DESIGN AND MANAGEMENT OF CONTINENTAL WILDLIFE RESERVES: LESSONS FROM THE EVERGLADES

JAMES A. KUSHLAN

US National Park Service, South Florida Research Center, Everglades National Park Homestead, Florida 33030, USA

ABSTRACT

Evidence from the attempt to preserve wading birds in Everglades National Park suggests that application of biogeographic theory to design and management of continental wildlife reserves requires considerations additional to those previously proposed. Shape and areal extent alone are inadequate criteria for reserve design. Unlike islands, continental reserves are not necessarily self-contained ecosystems driven by endogenous processes. The isolation of a continental reserve may lead to a phenomenon of ecosystem degeneration, the extent and rapidity of which depends on the ecological condition of adjacent habitat. Management strategies to preserve maximum species richness are seldom totally acceptable and often inherently unattainable. Conflicts between species management and ecosystem management illustrate the need for instituting an array of management strategies on a regional basis for preservation of both endangered species and ecosystems.

INTRODUCTION

Several recent proposals concerning the design of wildlife reserves have been inspired by the potential usefulness of island biogeography theory (MacArthur & Wilson, 1967; Terborgh, 1974; May, 1975; Sullivan & Shaffer, 1975; Simberloff & Able, 1976). The well-known island biogeographic concepts central to these proposals are that local extirpation may be a relatively common event, that the species structure of an island may be dynamic, and that big reserves are better than small ones because they support relatively large and extinction-resistant populations (Preston, 1962; Simberloff & Wilson, 1969; Diamond, 1971, 1972; Terborgh & Faaborgh, 1973; Lynch & Johnson, 1974; Willis, 1974; Elton, 1975;

Biol. Conserv. (**15**) (1979)—

Terborg, 1975). These concepts have been applied to the design of continental nature reserves on the premise that such reserves are, or are potentially, habitat islands. It has generally been proposed that continental reserves should be large, roundish, clumped, and connected by corridors (Terborg, 1974, 1975; Wilson & Willis, 1974; Diamond, 1975; May, 1975; Sullivan & Shaffer, 1975). However, derivation of these proposals from basic concepts is not unambiguous, and alternative contradictory proposals can also be derived (Simberloff & Able, 1976). In these proposals to date, only minor consideration has been given to the intrinsic ecological differences between continental areas and islands and none to the management options associated with affecting the necessary preservation of a continental wildlife reserve. Because of these difficulties, application of biogeographic theory to the design and management of continental wildlife reserves may require additional considerations.

THE EVERGLADES

The relation of design criteria, ecological characteristics, and management strategy of continental reserves to the adaptation and the extirpation potential of various species is demonstrated by the attempt to perpetuate ciconiiform wading birds in Everglades National Park, Florida. This reserve of 5670 km^2 contains seven to nine times the minimal area proposed for continental reserves by Sullivan & Shaffer (1975). The freshwater and estuarine marsh and swamp habitat heavily used by wading birds comprises about 4250 km^2. The Park is bounded by undeveloped areas now included in the Big Cypress National Preserve (2370 km^2) and three shallow Everglades marsh reservoirs called Water Conservation Areas (3490 km^2) (Fig. 1). Together these extend the effective area of preserved interior and coastal wetlands to over 10,000 km^2, thereby encompassing much of the southern Florida region.

Wading birds, including 16 species of herons, bitterns, ibises, spoonbills and storks, are historically abundant and ecologically important components of the regional ecosystem (Kushlan, 1976*a*). Their populations have changed markedly over the past century (Robertson & Kushlan, 1974; Kushlan & White, 1977). Robertson (1965) has suggested that populations in the 1870s may have been as high as 2·5 million birds before being reduced by hunting pressure. They recovered somewhat by the 1930s when birds numbering in the hundreds of thousands were reported to nest in the area. Everglades National Park was established in part to protect these birds yet by 1975 populations of the nine most abundant species stood at about 130,000 birds with indications that some may be stabilising (Kushlan & White, 1977). Population changes within the Park were more drastic than those regionwide. In at least some years of the 1930s nearly all the birds nested near the southern Everglades in what is now Everglades National Park, but by 1975 the Park nesting population represented only 20 % of the reduced regional total.

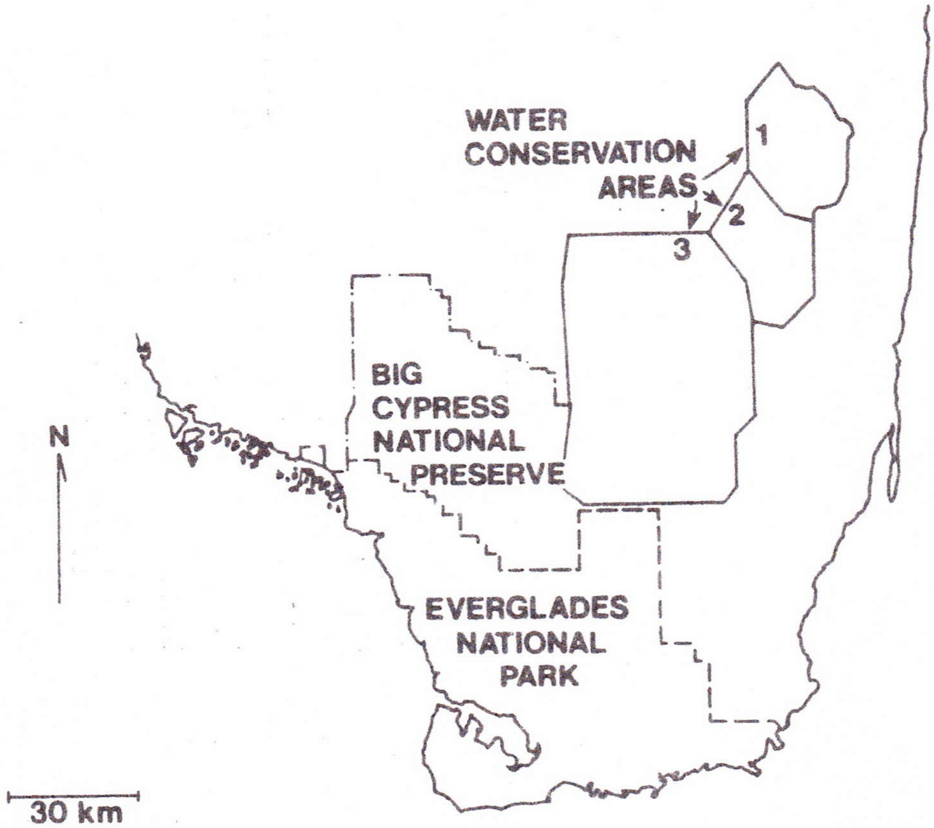

Fig. 1. Map of southern Florida showing contiguous reserves, Everglades National Park, Big Cypress National Preserve, and Water Conservation Areas in and near the Everglades.

Recent studies have given some insight into these population changes. The pattern of population change differed among individual species of wading birds. The white ibis *Eudocimus albus*, the most numerous species nesting in the large inland colonies, responded to changing environmental conditions by shifting colony sites from the Park to other areas where food becomes more available (Kushlan, 1976*b*; Kushlan & White, 1977), and now nests at colonies in the marshes of the southern Everglades only irregularly (Fig. 2a). The regional population of this species appears to persist because much of it has moved out of the Park to other areas within the region. The wood stork *Mycteria americana* on the other hand has not significantly changed nesting locations in the Park. Its nesting population there has declined from the mid 1960s, and it has nested successfully only twice in the past decade (Fig. 2b). Both the

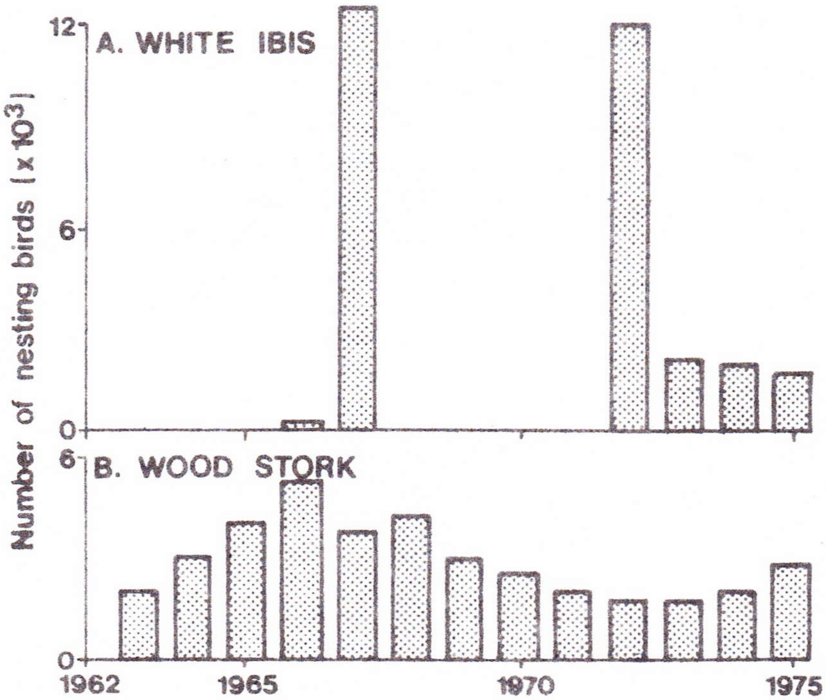

Fig. 2(*a*). Population of white ibis nesting in the Everglades of Everglades National Park from 1962 through 1975. (*b*) Population of wood storks nesting in the Everglades of Everglades National Park from 1962 through 1975.

timing of nesting and the reproductive success of wood storks are correlated with hydrologic conditions in the Park, and a recent shift to nesting later in the year has led to the more frequent failure rate (Kushlan *et al.*, 1975). Unlike the ibis, the remnant wood stork population attempts to nest in the Park most years but depends on critical water conditions that have occurred too infrequently to permit successful nesting at a natural rate.

These recent changes and shifts of nesting wading bird populations appear to be associated with changes in the functional characteristics of the southern Everglades ecosystem, especially those resulting from the establishment of a levee system that nearly enclosed Everglades habitat north of the park, forming the Water Conservation Areas (Fig. 1) and altered the flow of surface water into the park from upgradient areas. Hydrologic alterations involved interrupting most surface water flows into the southern Everglades, canalising continued water flows, moving discharge points out of the natural centre of the Everglades marsh, discharging on a fixed monthly delivery schedule rather than allowing for natural variation, and altering discharge-water level relationships. As these changes were associated with reduction in the Park's nesting wading bird populations, it is apparent that they altered the Park's ecological system and the viability of some of its component wildlife populations.

DESIGN CRITERIA

The difficulty of perpetuating some wading bird species in a large reserve and even within a larger system of contiguous reserves demonstrates several important concepts in continental reserve design: inadequacy of reserve size alone as a design criterion; the importance of environmental heterogeneity and maintenance of a reserve's functional characteristics; the role of timing and extent of isolation in determining the course of ecosystem degeneration; the importance of considering individualised population responses; and the management implications associated with distinguishing between local and regional extirpation of wildlife populations.

Attempts to determine size criteria for continental reserves have been generally unsuccessful (Richard, 1974), and size plays a particularly central role in the application of biogeographic theory to reserve design. Applying theory has not proven overly useful for continental reserves because biogeographic parameters derived from islands are not validly transferable to continental reserves owing to intrinsic differences in the dynamic characteristics of the two types of systems. Especially, area plays less of a role in determining species number on continents than on islands (Preston, 1962; MacArthur & Wilson, 1967). Also continental reserves, with a few exceptions (Vuilleumier, 1970; Brown, 1971; Diamond, 1975), seldom provide an analysable series of biogeographically and ecologically equivalent points of differing areal extent from which parameters characteristic of pertinent continental habitat patches can be derived. More autecological approaches such as setting reserve limits at the critical area requirements of extinction-prone species have also been attempted (Terborgh, 1974; Sullivan & Shaffer, 1975; Simberloff & Able, 1976). However areal extent, even when linked to the requirements of hypersensitive species, does not provide adequate design criteria because, as is suggested by evidence from preserving wading birds in the Everglades, it does not necessarily allow for continuance of the ecological processes required by particular species. Much of the relation between species diversity and area appears to be due to the correlation of area with habitat heterogeneity. Although in homogeneous systems, area alone may correlate with diversity (Simberloff, 1976), such homogeneity is seldom characteristic of continental reserves. In fact, preservation of natural heterogeneity and of specific habitat types often dominates the politics that dictate current design criteria for reserves.

More critical to reserve design than size alone is the preservation of the ecological integrity of the demarcated continental reserve. In this way too, continental reserves differ importantly from oceanic islands. Oceanic islands are more or less self-contained ecosystems in which the driving biological processes are generally endogenous. Although some potential continental reserves such as those on mountain tops or in lakes may function endogenously, most continental reserves do not. Functional insularity is determined by the degree of dependence of a reserved ecosystem on external forces and on the timing of the reserve's isolation from adjacent wildlife habitat. At the time an area is demarcated as a reserve, the species present function within the ecological structure of that ecosystem. If a reserve such as the Everglades is contiguous with adjacent preserved or otherwise not entirely obliterated habitat, its population pool depends not only on localised preserved resources but on those of nearby habitats and perhaps on the entire remaining regional ecosystem. The impact of ecological changes within the reserve on wildlife populations depends in part on the amount of change in adjacent areas, and conversely change in adjacent areas affects populations in the reserve. If a reserve gradually becomes isolated, the changes there may be slow. If it is rapidly isolated, changes within may be rapid.

At whatever speed functional or spacial isolation occurs, a system-level degeneration takes place within the reserve. Isolation from the buffering of contiguous habitats results in quantitative and qualitative alteration of the functional relations within the reserve, including changes in population levels, changes in ecological interactions, and alteration of forcing functions, all of which lead to system level degeneration toward a new dynamic condition. This will occur particularly in systems that depend on contiguous areas for critical environmental processes, such as upland discharge into the southern Everglades. Such ecosystem degeneration is analogous to the relaxation of species richness occurring after an island achieves physical isolation (Diamond, 1972). The consolidation of a new ecological system in a demarcated continental reserve requires time and will not be entirely achieved until changes in nearby land areas cease having additional impact. Only at such time and at a new level of ecosystem organisation do the functional characteristics of a continental reserve become sufficiently like an insular reserve to exhibit an island-like ecological self-containment, and it is only then that species extirpations caused by size constraints alone can be expected to occur. Miller & Harris (1977) suggested that such extirpations might be explained by species-area relations alone. More fundamentally, ecosystem processes rather than size or shape provide a major constraint on the design of continental wildlife reserves. Everglades National Park has been within its degeneration stage. As it and its surrounding reserves have been altered, its functional characteristics have changed and its species populations responded.

Individualistic responses of populations are crucial to understanding constraints on reserve design. In the Everglades, as would be predictable (Diamond, 1974; Willis, 1974), the largest, most specialised, and presumably most K-adapted species of wading bird, the wood stork, is being most severely impacted. It is also, probably not coincidentally, the species that is most dependent on precise maintenance of the hydrologic characteristics of the ecosystem. Other species have responded to the degradation of the preserved ecosystem by moving out of the reserve and by changing their reproductive tactics.

Whether extirpation of a species is a local or a regional phenomenon is also a critical factor in reserve design and is determined by the nature of the regional reserve system. Multiple reserves provide for correction of random extinction but may also perpetuate a species throughout the region because of the benefits derived from a single reserve. Changes in the functional characteristics within separate areas may benefit a species in one reserve but hinder its use of another. A species may persist as a viable population in only one area but may continue to occur in adjacent reserves as a fugitive. Recognition of these complex relationships between local persistence and regional persistence and between species preservation and ecosystem preservation is crucial to establishing and carrying out management objectives for reserves.

MANAGEMENT OBJECTIVES

Biogeographic theory concerns a structural parameter of a system, its species richness. Because of the key role played by species richness, application of island concepts to nature reserves is premised on accepting a management goal of preserving maximum species richness (Terborgh, 1974; Wilson & Willis, 1974; Sullivan & Shaffer, 1975). This is generally, but not always (Wilson & Willis, 1974) meant to be the richness of naturally occurring species. It is generally accepted that the preservation of ecosystem processes (or of entire biological communities) is necessary for species preservation, and it has also been argued that preserving ecosystem processes would be accomplished if the goal of maintaining species richness were achieved (Lamprey, 1974). Neither is necessarily true. The preservation of a sensitive species does not require preservation of a natural ecosystem. It may also be accomplished, at a high cost, by highly artificial manipulative management. On the other hand, a management objective to maintain species richness would not necessarily maintain ecosystem processes, since each sensitive species would have to be managed independently and therefore the natural ecosystem function may need to be altered to accommodate its needs.

Largely for these reasons, preserving species richness, as assumed by biogeographic theory, is not the accepted management strategy of many extant reserves. Single species management may be necessary to perpetuate a species for which available natural habitats no longer support a critical population. Such a reserve may be actively manipulated to conserve that species with the remainder of the ecosystem being altered and total species diversity reduced. On the other extreme, the management objective may be to preserve ecosystem processes as is, for example, the established policy of the United States National Park Service for natural areas (US National Park Service, 1975). Such an objective may not in itself perpetuate all species. Environmental conditions surrounding a reserve and changed equilibrium populations of its own species complex may mean that even the best management strategy may result in only an approach to, rather than restoration of, natural conditions. In the Everglades we can predict that the white ibis will probably maintain its regional population but cannot predict whether the wood stork will or will not do so. Thus in any given case it is possible that even the best ecosystem management available may not be sufficient to perpetuate a hypersensitive species in an ecosystem management reserve.

Thus arises a management dilemma. The closest approach to maintaining most of the natural processes within a reserve may not be sufficient to maintain natural species richness in even large parks such as the Everglades and the relatively early loss of larger, more specialised members of ecological guilds becomes probable. In the face of such local extirpations, important management decisions must be made which in part depend on how such an extirpation relates to regional, national, or perhaps worldwide loss of a species. A decision might be made that the management strategy of a reserve attempting to perpetuate natural processes should be altered for the benefit of that highly endangered species. In the case of the wood stork in the Everglades this might mean accelerating drying rates in the Everglades or provisioning artificial fish ponds. Alternatively the original strategy may be adhered to in an attempt to achieve the closest approximation of natural conditions thereby preserving most components of the system while possibly losing sensitive species. In such a case single species management would not be attempted unless as an index to the restoration of natural ecological conditions. That such a management choice is difficult to make reflects a basic dilemma in setting management objectives for reserves. This dilemma is also illustrated by current emphasis in the United States and elsewhere on preserving endangered species that encourages or requires such species-level management for endangered species even within ecosystem management reserves (Anon., 1977). A combined strategy of managing large reserves to maintain ecological processes and risking loss of species there while establishing additional reserves managed for the perpetuation of a particular endangered species may be a partial solution to preserving both species and ecosystems within a region. Thus on the species level, regional or national persistence of a species becomes a primary objective, and some reserves are then to be managed as critical habitat to prevent area-wide extirpation. On the ecosystem level, other preserves function under separate but related objectives to preserve natural, generally self-contained ecosystems in which evolutionary processes are allowed sway. Recognising the possibility of extirpation within an ecosystem reserve in no way countermands the necessity to manage initially in order to maintain a naturally functioning ecosystem, including its entire natural complement of species. Nor does it reduce the desirability to maintain the overall rate of species extinction and evolutionary change at natural levels. It does, however, pose the possibility of failure to preserve species and requires formulation of alternative strategies, on regionwide bases, for the preservation of both endangered species and of ecosystems in continental wildlife reserves.

ACKNOWLEDGEMENTS

The studies upon which this report is based were supported by the US National Park Service. A paper based on this report was given at the First Conference on Scientific Research in the National Parks, New Orleans, 1976 sponsored by the American Institute of Biological Science. I thank G. E. Davis, G. Y. Hendrix, and W. B. Robertson, Jr for comments.

REFERENCES

ANON. (1977). Wildlife protection: Section 7 of the endangered species act comes of age. *Environ. Law Reporter*, 7, 10049–52.

BROWN, J. H. (1971). Mammals on mountain tops: Nonequilibrium insular biogeography. *Am. Nat.*, **105**, 467–78.

DIAMOND, J. M. (1971). Comparison of faunal equilibrium turnover rates on a tropical island and temperate island. *Proc. natn. Acad. Sci. USA*, **68**, 2742–5.

DIAMOND, J. M. (1972). Biogeographic kinetics: Estimation of relaxation times for avifaunas of southwest Pacific islands. *Proc. natn. Acad. Sci. USA*, **69**, 3199–203.

DIAMOND, J. M. (1974). Assembly of species communities. In *Ecology and evolution of communities*, ed. by M. L. Cody and J. M. Diamond, 343–444. Cambridge, Mass., Belknap Press.

DIAMOND, J. M. (1975). The island dilemma: Lessons of modern biogeographic studies for the design of nature reserves. *Biol. Conserv.*, 7, 129–46.

ELTON, C. S. (1975). Conservation and the low population density of invertebrates inside neotropical rain forest. *Biol. Conserv.*, 7, 3–15.

KUSHLAN, J. A. (1976*a*). Wading bird predation in a seasonally fluctuating pond. *Auk*, **93**, 464–76.

KUSHLAN, J. A. (1976*b*). Site selection for nesting colonies by the American white ibis *Eudocimus albus* in Florida. *Ibis*, **118**, 590–3.

KUSHLAN, J. A. & WHITE, D. A. (1977). Nesting wading bird populations in southern Florida. *Fla Sci.*, **40**, 65–72.

KUSHLAN, J. A., OGDEN, J. C. & HIGER, A. L. (1975). *Relation of water level and fish availability to wood stork reproduction in the southern Everglades, Florida*. Tallahassee, Florida, US Geological Survey, open file Report 75-434.

LAMPREY, H. F. (1974). Management of flora and fauna in national parks. In *Second world conference on national parks*, ed. by H. Elliott, 237–49. Morges, Switzerland, IUCN.

LYNCH, J. F. & JOHNSON, N. K. (1974). Turnover and equilibria in insular avifauna, with special reference to the California Channel Islands. *Condor*, **76**, 370–84.

MACARTHUR, R. H. & WILSON, E. O. (1967). *The theory of island biogeography*. Princeton, NJ, Princeton University Press.

MAY, R. M. (1975). Island biogeography and the design of wildlife preserves. *Nature, Lond.*, **254**, 177–8.

MILLER, R. I. & HARRIS, L. D. (1977). Isolation and extirpations in wildlife reserves. *Biol. Conserv.*, **12**, 311–15.

PRESTON, F. W. (1962). The canonical distribution of commonness and rarity, Part II. *Ecology*, **43**, 410–32.

RICHARD, P. W. (1974). National parks in wet tropical areas. In *Second world conference on national parks*, ed. by H. Elliott, 219–27. Morges, Switzerland, IUCN.

ROBERTSON, W. B., JR. (1965). Inside the Everglades. *Aud. Mag.*, **67**, 274–9.

ROBERTSON, W. B., JR. & KUSHLAN, J. A. (1974). The southern Florida avifauna. In *Environments of south Florida: Present and past*, ed. by P. J. Gleason, *Mem. Miami geol. Soc.*, **2**, 414–52.

SIMBERLOFF, D. S. (1976). Experimental zoogeography of islands: Effects of island size. *Ecology*, **57**, 629–48.

SIMBERLOFF, D. S. & ABLE, L. G. (1976). Island biogeography theory and conservation practice. *Science, N.Y.*, **191**, 285–6.

SIMBERLOFF, D. S. & WILSON, E. O. (1969). Experimental zoogeography of islands: The colonization of empty islands. *Ecology*, **50**, 278–96.

SULLIVAN, A. L. & SHAFFER, M. L. (1975). Biogeography of the megazoo. *Science, N.Y.*, **189**, 13–17.

TERBORGH, J. (1974). Preservation of natural diversity: The problem of extinction prone species. *BioScience*, **24**, 715–22.

TERBORGH, J. (1975). Faunal equilibria and the design of wildlife preserves. In *Tropical ecological systems, ecological studies*, **11**, 369–80. Berlin, Springer-Verlag.

TERBORGH, J. & FAABORG, J. (1973). Turnover and ecological release in the avifauna of Mona Island, Puerto Rico. *Auk*, **90**, 759–79.

US NATIONAL PARK SERVICE (1975). *Management objectives of the National Park Service*. Washington, DC, US Department of the Interior.

VUILLEUMIER, F. (1970). Insular biogeography in continental regions. I. The northern Andes of South America. *Am. Nat.*, **104**, 373–88.

WILLIS, E. O. (1974). Populations and local estinction of birds on Barro Colorado Island, Panama. *Ecol. Monogr.*, **44**, 153–69.

WILSON, E. O. & WILLIS, E. O. (1974). Applied biogeography. In *Ecology and evolution of communities*, ed. by M. L. Cody and J. M. Diamond, 522–34. Cambridge, Mass., Belknap Press.