COLONIAL WATERBIRDS

JOURNAL OF THE COLONIAL WATERBIRD SOCIETY

VOL. 15, NO. 1 1992 PAGES 1-167

GUEST EDITORIAL

Population Biology and Conservation of Colonial Wading Birds

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Colonial Waterbirds 15(1): 1-7, 1992

Over the past several decades, the biology and conservation of colonial wading birds have attracted considerable attention, both scientifically and popularly. Scientifically, these birds (colonial herons, storks, ibises, and relatives) have proven useful in addressing many biological questions such as coloniality, foraging effectiveness, sibling competition, and promiscuity. Popularly, colonial wading birds have proven useful as symbols of wet and wild places.

As is the typical course of both scientific inquiry and popular attention span, specific interests have waxed and waned. Through the 1960's, pioneering investigations showed the usefulness of using colonial wading birds for studies such as behavior, migration, population fluctuations, and reproductive biology (e.g., Lorenz 1938, Noble *et al.* 1938, Schuz 1938, Meyerriecks 1960, Weller 1961, North 1963, Kahl 1964, Lack 1966, Jenni 1969). In the 1970's, special attention was paid to population surveys, wading birds as indicators of environmental conditions, foraging ecology, and contaminants (Kahl 1971, Voisin 1976-77, Payne and Risley 1976, Custer and Osborn 1977, Burger 1978, Kushlan 1978, Ohlendorf *et al.* 1978, Blacklock and Slack 1979). In the United States, agencies funded extensive coastal surveys (Spendelow and Patton 1988), one result being the founding in 1976 of the Colonial Waterbird Society (originally "Group") and its journal (Burger 1981, Morris 1991).

In the late 1970's and 1980's, while financial support for surveys faltered, interest in biological studies persisted (Burger 1982, Erwin 1983, Kushan 1986a, 1989, Rodgers *et al.* 1987), and a relatively mature knowledge base permitted monographic studies of the species groups (Hancock and Kushlan 1984, Hancock, Kushlan, and Kahl 1992). Activities internationalized as western and eastern hemisphere researchers increasingly asked similar questions with similar techniques, prodded on by multinational interest groups (Hafner *et al.* 1986, Luthin 1987). Management options became better defined (Parnell *et al.* 1988).

Despite these many advances, evidence also has accumulated of limits to the use of colonial wading birds in addressing many biological questions that otherwise might be of interest. It is rather wise to choose a study system or research model system that is suitable to answer the question being asked. Although wading birds may be wonderful for some studies, they are very difficult for others. That so many questions of wading bird biology and conservation remain unresolved can be attributed in part to these birds being very hard to study in some situations.

In the scientific enterprise, research questions are pursued until the questions cease to hold broad interest among scientists or until technology limits the scientist's ability to answer them properly. This, in part, is why specific interests in colonial wading birds have waxed and waned.

Another reason is that financial resources have waxed and waned. So it is appropriate every once in a while to examine the technical obstacles constraining resolution of research questions and to suggest which research questions might still be of some interest.

BREEDING BIOLOGY

Much is now known about courtship behavior and breeding biology of most North American and European species of colonial wading birds, sufficient to understand the group in broad stroke. However, there remain wide information gaps for many rare or tropical species (Hancock and Kushlan 1984, Hancock, Kushlan, and Kahl 1992). The Zigzag Heron (*Zebrilus undulatus*), the Agami Heron (*Agamia agamia*), the Slaty Egret (*Egretta vineceigula*), Swinhoe's Egret (*E. eulophotes*), tiger herons (*Tigrisoma* spp.), small bitterns, east Asian storks, and the rarer *Bostrychia* ibises come to mind. Considerable attention could profitably be applied to these little-known species.

For nearly all species, among the more crucial unresolved questions related to breeding biology are those concerned with ecological constraints on reproductive success. Particularly desirable is to determine limits of their ability to accommodate to changing environmental conditions. Such studies are needed to provide a basic understanding of the colonial wading bird adaptive strategy as well the habitat conditions required for their conservation.

"What is the reproductive success of a colonial wading bird?" is an often-asked research questions over recent decades. Many values for clutch size, nesting success, and nestling mortality are available in the literature (see Hancock and Kushlan 1984, Hancock, Kushlan and Kahl 1992). However, the utility of these values is undermined by their unknown accuracy. Among additional constraints are difficulties of finding all nests, identifying owners, revisiting nests sufficiently frequently to determine mortality (most studies report a large proportion of unknowns), the short period the birds are in the nest (most studies go for no more than 14 days of the 30-50 days of nestling development), and determining the relevance of hatchling studies to population regulation. These matters are intrinsic constraints of using the wading bird study system, but that does not render them any less troublesome.

The most appropriate measure, of course, is per capita life- time reproduction. Within a single season, the most appropriate measure of population reproductive success is survival of young to the point of leaving the colony in relation to the number of reproductive adults in the population. Clearly, neither of these results is practical for most colonial wading birds in most settings. This constrains the utility of the wading bird study system to address population dynamics questions.

If our interest is in the wading birds themselves rather than population dynamics, only a population index is possible in most cases. Such an index may be short-term survival, or it may be a surrogate such as growth rate. Although the relationship of such indexes to population parameters is tenuous, they may be used to ask comparative questions. For example, one could ask if two groups suffered similar mortality within a nestling stage.

From a research perspective, the effect of investigator disturbance needs to be explicitly addressed, because investigator-enhanced mortality or injury can severely bias the data (Tremblay and Ellison 1979, Rodgers and Burger 1981, Parsons and Burger, 1982, Vos *et al.* 1985, Frederick and Collopy 1989). Yet the quantitative effect of investigator bias has seldom been factored into analysis. In individual studies, the investigator needs to be able to ask: "To what extend will disturbance bias the data set?" Answering this question usually requires experimentation to partition variance in mortality (or other measured variable) into that associated with investigator activity and that associated with the natural causes under study.

From a conservation perspective, investigator disturbances involving capturing and marking young birds can be very serious indeed. Scientists should be compelled to ask: "What are the effects of investigator intrusion on the conservation needs of this population?"

FORAGING ECOLOGY

As is the case for breeding biology, much is now known about foraging be-

havior and food habits of colonial wading birds. This is one research area where the bird's habits (particularly a tendency to regurgitate their food onto a waiting field worker) have proven especially conducive to research. An area remaining poorly known is food choice variability, i.e., how individuals, colonies, or population segments vary their diet. Understanding interactions of prey availability, energy demand, and individual decision-making in the face of changing environmental conditions could be profitably pursued.

A second area of foraging research needing additional attention (also relating to questions of reproductive success) is how foraging opportunities and limitations constrain reproductive success. To the extent that energy availability influences reproductive success and, in turn, reproductive success influences population stability, such questions may be keys to understanding the population dynamics of these species.

POPULATION SIZE AND TRENDS

Ever since people have been interested in colonial wading birds, among the most-asked questions is: "How many are there?" The first point to make is this: It is seldom an important or even answerable question. For very few species of animals do we know population size with any degree of certitude. Yet such numbers are often demanded with regard to colonial wading bird populations by government agencies footing the bill or by the popular press. Spendelow and Patton (1988) provided the definitive analysis of the 1970's census work by many hundreds of investigators along coastal United States. They dealt with a bewildering array of numbers of differing and poorly documented accuracy. Although this work is undoubtedly the best possible attempt at a numerical assessment of these populations, the tally required such interpretation, calculation, and categorizing that it seems unlikely that meaningful trends could be derived in the future. The most important questions should be asked before beginning a census study: "What is the purpose of a census? What question is the data to answer? What statistical test will be used?"

It is probably surprising to many that a reliable, consistent, and accepted way of censusing a colonial wading bird population is not yet available. First of all, we should not forget that there even remain fundamental difficulties in defining a colony (Buckley and Buckley 1980, Kushlan 1986b). However defined, colonies are more often than not large, multispecies, three-dimensional, asynchronous, widely spaced, and nearly inaccessible. Because of these factors, the most convenient censusing methods may be very poor except for those few colonial wading birds that are large, visibly colored, and nest on top of trees, such as some storks and large herons. Even for these, a total enumeration of the population is seldom possible. Consider the additional Grey Heron (*Ardea cinerea*) nests being found by English atlas workers (J. Hancock, pers. comm.).

The next best approach is to seek an estimate of the population. A census technique whose purpose is to provide a population estimate must have known precision (how close repeated measurements are to each other) and accuracy (how close measurements are to the real value). That very few colonial wading bird censuses meet these criteria has been known for some time, the point being persuasively argued by Hutchinson (1980) over a decade ago (see also Erwin *et al.* 1984, Erwin 1985, Kushlan 1985). When accuracy and precision of the method are known, sample size and the sensitivity of detecting differences between subsequent measurements can then be calculated. Without these, it is impossible to know if the population estimate can meet the goals set for collecting the data in the first place.

If a fully characterized estimate is seldom possible, the next best approach is to use an index that can be compared from time to time or from location to location. Nearly all counts of colonial wading birds are indicies, not enumerations or even estimates. Erwin (1985) discusses how standardization of such indices is essential, along with knowledge of precision. Such indices only provide comparative, not absolute, information. (They cannot be used to assert population size.) Furthermore, standardization of most currently used techniques may not be practical because of the number and intractability of variables to be rendered constant.

Admittedly, this problem is by no means unique to colonial wading birds: many population studies in which complete enumeration is impossible suffer from untested assumptions. However, we can take heart that sampling theory is very well developed; and in this respect, I suggest that more attention be given to considering censusing colonial wading bird populations by making population estimates using mark-recapture analysis (Seber 1982, 1986, Brownie 1987). Such well-known models have progressed far beyond the simple Lincoln index calculation and not only provide error estimates but permit hypothesis testing. This approach was, in fact, used in the most successful population study of a colonial wading bird, that of British Grey Herons by North and Morgan (1979). Individual censuses of multiple observers (as long as they can surreptitiously "mark" colony sites or nests they encounter) can make use of mark-recapture analysis (see the recent papers by Nicoll 1992, and Lebreton *et al.* 1992 for further discussion).

Censusing has a very important downside. That investigators conducting censuses can disturb nesting colonial wading birds has long been appreciated (Rodgers and Burger 1981). Entering or even approaching a colony of nesting wading birds inevitably disturbs adults and places their eggs and young at risk. Unfortunately, the study of investigator disturbance has progressed only slightly in recent years. We generally know the role of habituation, stage of nesting cycle, time of day, predators, and distant vs. on-site techniques, but we have very little information of the quantitative effect of disturbance on the data themselves.

With respect to conservation, officials charged with protecting colonial wading birds will ask: "What is the loss and is the census information worth that loss?" From a conservation perspective, understanding investigator effects is a subset of a larger question: "How does human activity affect nesting success?" This is an especially critical issue in developed regions, such as North America, where conservation agencies, faced with land development and increased use of coastal environments by people, have to decide how close to colony sites human activities should be permitted. Understanding this more general question is a crucially important area of research.

POPULATION DEFINITION

Even if a population estimate or trend could be expressed within acceptable confidence limits, it remains unclear exactly what constitutes a biologically meaningful portion of a wading bird population. The number of birds present at a colony site is at best of local or transient interest. The number of birds at feeding sites, especially outside of the nesting season, seldom reflects the reproductive population. The group of birds in a geographic area or within a political boundary seldom constitutes an entity of biological interest.

For most research, the biological entity of interest is the "population," more specifically the deme - the local interbreeding population. Determining what constitutes a deme is one of the more important questions facing colonial wading bird biologists. An exciting new tool is the use of biochemical techniques to determine patterns of relatedness among birds nesting at different colony sites. Recent studies of allozyme variation have indicated that a wading bird deme is considerably more expansive than a colony (Stangel *et al.* 1990, 1991). These studies demonstrated the existence of genetic variability that could reflect gene flow. Furthermore, techniques of higher resolution are available. The use of biochemical markers to assess demic boundaries is an important area of research.

Identification of wading bird demes is also a critical area of conservation research, particularly in addressing the question of what constitutes the most appropriate management or conservation unit.

WINTERING HABITATS

One would think that it would be well known where temperate wading birds go in winter and where tropical wading birds go when their marshes are too flooded or too dry. However, we understand these matters very poorly. That North American colonial wading birds winter in the West Indies and Central America has been known for some time (Cooke 1946, Coffee 1948, Byrd 1978, Ryder 1978). Yet, in the Western Hemisphere, consequences of winter residency have scarcely been incor-

porated into an appreciation of population biology or conservation.

This oversight is certainly not the case for other water birds or for some wading bird populations outside North America. Shorebird conservationists have spent the last decade examining migration patterns, stopover sites, and habitat needs, and are now in the process of defining a sister-reserve system to assure population stability. In Europe, it was persuasively demonstrated that winter conditions influence breeding population sizes the following year (Lack 1966, North and Morgan 1979, Dallinga and Schoenmakers 1987). There is every reason to believe that this is the case in the Western Hemisphere as well. If so, concentrating research on nesting grounds can address only a portion of the questions needed to understand population biology. Increased study of the wintering areas and habitats of migratory wading bird species is essential.

These questions may be addressed by reinspection of existing ringing data. Evaluations of ringing studies of North American wading birds have been limited by infinitesimally small recovery rates, a high proportion of shooting returns, and the birds' tendency to change nesting sites from year to year. Widespread ringing studies could be reinstituted to great benefit, especially ringing programs on the migration routes and wintering grounds as have been established for shorebirds.

An especially effective approach is to use telemetry. Airplane-based telemetry has proven valuable in tracing migration and wintering patterns (Comer *et al.* 1987). Satellite-based telemetry may be the critical technology advancement that will open this question to study. Tracing migratory patterns and survival relative to environmental conditions on the wintering ground constitutes a high priority for future research.

CONSERVATION BIOLOGY

In the best of all worlds, one would develop and implement a conservation program for each species based on a thorough understanding of interdemic population dynamics, including size and trend and how survival and mortality constrain population stability. It is a pity that we do not live in such a world. At this point what can be done is to raise questions to be addressed in developing conservation programs in a flawed world.

Is active management needed? It seems clear that, for most species, passive habitat protection will be inadequate to assure long-term survival, especially considering increasing competition with humans for space and for water worldwide (Parnell *et al.* 1988). Active management will probably need to include: protection and active manipulation of colony sites; protection, active manipulation, and even restoration of feeding habitat, and protection and active management of wintering sites. How these management programs should be accomplished requires detailed, site-specific study.

Is habitat the key for stability of colonial wading bird populations? As these species nest and often feed together, it is both the advantage and the challenge that colonial wading bird management can be enacted on a regional habitat basis. Programs for preserving and manipulating environmental conditions, such as plant structure, water depth or food supply, can be enacted in ways that should support all species simultaneously.

How do we plan conservation? The ideal management plan would involve meeting the habitat needs of all cohabiting colonial wading bird species over an area sufficiently large to encompass the biological limits of each population. This process requires regional approaches to colony and habitat management. Understanding the potential of and constraints on such regionally-based conservation planning is an important area of research.

RESEARCH LIMITS

Not all species are equally useful for all types of studies. In the previous discussions certain limits of the wading bird study system were noted. It is unwise and counterproductive to push any study system or model beyond the limits of tractability. Certainly, there are some questions that are not best addressed using colonial wading birds. There are some questions that cannot be answered using colonial wading birds given the present state of technological development. There are

some questions that can be answered using colonial wading birds but are not of wide interest or conservation importance. And then there are questions that can be answered in exciting and interesting ways by using the wading bird model system.

This paper has suggested some of the questions that could benefit from further study and suggested some of the constraints that need to be either accepted or overcome. Colonial wading bird studies can continue to contribute to understanding biology and conservation if they seek to address answerable questions of basic importance through appropriate methods and statistically valid analyses.

ACKNOWLEDGEMENTS

I thank R. Michael Erwin and James A. Hancock for helping to clarify points raised in this paper, although they bear no residual responsibility for its content.

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