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Introduction: Biology and Conservation of the American White Pelican

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Abstract.—Two separate, large-scale management units for the American White Pelican (*Pelecanus erythrorhynchos*) in North America are proposed: the eastern and western metapopulations, separated by the North American Continental Divide. The populations on either side of this barrier are subject to contrasting ecological conditions, movement patterns suggest strong geographic separation and each is likely demographically distinct. Subdivisions within these demographic units need to be more precisely defined in the future. Yet, because of the highly colonial nesting habits of the American White Pelican, conservation can still be effective if directed toward separate breeding colonies. Our intent is to provide a compilation of current knowledge regarding species status, distribution and ecology. Herein, further study is recommended: (1) to determine genetic characteristics and the degree of genetic separation of the various geographic divisions in the range of the species to help ultimately better define "evolutionarily significant units" for American White Pelican conservation, (2) to study movements and genetic exchange among and between these divisions, and (3) to study movement patterns and genetic mixing among these divisions during long- and short-term changes in environmental conditions.

Key words.—American White Pelican, *Pelecanus erythrorhynchos*, management unit, metapopulation, breeding colony, sub-colony, aggregation.

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"*I know of no more magnificent sight in American bird life than a large flock of white pelicans in flight.*"

A. C. Bent (1922:289)

The American White Pelican (*Pelecanus erythrorhynchos*) will always be a symbol of the "old" American West, epitomizing freedom, wildness and the ability to survive in harshness (*sensu* Darling 1956). Like other bird species in the same habitats, the American White Pelican (AWPE) has evolved under dynamic wetland conditions characteristic of their breeding areas (for example, see Jehl 1988), as well as coastal freshwater and estuarine habitats used during the non-breeding season. The pristine conditions of these wetland habitats, representing in a larger sense, geologically recent ecological conditions of drying and saline lakes following the last North American glaciation (Jehl 2001), have been significantly altered by humans seeking water supplies for growing numbers and draining wetlands for expanding agriculture (Minckley and Deacon 1991). Periodic drought and water shortages (Service 2004), saline and alkali conditions, long distances between supporting habitats and ever-changing and dynamic conditions, all characterize conditions in AWPE breeding areas.

East of the North American Continental Divide and until the advent of modern agriculture, the AWPE epitomized primitive wildness, mostly feeding on commercially unimportant food species (Keith 2005). In contrast, supporting habitats in the east are less saline, more predictable, and more closely spaced. Ironically, too much rather than too little water has been cited as a major factor in the reduction of breeding success (Evans 1972). Due mainly to variation throughout its range in water conditions which affect prey and access to breeding islands by predators, the AWPE is still universally considered a "boom and bust" species (Diem and Pugasek 1994). And overall, the AWPE has historically been a species *not* in direct conflict with humans, but instead has most often been the indirect victim of human activities (despite a short history of direct persecution; Keith 2005; Sovada *et al.* 2005).

Water-use and water-development are likely to be critical elements influencing the long-term survival and metapopulation

health of western AWPE. In the east, however, other factors are rapidly becoming important considerations in the management of AWPE, such as mitigating a growing aquaculture/pelican conflict (King 2005) and disease issues (Rocke *et al.* 2005). Wintering habitats have also been degraded in many instances by humans for many reasons (e.g., Salton Sea, California; Shuford and Molina 2004).

There are four major reviews on the biology of the AWPE (Bent 1922; Palmer 1962; Johnsgard 1993; Evans and Knopf 1993); however, information is still lacking in many areas of the species' natural history, distribution and demography. Despite being one of the more interesting and inspiring species of North American birdlife, conservation of the AWPE is also somewhat paradoxical. In the west, the AWPE was originally much more widespread and abundant (Boellsdorff *et al.* 1988: their Fig. 2; Keith 2005; Shuford 2005), becoming greatly (and perhaps permanently) reduced in number and distribution in post-settlement times. The AWPE is as abundant as it is today, and perhaps even increasing, largely because of protection afforded from intensive and ecologically insensitive agricultural and other land developments in the 20th Century. The U.S. National Wildlife Refuge System (Johnsgard 1993), as well as other federal and state/provincial protected areas, have been key in protecting the numbers of AWPE we still have, and these initial actions should be recognized as a wildlife management success story. In recent decades, however, federal agencies have had to turn attention to growing man/pelican interactions, in particular focusing on the economic impacts of increasing numbers of the AWPE on a growing aquaculture industry in the American southeast (King 2005), as well as other emerging issues, such as disease (Rocke *et al.* 2005) and continuing habitat degradation.

Given recent issues being raised about the management of the AWPE, we convened a symposium by active and recent AWPE researchers at the 29th Annual Meeting of the Pacific Seabird Group, Santa Barbara, California, 20-23 February 2002. Many biologists and managers who have in the recent past or are currently conducting studies on the AWPE met to discuss the state of our knowledge. The following papers represent scientific contributions from that symposium, also including important recent updates since 2002.

Herein, we present local, site-specific studies (Fig. 1) representing: (1) a very disjunct and isolated breeding colony (Stum Lake, British Columbia, Canada); (2) western breeding numbers in a state of long-term "deterioration" (California); (3) relatively new and growing breeding colonies such as Medicine Lake, Montana; and (4) a large, flourishing breeding colony (Chase Lake, North Dakota, perhaps the most important single breeding aggregation within the entire geographic range of the AWPE). We hope that symposium contributions will stimulate research that will contribute to our overall understanding of ecological interactions, demographics and status throughout the range of the AWPE, as well as to stimulate further publications.

DISTRIBUTIONAL DEFINITIONS

American White Pelican Metapopulations

McCullough (1996) has stated: "*In view of the continuing evolution of the metapopulation idea, it perhaps is neither desirable nor possible to give a rigorous definition to the term.*" But for utility, we have attempted to define regional-scale management units for AWPE, examining how they are distributed geographically (Fig. 1). The discussions in Hanski and Gilpin (1991), with a caveat from Harrison (1994) provide that: . . . "*success [in conservation] may only be possible for extremely well-studied species.*" Previous lack of a realistic regional-scale definition for conservation practice in AWPE probably arises out of the controversies regarding precise definitions needed in the use of various terms of theoretical models (Harrison and Hastings 1996) compared to definitions more commonly used in field practice. Hopefully this will lead field biologists to strive harder to better define these parameters through more detailed research and as they apply-to and test the ideas and models provided by theoreticians. We believe the issues of consistency and relevance are extremely important and that more precise

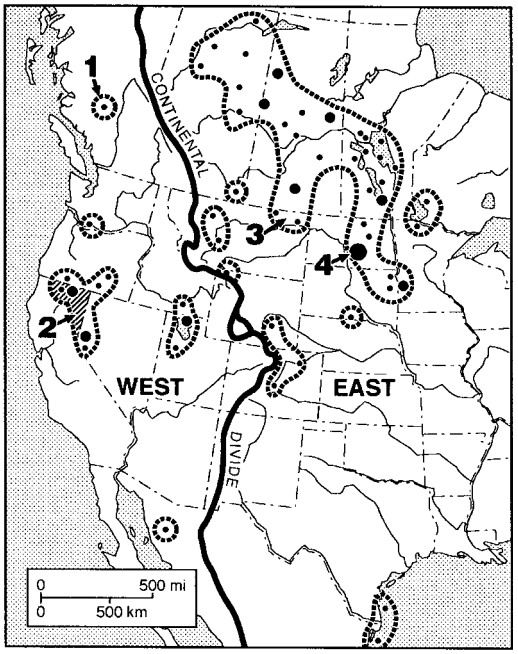

Figure 1. A diagrammatic map depicting the current breeding range and approximate breeding colony locations of the AWPE in North America (various-sized dots indicate relative numbers) (Johnsgard 1993; Evans and Knopf 1993; King and Anderson 2005), showing proposed "western" and "eastern" metapopulations. Short-dashed lines that surround more than a single colony or single colonies widely separated from other units may or may not represent examples of separate populations. The largest area surrounded by short, dashed lines in the eastern metapopulation is shown for discussion purposes only and it likely contains multiple genetic and/or ecological sub-units, or it may encompass additional, nearby colonies shown here as separated. Numbers on the map indicate the locations of specific units detailed in separate papers of this symposium: 1 = Stum Lake, British Columbia, Canada; 2 (hatched area) = colonies currently located within the state of California; 3 = the colony in Montana at Medicine Lake; 4 = the largest colony in North America, Chase Lake, North Dakota.

parameter definitions will have important implications regarding the applied conservation future of the AWPE and other species. Yet, we also heed Caughley (1977) in that ". . . *the animals rather than the mathematics are the subject of study and the conclusion must be biological, not mathematical . . . Common sense is the most important requirement; it holds mathematics to reality.*"

Vermeer (1977) first proposed separation in the total breeding range of distinct east-west segments of the AWPE, based mostly on band-recovery data and now further supported by Anderson and Anderson (2005). In the most recent comprehensive review of the AWPE, Evans and Knopf (1993) also divided the species into two major geographic regions of North America separated by the Continental Divide (see Fig. 1, diagram mostly from Evans and Knopf 1993).

Each of these two geographically distinct portions of the breeding range corresponds to the definition of Hanski and Gilpin (1991) as metapopulations (Table 1), or "*a population of populations*" (originally after R. Levins). "*Metapopulations are systems of . . . local populations connected by dispersing individuals" or a "set of local populations*" (Hanski and Gilpin 1991); or as defined by Newton (1998): ". . . *any population composed of a number of discreet and partly independent subpopulations that live in separate areas but are linked by dispersal.*" The degree of dispersal (implying genetic exchange) is a key element in this definition of the metapopulation (Hastings and Harrison 1994). For the AWPE, there are hints of a very small, but possibly intermediate situation in Montana (Hendricks and Johnson 2002; Fig. 2).

As abundantly demonstrated for the AWPE (Keith 2005; Shuford 2005), colonies, especially in the western metapopulation, have been subject to severe fragmentation and redistribution. McCullough (1996) listed two important criteria relating to the "metapopulation idea": spatially discreet distribution and significant extinction probability in one or more of the local patches in the geographical distribution. The east and west metapopulations of AWPE certainly have distinct conservation issues. It is also apparent that the western AWPE metapopulation is much smaller in geographic extent, number of subdivisions and numbers of individual birds (King and Anderson 2005) compared to the eastern AWPE metapopulation (depicted in Fig. 1). Differences between the two metapopulations are therefore likely due to: (1) a much reduced western metapopulation compared to the original, pre-settlement distribution, (2) differences between habitat configurations and critical life-history-related ecological conditions in the east and west (number of available lakes, precipitation levels, food distribution, changes brought about through man, etc.), or (3) a combination of both of these factors.

Table 1. Suggested definitions of various geographical subdivisions in western and eastern portions of the range of the American White Pelican in North America.[a]

Scale	Suggested terms used	Criteria
Regional	**Metapopulation:** western, eastern	Separation by a well-defined barrier[b] with very small dispersal between- compared to within-metapopulations
Local, interactive	**Population**, **sub-** or **local-population**	Dispersal among populations much greater than among metapopulations[c]; subject to further subdivision
Single geographic location	**Colony** or **sub-colony**	One or more colonies or sub-colonies associated with a single geographic feature[d]
Away from colony	**Non-breeding flocks**	Groups of individuals gathered anywhere away from colonies during the non-breeding season

[a]Items shown in bold indicate the terms used in the reports following. They are subject to further refinement as new data are obtained (for example, genetic studies).
[b]For the AWPE, the North American Continental Divide has been defined as a major barrier between east and west (see text).
[c]Smaller units might be usefully defined in the future (see text).
[d]Usually these are defined by one lake or one system of water bodies, or some dominant geographic feature.

Smaller Units Within AWPE Metapopulations

Units within metapopulations are more difficult to define or propose (as suggested by Coulson 1985) without more data on specific dispersal and genetic exchange. Definitions of the subunits, or the use of terms that define them, within a metapopulation ("a population of populations") vary widely in the literature, most commonly called either "populations" or "sub-populations." The term "local population" was defined by Mayr and Ashlock (1991) and Mayr (1963) in the context of evolutionary biology as "*the individuals of a given locality which potentially form a single interbreeding community*" or gene pool. Caughley's (1977) definition of "population" is: ". . . *a biological unit at the level of ecological integration where it is meaningful to speak of a birth rate, a death rate, a sex ratio and an age structure in describing the properties of the unit.*"

Limits (or borders and edges) of units commonly called populations, sub-populations or local populations in the literature are not well defined, either geographically, ecologically or genetically (Figs. 1 and 2 depict some possibilities). Newton (1998) aptly recognized the "gray zones" of definition between smaller and larger demographic units as a "*continuum*", but he aptly applied principles of population biology to various levels or samples. This is the idea that numbers of birds in a "study area" (which almost universally has artificially delineated boundaries) can still be considered a demographic sample (Ricklefs 1979) if even its wider boundaries are not known. Yet, while further definitions of smaller demographic units within each sub-metapopulation grouping of AWPE would be useful, we cannot provide them here because it is extremely difficult to make precise definitions in light of the fact that there are likely these gradations of mixing (the continuum *sensu* Newton 1998), especially among the smaller units. Therefore here, we rely on the judgments of individual authors in their terminologies for these sub-units in the following papers.

In fact, high variability best describes the nature of AWPE breeding habitat. Due to natural variation in water conditions, AWPE have periodically moved breeding and feeding areas, so that breeding aggregations are not so fixed in location as with many marine birds. Such moves have been increasingly made more common due to the activities of humans. Thus it is likely that this high degree of mobility has resulted in a high degree of intermixing among populations, despite their general philopatric tendencies. However, it is unclear to what extent and how movements might occur, especially across the Continental Divide.

Breeding Colonies of the AWPE

In all instances, highly colonial breeding aggregations of the AWPE at any given time are always associated with some geographical

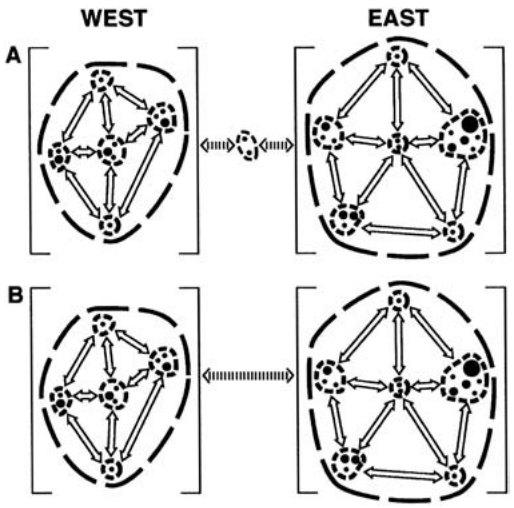

Figure 2. Diagrammatic representations of hypothetical AWPE range-wide sub-divisions (compare to Fig. 1) in metapopulation terms (the two models A and B, are the two that we currently believe best represent the AWPE). These diagrams were modified from a larger set of possibilities presented by Buckley and Downer (1996) and one of their models (B) was modified from Harrison (1994). Hypothetical populations are enclosed in short-dashed lines and metapopulations in long-dashed lines. Arrows indicate that genetic exchange is possible but they do not indicate how much.

features that function as conspicuous but "safe" havens for their nidicolous young (after Lack 1968:118). Wittenberger and Hunt (1985:3) defined a "colony" as "*a place where a number of individuals or pairs regularly roost at a more or less centralized location from which they recurrently depart in search of food.*" Unfortunately, the adaptive and ecological distinctions between breeding and roosting "colonies" are great, as are the degrees of distinction among the boundaries of colonies or the degrees of integration between these units (Coulson and Dixon 1979). Seigel-Causey and Kharitonov (1990) applied the colony-idea to "*primarily nesting aggregations*" as we will here. Therefore, the idea of "breeding colony" is a useful and meaningful term to apply to breeding aggregations of the AWPE; and, the study of the adaptive significance of coloniality in birds like the AWPE is still a fruitful area for research (Danchin and Wagner 1997).

Those geographical features where breeding occurs also have a name associated (or a name can be associated) with them (usually an island or peninsula, but sometimes also with a given body of water or some other dominant, geographically-named feature). This is where the terms "colony and/or sub-colony" often enter discussions relating to ecological conditions or even demographic performance; and they are usually named by agencies or researchers working on specific groups at specific locations.

Individual AWPE might move back and forth frequently (especially from year-to-year) among specific geographical breeding sites under varying conditions (Moreno-Matiella and Anderson, 2005), in which new breeding colonies or sub-colonies will have arisen or disappeared. But without specific behavioral, demographic and genetic data it is difficult to determine whether these colonies represent consistent isolated units or form ever-changing parts-of wider demographic units without constant mixing (Coulson and Dixon 1979). The terms "colony" and "sub-colony", as used by the authors in this symposium, refer mainly to breeding aggregations at specific geographic localities (often given the name or description of that location or feature) or even separate geographic features (with separate names) within a broader geographical location. But they may also provide useful evaluations for demographic evaluation if they are representative *samples* of a demographic unit (after Ricklefs 1979). Many colonies associated with given localities have much antiquity and historical consistence, as well as very large numbers of breeding pairs (for example, Chase Lake, North Dakota; see Bent 1922; Palmer 1962; Johnsgard 1993), especially when located in areas that are officially designated as protected areas or refuges by management authorities. They are therefore highly likely to be representative samples of the local geographic area with similar ecological conditions. Alternatively, small numbers of breeding AWPE may be highly isolated (as is the case at Stum Lake, British Columbia; VanSpall *et al.* 2005) so such a colony might also therefore represent a valid population sample. However, the word "colony" is not automatically interchangeable with population or sub-population (or local population).

The metapopulation divisions we have depicted in Fig. 1 represent no particular year or even the current situation, but rather, a typical, average "snapshot" for discussion purposes. Breeding colonies and sub-colonies at various locations over time will be "blinking-in and blinking-out" (McCullough 1996). A recent example is the temporary nesting colony mapped in Sonora, Mexico (Fig. 1). This colony was most recently active (fledged young) in April 2000, but it disappeared in 2002 after the reservoir on which the colony was located, dried-up during a drought (P. Moreno-Matiella, unpublished data).

Conservation Strategies Relating to the AWPE

Modern and more meaningful approaches based on population biology and actual geographical distribution during the breeding and non-breeding seasons are beginning to represent units that encompass multiple-political regions, more ecologically-meaningful units such as: (1) multi-state National Wildlife Refuge (NWR) complexes (e.g., the Klamath Basin NWR of California and Oregon); (2) the "Flyway Council" approach (consisting of multiple state and country representation in the management of migratory waterfowl, including the AWPE); (3) "joint-ventures" under national management plans such as the North American Waterbird Conservation Plan 2002 (Kushlan *et al.* 2002); or (4) the regional Intermountain West Waterbird Conservation Plan within it, a plan that encompasses nearly the entire western metapopulation of the AWPE (Ivey and Herziger 2005).

We suspect that, given adequate data plus effective conservation of numbers of present AWPE, future conservation biologists will also better develop the ability to define multiple "evolutionarily significant units" (Moritz 1994; Fraser and Bernatchez 2001) for the AWPE. But in conservation practice, it will not be necessary to wait. Conservationists can immediately increase management, protection, enhancement and restoration of individual colonies and sub-colonies throughout the AWPE range (Hastings and Harrison 1994), as well as preserve or enhance the necessary connectivity and adequacy of their non-breeding habitats. Disjunct and separated colonies of the AWPE in the current breeding range (and taking into account documented historical areas that no longer exist since the 19th Century) should still be classified as "management units", not because the birds might not mix to some extent with birds from other areas, but because conservation and management issues will be different between different geographic areas. Because specific numbers of birds occur at specific colonies, and the AWPE is highly colonial, monitoring of numbers and understanding ecological relationships in each separated part of the breeding range will be critical for long-term management and conservation purposes for maintaining and restoring numbers.

"*We console ourselves with the comfortable fallacy that a single museum-piece will do, ignoring the clear dictum of history that a species must be saved in many places if it is to be saved at all.*"

Aldo Leopold (1966:180)

AWPE Away from Breeding Locations

There is no practicality or usefulness in defining wintering or loafing groups of AWPE away from breeding sites with the term "population" because their behavioral and genetic associations have not been identified or even speculated, and such groups are usually temporary. General conditions on the wintering grounds could certainly affect single and/or multiple populations (Newton 2004; Esler 2000) and should not be ignored; but until specific data are forthcoming that AWPE aggregations on wintering grounds or at staging or loafing areas represent population samples or behaviorally cohesive groups (one aspect of "colonies" as defined by Wittenberger and Hunt [1985]; or communal roosts), we recommend that such groups of AWPE at least for census purposes be termed simply "non-breeding flocks." Yet, important locations used by non-breeding flocks must also be considered in any conservation management strategy.

FUTURE NEEDS

It is apparent that future studies on the following (in addition to continued and expanded studies on statuses, behavior and ecology of metapopulations and other demographic subdivisions) are needed to determine:

(1) the effectiveness of the North American Continental Divide as an isolating barrier;
(2) the genetic composition and variability among and between metapopulations and their sub-units (specific, local DNA studies);
(3) the degree to which recruits to the breeding areas are philopatric (return to their place of birth) and the extent to which annual exchanges of breeding adults occur between geographical areas and locations;
(4) the degree to which genetic exchange occurs through recruitment of first-breeding individuals across our hypothesized metapopulations and other units;
(5) the actual patterns of dispersal and movement during the course of normal and unusual breeding seasons (drought versus wet years, for example); and,
(6) how these parameters might change in light of expanding or declining numbers and large-scale and small-scale changes in long-term conditions (man-induced local conditions such as aquaculture or larger-scale conditions such as climate change).

Many of these questions can be explored through more extensive and regular banding and marking programs (of course, with durable bands and markers, with breeding colony and even sub-colony specific codes, and regular seasonal surveys in the colonies and sub-colonies) that should become routine annual tasks of many management agencies, along with currently routine, long-term monitoring of annual breeding numbers and productivity. We hope that this series of papers will stimulate further research and more intense and direct conservation for the American White Pelican.

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