



Observations on species limits in the Great Egret (*Ardea alba*) complex

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Abstract

The Great Egret (*Ardea alba*) has recently been split by some authors into two species, the widespread nominate form and Eastern Great Egret (*A. modesta*) of the Indo-Pacific region, based on a misinterpretation of available genetic and behavioral information. DNA-DNA hybridization data show only that *modesta* and the New World form *egretta* are likely to be separate species. Genetics of the Palearctic nominate form and the African *melanorhyncha* have not been studied. A display called Aerial Stretch, supposedly unique to *modesta* and definitely absent in *egretta*, may also be present in *alba* and *melanorhyncha* but has not been well studied. Striking differences among the four forms in soft-part coloration during “high breeding” could serve as isolating mechanisms between species, but the Eastern Hemisphere forms are closer to each other than any is to the American one, and *alba* and *modesta* differ more in intensity of color than in hue. While the complex may comprise as many as four species, currently available data only support a split of American Egret from Great Egret.

Key words: Aerial Stretch; American Egret; *Ardea alba*; *Ardea modesta*; *Ardea egretta*; isolating mechanisms; herons; heron taxonomy.

Introduction

The Great Egret (*Ardea alba*, sometimes placed in a separate genus *Casmerodius*) has long been regarded as a nearly cosmopolitan species with four essentially allopatric subspecies: *alba* (southern Palearctic from central Europe to Russian Far East), *modesta* (India to northeastern China and Japan to

Australia), *melanorhyncha* (sub-Saharan Africa and Madagascar), and *egretta* (North and South America). The form *maoriana* of New Zealand is no longer recognized by most authors. The current IOC list of birds of the world (Gill and Donsker 2010) separates *modesta*, under the poorly chosen English name Eastern Great Egret [within a cosmopolitan complex, “eastern” and

“western” are meaningless], from the “Western Great Egret” following Christidis and Boles (2008), with *egretta* remaining a subspecies of *Ardea alba*. This taxonomy represents a serious misinterpretation of the very limited genetic and morphological data available. The genetic information comes from a single DNA-DNA hybridization study (Sheldon 1987) that included only *egretta* and *modesta*. That study found that *modesta* differed from *egretta* to the same degree as it differed from broadly sympatric *A. intermedia*, and suggested that *modesta* and *egretta* should be considered separate species. Some influential authors (Kushlan and Hancock 2005, Christidis and Boles 2008) have wrongly extrapolated from Sheldon’s work that *modesta* should be split from *alba*, but Sheldon suggested only that American *A. egretta* should be split from Old World forms, as represented in his study by *modesta*. The morphological distinctness of *egretta* within the complex clearly supports that interpretation.

Potential Isolating Mechanisms

None of the authors who have split *modesta* have considered any potential isolating mechanisms other than a single “Aerial Stretch” display supposedly unique to *modesta* (Hancock 1984; Kushlan and Hancock 2005). However, Brown et al. (1982) described a somewhat similar and possibly homologous flight display in *melanorhyncha* without naming it, and M. Bartosik (pers. comm.) believes it may be the same as an aggressive flight display he has observed repeatedly in Europe (<http://www.pbase.com/mbb/image/124555868>). Although Kushlan and Hancock (2005) considered breeding biology of the Great

Egret complex to be “well studied”, all detailed observations yet published have involved *egretta*, *melanorhyncha*, or *modesta*, with the nominate form still relatively unknown. So we simply do not know whether *alba* or *melanorhyncha* use an Aerial Stretch, and absence of evidence is not evidence of absence. On the other hand, no such display has been reported for the very well-studied *egretta* (Mock 1978, McCrimmon et al. 2001).

Probably the most significant species recognition feature among all-white egrets that breed in mixed-species colonies is the coloration of the soft parts during the peak of the breeding cycle, when colors may change or intensify strikingly (Mock 1978, Kushlan and Hancock 2005). In the case of Great Egrets, all forms have black legs, yellow eyes, yellow bills, and yellow or yellowish-green facial skin for most of the year. But at the peak of courtship and territory establishment, they attain “high breeding” colors that differ among the various named forms. These colors have been poorly documented because they are highly ephemeral, and often appear only within breeding colonies where they are difficult to photograph. Furthermore, they exhibit broad individual, as well as seasonal, variability. Birds with incoming or fading “high breeding” colors can exhibit a confusing array of combinations and shades.

American Egrets, as they were long known, retain their all-black legs; the bill turns orange-yellow, with a variable amount of black on the culmen (sometimes covering most of the upper mandible, sometimes none); the loreal skin becomes bright apple green; and the eyes may have a rim of red around the periphery (Mock 1978,

McCrimmon et al. 2001) or may become nearly all red (<http://virtua-gallery.com/wp/2009/06/great-white-egret-with-twig/>). In *alba* and *modesta*, which may intergrade in northeast China and Japan (McCrimmon et al. 2001, Collar and Pilgrim 2007), the only known zone of contact among any of these forms, the bill becomes mostly black with variable amounts of yellow or red at the base of both mandibles, which darken from the tip backward rather than the culmen down as in *egretta*; the upper leg usually becomes red-orange, fading to dull pinkish yellow, in *alba* and pink to red in *modesta* (see photo in Collar and Pilgrim 2007; <http://www.flickr.com/photos/lipkee/2357186851/in/photostream/>); the loreal skin becomes bright green in *alba*, but blue-green or turquoise fading to pale green in *modesta*, and, reportedly, the iris briefly becomes entirely bright red at least in some *modesta* (Snow and Perrins 1998, Marchant and Higgins 1990, Kushlan and Hancock 2005). However, I have been unable to locate any photos showing the red eyes of *modesta*. Whether *alba* ever attains a red iris is unclear from the literature or available photographs. Iris color is the most briefly held of the high breeding changes, occurring just before egg laying (Hancock and Kushlan 1984), so birds of any form may have yellow eyes while retaining or developing their other high breeding colors. High-breeding *melanorhynchus* retains its all-black legs, the bill becomes all black darkening from the tip and fading in reverse as in *alba* and *modesta*, loreal skin turns blue-green, and eyes become brilliant red (Brown et al. 1982, Kushlan and Hancock 2005). Again, the red iris fades quickly. Clearly, all the Eastern Hemisphere forms resemble each other more closely than any resembles *egretta*, and *alba* and *modesta* are closest to each other of any pair, with

colors that, except for the lores, differ in intensity more than in hue. So Great Egrets fall into three groups on the basis of high breeding coloration: *alba/modesta*, *melanorhynchus*, and *egretta*. Each group should be field-identifiable during the breeding season, but separating *alba* from *modesta* can be problematic because of individual variation. For example, J. A. Kushlan (pers. comm.) believes that some birds recently photographed in central Europe that appear to be vagrant *modesta* (J. Šírek pers. comm.) may be color extremes of *alba*. Likewise, whether a *melanorhynchus*-like egret that appeared on the East Coast of North America (Adams and Hafner 2008), or a Great Egret with pale upper legs reported from the West Coast (<http://skygardener.zenfolio.com/p469412472/h1e38cc0b#h11405fcb>) are true vagrants of Old World forms or simply individual variants has not been determined.

Discussion

Given currently available information, the Great Egret clearly was split in the wrong place by Kushlan and Hancock (2005) and Christidis and Boles (2008). Considering the distribution of high breeding color differences and possible intergradation between *modesta* and *alba*, splitting *modesta*, while retaining *egretta* within *alba* is unreasonable. Certainly Sheldon (1987) does not support such a classification, as Collar and Pilgrim (2007) clearly acknowledge. They also point out that even Kushlan and Hancock (2005), the first to formally propose this arrangement, were equivocal about it and suggested that further genetic data were needed. That is an understatement. Although Christidis and Boles (2008) understood that Sheldon's

(1987) data only supported a split between *modesta* and *egretta* and did not address relationships among the other Old World forms, they nevertheless retained *egretta* in *A. alba* while splitting *A. modesta*, presumably based on a single poorly studied display that may not, after all, be unique to one form. They completely ignored the striking soft-part color differences in the complex and gave undue weight to very flimsy behavioral evidence. Currently available data support only the splitting of *egretta* from *alba* (including *modesta*), and even that split may be premature considering that it is based on a now-obsolete genetic technique, although McCracken and Sheldon's (1998) more recent results offer some confirmation without directly addressing this particular taxonomic issue. Modern genetic studies of all five named forms are urgently needed, as are thoroughgoing investigations of mating displays, before species limits in this complex can be fully hypothesized.

For now, compilers of checklists and authors of field guides have only two reasonable taxonomic options with regard to the Great Egret complex: either retain a single Great Egret species pending definitive and complete genetic and behavioral studies of all forms; or recognize Great Egret (*A. alba*), including subspecies *modesta* and *melanorhyncha*, and American Egret (*A. egretta*) based on Sheldon (1987) and demonstrated potential isolating mechanisms of differing high breeding colors, color ontogeny, and lack of the Aerial Stretch display. Recognition of *A. egretta* as a separate species would call attention to the widely cited but mistaken use of Sheldon (1987) to separate only *modesta* from *Ardea alba* and end the trend in that direction among list-makers. The *alba/egretta* split is reasonable without genetic information

because of the wide geographic separation of the two forms and the presence of at least two kinds of isolating mechanisms (Pratt 2010). If *alba* and *modesta* are ultimately shown to intergrade in northeastern Asia, then the case for separating them at the species level will be further weakened. Alternatively, if these taxa are found to be allopatric or parapatric, and supposed differences in mating displays among *alba*, *modesta*, and *melanorhyncha* hold up to further scrutiny, then the four current major subspecies of Great Egret might well all be considered biological species regardless of what future genetic studies show.

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