The Great White Heron is a species

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Abstract

The Great White Heron was considered a separate species for nearly 140 years from the time of its original description (1835) by John James Audubon as *Ardea occidentalis* until 1973 when it was synonymized with the Great Blue Heron (*Ardea herodias*) by the American Ornithologists' Union Committee on Classification and Nomenclature. Recent studies and syntheses have supported its re-elevation to full species status, a finding accepted by international authorities. In 2020, American Ornithological Society's North American Classification Committee declined to accept a change in status. The present paper summarizes arguments and presents further information that support recognition of the Great White Heron, *Ardea occidentalis*, as a species distinct from the Great Blue Heron.

Key words: Ardea herodias, *Ardea occidentalis*, Ardeidae, assortative mating, Caribbean, genetics, Florida Bay, Great Blue Heron, Great White Heron, morphology, taxonomy.

The Great White Heron has been an intriguing bird since its discovery for science in Florida Bay by John James Audubon in 1832 (Kushlan 2015). It was not unknown to locals before this event, as Audubon's experienced local guide was the one who showed the birds to him; it was one of the great scientific findings of Audubon's Florida expedition — the discovery of what was considered to be North America's largest heron (Kushlan 2020). Audubon's plan was to illustrate all North American bird species at their natural size; but the Great White Heron is huge. To compensate, the printer suggestively and uniquely allows the heron's bill tip to transgress the plate's outer border (Fig. 1). Audubon commissioned the background to show Key West with the town and the heron being highlighted by a dramatically darkened sky, making this one of his most striking images.

Audubon's discovery was a natural history sensation, and the Great White Heron was accepted as

Figure 1. Portrait of the Great White Heron by John James Audubon from *Birds of North America*, Plate 281 (1835a).

a bona fide species for nearly 140 years from 1835, when Audubon published his plate, its formal description, and an account of its discovery and life history, to 1973 (Audubon 1835a, b; American Ornithologists' Union [AOU] 1973). In 1973, the AOU Check-list Committee decided to consider it a subspecies of the Great Blue Heron (*Ardea herodias*). Evidence presented for the decision was thin then, and subsequent research has further undermined this fifty-year-old decision (McGuire 2001, 2002, Sibley 2007, McGuire *et al.* 2019, Remsen 2019, BirdLife International 2020a). In 2020, the American Ornithological Society's North American Classification Committee (NACC) declined by a 5 to 4 vote to recognize the Great White Heron as a species (Chesser *et al.* 2020). Yet studies have presented compelling evidence based on morphology, mating behavior and genetics to conclude that the white-colored *Ardea* found in extreme southern Florida is a distinct and valid species. Assigning the appropriate taxonomic rank has importance for understanding the evolution of the Ardeidae and the genus *Ardea* but also has crucial conservation importance, owing to the Great White Heron's decreasing population size and endangered status (BirdLife International 2020a).

In this paper, we use the names *occidentalis* and Great White Heron for the population of predominantly white-plumaged herons breeding in southern Florida and rarely elsewhere in the Caribbean. At the present time *occidentalis* is recognized as the subspecific epithet applied to these birds by the NACC and the common name of Great White Heron is available to also refer to the subspecies. We use the specific epithet *herodias* to refer to the dark-plumaged Great Blue Heron populations including its other recognized subspecies *fannini* of the Pacific Northwest, *wardi* of the southern United States and northern Mexico, and nominate *herodias* occurring north of *wardi* (Dickerman 2004, Kushlan and Hancock 2005). We use the name *wurdemanni* and Würdemann's Heron to refer to darkish but decidedly pale birds that occur within the range of the Great White Heron. These birds are recognizably different from other dark Great Blue Herons by their variously grayish bodies and washed-out neck and head coloration. These birds were once considered a separate species *Ardea wurdemanni* and more recently to be hybrids of Great White and Great Blue herons, although alternative explanations are available, as discussed below. In some studies, any dark specimen collected in Florida Bay tends to be treated as a Würdemann's Heron irrespective of plumage character. Abbreviations in selected quotes include GBHE for Great Blue Heron and GWHE for Great White Heron.

Taxonomic History

Holt (1928) presented convincing evidence in favor of the specific distinctiveness of the Great White Heron that led to its status being formally recognized by the AOU. This state of affairs lasted until the Check-list report of 1973 when the committee declared *occidentalis* and *A. herodias* to be conspecific (AOU 1973). The Committee's notification cited Mayr (1956), Meyerriecks (1957) and Bond (1961) in supporting the decision, although it offered no details on how it used these references, leaving it to the reader and posterity to discern his method. This is perhaps an example of how the prestige of an author may have influenced acceptance of his conclusion.

Mayr (1956) states that while naturalists who have studied the heron in the field considered *occidentalis* and *herodias* as separate species, "It is museum workers like Ridgway and me who are inclined to consider the Great White Heron as conspecific with the Great Blue …" (p. 71). Given that Mayr goes on to accept the museum point of view, the implication certainly is that he discounted observations in nature as being less compelling than those derived from museum specimens. No doubt, given Mayr's stature, his opinions carried weight. Mayr cited only two references, Holt and a theoretical chapter of his own. He did not provide a citation to further explicate Ridgway's views although Holt (1928) did. So Mayr (1956) likely was alluding to Ridgway (1880) in which Ridgway states that J. W. Velie of the Chicago Academy of Sciences found "in two instances, once in 1872, and again in 1875, … half-grown young, one each of *A. occidentalis* and *A. würdemanni*, in the same nest! This evidence is all that was needed to settle the question of the identity of the two forms in question, and there cannot now be any doubt that they represent two phases of one species, …" (pp. 122-123). Ridgway's conclusion, based on a second party observation of two mixed-color broods, certainly did not rise to the level of concluding that "cannot now be any doubt." (p. 123).

In fact, details of Velie's records in Florida beyond Ridgway's conclusions are decidedly obscure. The record of Velie's observations derive from a speech by the wealthy manufacturer, philanthropist and Academy president Eliphalet Wickes Blatchford in a speech at the Chicago Academy of Sciences. Blatchford's (1878) references were in connection with the president's annual report describing expansions of the Academy's collection and singling out the work of Dr. Velie for commendation. He reports that Velie collected broadly including shells, mammals, birds and eggs along the Florida Gulf coast in 1872, 1875, 1876 and 1877 ranging over the years from Key West to Cedar Key. Despite Ridgway's assertions, Howell (1932) in his exhaustive review of the birdlife of Florida, including a thorough study of museum specimens, concluded there actually exists little information on Velie's work in Florida but inferred from the known range that his Great White Heron specimens must have been from the Florida Keys even though he recorded it as only going as far south as Cedar Key. Butler (1997) raises this doubt writing that Velie's specimens were from northern Florida. So, where Velie made his observation of heron nests remains unclear. Mayr's conclusion based on a third-hand report of Velie's observations of interbreeding is slim indeed and contrary to his previous assertion of the primacy of museum curators over "field" observation.

Although cited by AOU (1973) in support of its decision, rather than being supportive of Mayr (1956), Bond (1961) in fact disagreed that the extreme South Florida population was an endemic subspecies from North America but rather one that had evolved in the Caribbean and constituted an Antillean-derived subspecies, *repens*.

The AOU Check-list Committee also cited Meyerriecks (1957) in support of its decision (AOU 1973). Meyerriecks actually concluded that previously reported mixed mating in Florida Bay "are, at best, vague and inconclusive" (p. 472) while providing evidence, albeit meager, on the existence of assortative mating. Meyerriecks stated that although his observations "favors the view that *occidentalis* and *herodias* are conspecific," more study is required "before a final decision can be made" (p. 478). Such indecisiveness and call for more research by Meyerriecks before a decision should be made is hardly strong support for such change as the committee chose to make nor, as McGuire *et al.* (2019) remarked, would be the rather "vague historical assertions of Mayr (1956) and Bond (1961)" (p. 2).

The inclination of Mayr and opinions of Ridgway, Bond and Meyerriecks individually and together should not have been insufficient for the AOU Committee to have chosen to synonymize Great White and Great Blue herons. The Committee also states that for "additional morphological grounds" *occidentalis* "is entitled subspecies rank" and that the name Great White Heron is "available for the white morph" (AOU 1973, p. 413). It is not usual to retain a common name for one morph of a subspecies. It was perhaps acknowledgment of a century of public usage, or recognition of the importance of a national wildlife refuge named for the Great White Heron established in 1938 to protect it, or perhaps acknowledgment of the intrinsic silliness of calling a large white bird blue.

Since then, the taxonomic status applied to Great White Herons has varied somewhat but usually has followed the authority of the AOU Check-list. Payne and Risley's (1976) study of systematics of herons indicated uncertainty about the taxonomic status of *occidentalis*, but they had few specimens to analyze. They did not challenge the status quo and listed the Great White Heron as a subspecies of *A. heroidias*. As this work was in preparation for a new edition of the Check-list of the Birds of the World, conservatism seems not inappropriate (Payne 1979). Payne rejected recognition of *A. h. wardi* as a subspecies, stating that variation of *Ardea* (outside the Pacific Northwest) is clinal and that the only distinguishing feature of *occidentalis* is its proportion of white birds. AOU (1998) considered *occidentalis* as a white morph of *herodias*, with the group name *occidentalis*. AOU (1998) considered group names to consist of similar taxa "that perhaps should be split" (p. xii), suggesting that committee's uncertainty. Dickerman (2004) considered *occidentalis* as a subspecies of *herodias*. Both Zachow (1983) and McGuire (2001, 2002) attempted to deal with the confounding issue of clinal change in morphology and genetics of *Ardea* down the Florida peninsula. Zachow considered bone size variation to be clinal, but the preponderance of McGuire's morphological, geographic and genetic evidence suggests distinctiveness of the Florida Bay population. Kushlan and Hancock (2005), recognizing McGuire's then unpublished work, followed the AOU Check-list taxonomically but did offer the hypothesis that Great White Herons might have evolved in the West Indies and came into secondary contact with continental Great Blue Herons in South Florida. McGuire *et al.* (2019) in synthesizing morphological, behavioral and genetic information, concluded that the Great White Heron is specifically distinct from the Great Blue Heron.

Whether the two herons are taxonomically distinct or not, the question of the Würdemann's Heron remains. Würdemann's Heron is no longer mentioned by the latest check-lists (AOU 1957, 1998). However, although variable, it is quite distinctive from continental Great Blue Herons, well-known in Florida, and featured in current field guides (Sibley 2014, Dunn and Alderfer 2017). Sibley describes it as being intermediate between white and dark herons and it is generally considered to represent gene flow between *occidentalis* and *herodias* (McGuire *et al.* 2019). But an alternative hypothesis exists. If *occidentalis* were a separate species and interbreeding with continental Great Blue Herons is rare to non-existent, Würdemann's Heron might represent the dark morph of *occidentalis*. Given that assortative mating among white Florida Bay *occidentalis* and among dark continental *herodias* appears to be the rule, Würdemann-type herons documented within mixed broods need not indicate hybridization between white and North American gray birds.

Assessing Taxonomic Status

Plumage and Soft Part Coloration

Morphologically, *occidentalis* differs most obviously from other related taxa in its white plumage. The other subspecies, as far as is known, have entirely dark plumage. All-white plumage disadvantages taxonomists by offering no other color-based metric. There does seem to be a difference between *occidentalis* and *herodias* in length of occipital plumes. Holt (1928) reported occipital plumes of *occidentalis* and Würdemann's herons are similar in length but shorter than those of *wardi*. McGuire *et al.* (2019) reports shorter mean values for *occidentalis* compared to nominate *herodias* but slightly greater values for Würdemann's Herons. Given their role in communication including pair formation, differences in plume length could be of species-specific significance (Mock 1976, Kushlan and Hancock 2005, Voisin 2010).

McGuire *et al.* (2019), Remsen (2019) and NACC (2020) did not consider soft-part colors. However, Hancock and Elliott (1978) state that the loral skin color is dull greenish in *A. herodias* and bluish in *occidentalis*. Galvez (2014) calls the facial skin at the base of the bill "pale" turning bright yellow during breeding. The taxonomic importance of soft-part colors in birds, including herons, suggests soft-part coloration differences might be significant, and that more information may be desirable (Hancock and Kushlan 1984, Pratt 2010, 2011).

Also of importance are the relatively underappreciated differences in the extent of facial skin between *herodias* and *occidentalis*. Galvez (2014) made careful comparisons showing that *occidentalis*, unlike *herodias*, shows a larger amount of bare skin in the facial region, which exposes the upper edge of the lower mandible, creating what he calls a "grimace," which also makes the bill appear larger. This feature actually can be seen in Audubon's original drawing (Fig. 1).

Size

The subspecies *wardi* was described as larger than the subspecies *herodias*, a difference that is apparent in the field. Dickerman (1992, 2004) confirmed this through measurements of wing chord, and lengths of tail, culmen and tarsi.

Size differences between *occidentalis* and other subspecies are somewhat less clear. McGuire *et al.* (2019), owing to a limited number of specimens of *wardi* at their disposal, compared *occidentalis* with nominate *herodias*. They reported statistically significant differences in five of seven morphological characters, although they found *occidentalis* and *herodias* are similar in wing chord. Dickerman (2004), with a larger sample (35 vs. 8) of nominate *herodias*, found mean wing chord of *occidentalis* is larger than that of nominate *herodias* and smaller than *wardi* from Florida, an expected finding comparing a migratory population with a non-migratory one. Both studies found that that exposed culmen and tarsus are greater in *occidentalis* than in nominate *herodias*.

Zachow (1983) and Dickerman (2004) compared *occidentalis* to the adjacent subspecies, *wardi*. Zachow found from osteological measurements that *occidentalis* from Florida Bay were overall larger than *wardi* from mainland Florida. Dickerman (2004) compared 28 male and 20 female specimens of *wardi* from mainland Florida. His data indicate that *occidentalis* has shorter wing chords than both male and female *wardi* from Florida. He also found that, except for culmen length, *occidentalis* is smaller than *wardi* (Dickerman 2004). All studies have shown *occidentalis* has a larger bill, a feature apparent in the field.

There have been no comparisons of size differences within the range of *occidentalis*. To attempt to determine geographic variation in size within *occidentalis*, we compared several characters measured by McGuire (McGuire *et al.* 2019). Using data from Table S1 of McGuire *et al.* (2019) and McGuire's (2001) lists of individual specimens by the museum and catalog number, we determined specific localities for most specimens. We divided adult *occidentalis* specimens into two geographic groups, a southern series (n = 10 males; n = 4 females) from the lower keys defined as west of the water gap at the Seven Mile Bridge to Key West and a northern series (n = 8 males; n = 9 females) defined as any breeding locality east and north of Seven Mile Bridge of US Highway 1. Mean values of most characters of northern and southern samples were similar. However, for males the mean wing chord was greater for northern populations (mean = 496.7 mm, SD = 9.24, n = 5) than that for the southern populations (mean = 486.6 mm, SD = 10.62, n = 9). Although the difference is not statistically significant owing to the very small sample size, it is suggestive of a difference between more northern and more southern *occidentalis* ($t = 1.7786$, $P = 0.1006$, df = 12). The percent difference in wing chord of males contrasted with females is consistent with that reported by Dickerman (2004) for nominate *herodias* and *wardi*, but not for the southern *occidentalis,* suggesting that there may be a trend toward reverse sexual dimorphism in *occidentalis* such as found in the closely related South American *Ardea cocoi* (Cocoi Heron), in which females' wing chord is 1.7% greater than that of males (Wetmore 1965, Blake 1977, Payne 1979). These comparisons of differences in wing chord and sexual dimorphism, between *occidentalis* and eastern North American populations of dark-plumaged herons support the concept that *occidentalis* is on a different evolutionary trajectory.

Assortative Mate Choice

Importantly when considering the specific status of *occidentalis* and *herodias* is that McGuire *et al.* (2019) showed white and dark herons mate positively assortatively. This in fact had been known for some time, with hints dating back to Holt (1928) and Meyerriecks (1957). Robertson (1978) thoroughly monitored nesting by herons in Florida Bay for decades from an airplane. He found that mixed pairs occur "about" one order of magnitude below what is expected from a randomly mating population. Further, mixed pairs in his data did not distinguish *wardi*-type birds from *wurdemanni*-type birds. Similar surveys by Powell support

Robertson's finding of positive assortative mating (Powell and Bjork 1996). As a recent example, Lorenz and Rafferty (2016) reports that on one island there were 12 nests of dark pairs and 24 nests of white pairs. There were no mixed pairs. McGuire *et al.* (2019) found 97 of 114 (85%) pairs mated assortatively by plumage color. Clearly, most white herons pair with white herons and dark herons pair with dark herons.

Genetics

The McGuire *et al.* (2019) analysis of microsatellite DNA was performed with STRUCTURE, a software program that infers population structure, assignment of individuals to populations, hybrid zones and identifies migrants and admixed individuals (Pritchard *et al.* 2000). The analysis revealed two genetic groups, one including dark herons represented by the subspecies *fannini*, nominate *herodias* and *wardi*, and a second group including *occidentalis* from the keys and *occidentalis* and Würdemann's herons from Florida Bay.

Remsen (2019) writes: "In a comparative framework, the contact zone between these two [herons] resembles empirically that of Lazuli and Indigo buntings, Rose-breasted and Black-headed grosbeaks, White and Scarlet ibises, and others that we treat as separate species: gene flow is substantial but far from "free"; the contact zone is strongly dominated by phenotypically pure birds, and the frequency of mixed pairs is low. Free gene flow would produce a hybrid swarm at the contact zone; after 10 generations of random interbreeding, the chances of finding any pure birds in a closed system would be less than 1% (vs. at least 85% empirically in this system). Of course, the real-world contact zone is not a closed system, yet the level of immigration required to maintain 85% pure phenotypes seems unreasonably high." (p. 40). Remsen also writes that "when given the chance to pair, white birds pick white birds and blue birds pick blue birds to a much greater degree than expected by chance. In other words, these two taxa regard each other as "different" when it comes to mate choice. Thus, gene flow is reduced by assortative mating, and thus the two taxa should be ranked as separate species according to the most frequently applied operational definition of the BSC [Biological Species Concept]. I think the data are sufficient to place the burden-of-proof on treatment as the same species." (pp. 39-40).

Regarding mate choice, NACC members voting to recognize *occidentalis* as a species include such statements in their report as "The high degree of assortative mating is convincing …" and there is "significantly non-random mating" (NACC 2020). Others voting in the affirmative noted *occidentalis* and dark herons have been in contact "for centuries" but do hybridize frequently. Another member recognizing *occidentalis* as a species noted not seeing intergrades in Cuba where both *occidentalis* and dark herons breed while another NACC member stated there is some evidence of interbreeding, but not free interbreeding. Those against the proposal to recognize *occidentalis* as a species ranged from accepting there is evidence of assortative mating, but that 15% of disassortative mating and hybridization indicates high levels of gene flow for recognizing species.

Some members questioned the amount of assortative mating and noted concerns regarding Q-values revealed by STRUCTURE (NACC 2020). The program is widely used in genetic studies but should not be regarded as definitive proof of introgression (Ottenburghs *et al.* 2017). Further, STRUCTURE assignments are not infallible and may mismatch haplotypes and phenotypes (Oswald *et al.* 2018). One member wrote that the "similarity of Q scores of dark and white birds from the Florida Bay is quite striking, suggesting substantial backcrossing/introgression." Q-values (McGuire *et al.* 2019, Table 4) show that dark and white herons are represented by separate genetic clusters, with dark Florida Bay birds having intermediate ancestry values, albeit closer to white herons. These Q-values were, however, inferred from heron populations represented by samples of uneven size (sample sizes range from 11 to 77 in McGuire *et al.* [2019, Table 4]), which has recently been shown to produce biased results in ancestry analyses performed with STRUCTURE (Toyama *et al.* 2020). More balanced sample sizes might produce different Q-values, which might or might not qualify as "quite striking." Nonetheless, a strong signature of admixture would still be observable, suggesting ongoing gene flow between populations (Toyama *et al.* 2020, Toyama pers. comm., 2021).

Gene flow between *occidentalis* and dark herons, based on NACC comments, weighed heavily in their decision to consider *occidentalis* a subspecies (NACC 2020). However, gene flow happens between species (e.g., Servedio *et al.* 2011, Sonsthagen *et al.* 2016, Dannemann and Racimo 2018, Palacios *et al.* 2019). Gene flow in the form of hybridization occurs in an estimated 16.4% of species of birds (Ottenburghs *et al.* 2015). Further, patterns of gene exchange could be from "ghosts of introgression past" and not a genetic map of current relationships (Rowher *et al.* 2001, Rheindt and Edwards 2011). Evidence of admixture occurs in North American *Plegadis* species geographically close and distant from their region of sympatry (Oswald *et al.* 2018). The interchange between *occidentalis* and dark herons is, as Remsen (2019) stated, similar to ibises and North American buntings and *Pheucticus* grosbeaks. Genetic values and morphology make delineating species difficult in some taxa, with a considerable admixture of several species of gulls, some of which is historical (Sonsthagen *et al.* 2016), yet most species studied are not taxonomically controversial.

Check-list standards include that "hybridization of two forms across a narrow and stable contact zone … is now viewed as evidence of lack of free interbreeding" (AOU 1998, p. xiv). The hybrid zone for the Florida herons is both narrow and stable. Johnson *et al.* (1999), in describing the Comprehensive Biological Species Concept (CBSC), states: "An avian species is a system of populations representing an essentially monophyletic, genetically cohesive, and genealogically concordant lineage of individuals that share a common fertilization system through time and space, represent an independent evolutionary trajectory, and demonstrate essential but not necessarily complete reproductive isolation from other such systems." (p. 1478). The taxa *occidentalis* and *herodias* clearly represent independent evolutionary trajectories, likely reflecting the independent evolution of *occidentalis* in the West Indies.

Although genetic distances are low between samples of white and dark herons (McGuire 2002), perfectly good species are recognized with very low genetic distances (e.g., Gray and Chestnut teal [Christidis and Boler 2008]) and with genetic distances of zero (e.g., Chestnut-sided and Magnolia warblers [Avise *et al.* 1980]). Winker (2018) makes the persuasive conclusion that "genetic diagnosability alone is not a particularly useful criterion for diagnosing species …" (p. 455). Anas ducks and Larus gulls are a few examples that maintain the status of different species despite frequent interspecific hybridization. Response to some barriers such as saltwater vs. freshwater preference and reproductive barriers (choice of plumage color of mate) might contribute to the maintenance of narrow hybrid zones (Rheindt and Edwards 2011).

If *occidentalis* and *wardi* were in fact subspecies of the same species, the two interbreeding taxa would produce blended morphologies typical of intergrading subspecies. The only indication of potential blending is Würdemann's Herons. These herons are rare (Pranty 2005). Further, this plumage variation does not show any sort of cline, which would be expected with interbreeding subspecies. Assortative mating of white birds and of dark birds would not be expected to occur between subspecies (*contra* Chesser *et al.* 2020). Size, including sexual dimorphism, shows *occidentalis* is evolving on a different trajectory than found between nominate *herodias* and *wardi*.

Global Reclassification

Birdlife International re-examined the taxonomic status of the Great White Heron using the criteria of Tobias *et al.* (2010) (BirdLife International 2020a). Based on this independent quantitative analysis, BirdLife International concluded that *occidentalis* and *herodias* are separated by diagnostic plumage (white vs. gray), mate choice, timing of mating, and habitat (saltwater-island vs. fresh/brackish water-mainland), having shorter *occidentalis* plumes, longer bill, tarsus and middle toe than *herodias*, habitat choice and narrow hybrid zone. On this basis BirdLife International and the Handbook of Birds of the World accepted *Ardea occidentalis* as a separate species (BirdLife International 2020b).

Distribution, Population and Conservation

The Great White Heron breeding range is primarily South Florida, in Florida Bay, the Lower Florida Keys, eastward in Biscayne Bay, and sparsely along the Gulf of Mexico coast. Although there is no evidence of migration, stragglers can occur widely. It also occurs in small numbers as a rare breeder in Cuba and also in Yucatan. Other records that appear in the literature are not persistent breeding birds. These geographic differences in abundance are often overlooked in assessing the effective range; currently it is a bird primarily of extreme South Florida. It is unlikely to have evolved there in sympatry with the Great Blue Heron. More likely it evolved in the West Indies and colonized South Florida when the environment became acceptable post-Pleistocene bringing it into contact with *Ardea herodias* (Kushlan and Hancock 2005). Whereas the Great Blue Heron is rare in winter along the coast of South America and breeds only infrequently elsewhere in the Caribbean, the white *Ardea* population in the Los Roques off Venezuela may well be a morph of *Ardea cocoi*. Disregarding the insular Los Roques population 160 kilometers north of Venezuela and other rare records from the Caribbean, the known breeding range of the Great White Heron can be characterized as Cuba, Yucatan and extreme South Florida, with the preponderance of the population in Florida (Kushlan and Hancock 2005, BirdLife International 2020b).

The global population is tentatively placed at about 1,000-2,499 mature individuals, though the true population size may be closer to the lower end of the estimate or even below (BirdLife International 2020a, b). Data suggests the species is declining at a rate of c. 45% over the last three generations (24 years), or 33% over two generations (16 years).

In a recent periodic re-evaluation in conjunction with its application of the IUCN Red List process to birds, Birdlife International (2020b) evaluated the conservation status of *occidentalis*. Based on its analysis of population size and trend, range, and threats, BirdLife International recognized *Ardea occidentalis* as an endangered species, and it is now listed as such on the IUCN Red List of Threatened Species (BirdLife International 2020a).

Conclusions

Occidentalis is recognized as a distinct species. *Ardea occidentalis* by the IUCN Red List based on the standard criteria used for this listing and by its conservation status evaluation criteria is a globally endangered species (BirdLife International 2020a, b). *Occidentalis* differs from *A. herodias* morphologically in plumage color and facial soft parts. The two species overlap in size, but *occi-*

dentalis averages larger than *herodias*, especially in bill dimensions, and measurements indicate the two species are on independent trajectories in sexual dimorphism and geographic variation. Further, the two species differ genetically and breed assortatively. Mayr's (1956) paper is entitled "Is the Great White Heron a good species?" The answer to the question is clearly yes. The conservation implications of this recognition are immense; the Great White Heron is a species in need of directed conservation action.

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