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A review of the North American subspecies of the Great Blue Heron (*Ardea herodias*)

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Abstract.—Geographic variation in the great Blue Heron (*Ardea herodias*) was comprehensively reviewed by H. C. Oberholser (1912), who recognized nine North American subspecies–excluding the so-called Great White Heron (*A. occidentalis* = *A. h. occidentalis*). Oberholser's revision provided the framework generally followed in subsequent subspecific treatments of this species. However, Payne's (1979) brief general summary of this species' geographic variation rejects most of these North American taxa, recognizing as valid only the nominate subspecies and those of the Pacific northwest [*A. h. fannini*] and Florida [*A. h. occidentalis*]. My studies verify that *A. h. herodias* and *A. h. fannini* are taxonomically distinct, along with *A. h. wardi* in which I include *A. h. treganzai, A. h. hyperonca,* and *A. h. sanctilucae.* In addition, I regard *A. h. lessoni, A. h. adoxa,* and *A. h. olgista* as synonymous with *A. h. herodias,* as all are based on migrant specimens of this form. In addition, I suspect Payne is justified as recognizing the Caribbean *A. h. occidentalis* as valid, based on its white plumage and shorter head plumes.

The Great Blue Heron (*Ardea herodias*) nests in North America from southeastern Alaska, southern British Columbia, northern Alberta, central Saskatchewan, northern Manitoba, northern Ontario, southern Quebec, New Brunswick, and Nova Scotia southward to the Gulf states, southern Florida; on the coastal lowlands of Mexico south to Tabasco, Nayarit, and Baja California; and locally in the Caribbean Basin (A.O.U. 1998). There are no nesting season specimens of Great Blue Herons taken between the Yucatan Peninsula of Mexico and Venezuela. Oberholser (1912) recognized nine subspecies over this extensive area, these being *A. h. herodias* L., 1758 (type locality: America [= Hudson Bay, Canada]); *A. h. wardi* Ridgway, 1882 (Oyster [= Estero] Bay, Florida; *A. h. treganzai* Court, 1908 (Egg Island, Great Salt Lake, Utah); *A. h. fannini* Chapman, 1901 (Skidegate [Graham Island], Queen Charlotte Islands, British Columbia); *A. h. hyperonca* Oberholser, 1912 (Baird [Shasta Co.], California); *A. h. sanctilucae* Thayer and Bangs, 1912 (Espiritu Santo Island, Baja California); *A. h. lessoni* Wagler, 1831 (Mexico); *A. h. adoxa* Oberholser, 1912 (Curacao); and *A. h. olgista* Oberholser, 1912 (San Clemente Island, California). Not included in Oberholser's revision was the so-called Great White Heron (*A. occidentalis*), which is now widely regarded as a white morph of *A. herodias* (e.g., A.O.U. 1998). In addition, he did include the endemic *A. h. cognatus* of the Galapago Islands, which is the only nesting population of this species outside North America.

Oberholser's (1912) subspecies were based on differences in plumage coloration and measurements among populations, which in some cases included migrants from other areas. In fact, although Oberholser was aware of both migration and other forms of dispersal in this species, he appears to have underestimated the extent of

this phenomenon. For example, Bond (1935) found that Oberholser's *A. h. adoxa* from Curacao is based on a series of eight specimens, all of which are southward migrants of *A. h. herodias*. In addition, the adult female holotype (examined) for Oberholser's (ibid.) *A. h. olgista* from San Clemente Island is also an example of the nominate form, based on its dark coloration and a wing chord of 433 mm, even though previously synonomized with the locally nesting *A. h. "hyperonca"* (= *A. h. wardi*) by Grinnell and Miller (1944) and Hellmayr and Conover (1948). Hellmayr and Conover (1948) also listed *A. lessoni* Wagler as a synomym of *A. h. herodias,* simply noting "type in Munich Museum examined."

Oberholser's revision provided the framework generally followed in subsequent subspecific treatments such as A. O. U. (1931, 1957), Peters (1931), Friedmann et al. (1950), Palmer (1962) and Hancock and Elliot (1978).

More recently, Payne (1979) has treated overall geographic variation in the *A. herodias* complex (including *A. occidentalis*), although he did so only briefly, generally, and without measurements or references to subspecific names. He recognized only three taxa in North America: the widespread *A. h. herodias, A. h. fannini* of the north Pacific Coast, and the white-plumaged *A. h. occidentalis* of the Caribbean Basin. My revisionary work on the Great Blue Heron began in an attempt to identify then recently collected Mexican specimens in the 1960's. Since then I have examined most of the available adult specimens in North American collections. My findings generally agree with those of Payne, except that I also recognize the populations of paler and larger birds of southern and western North America as *A. h. wardi.* I did not examine plumage variation in nesting populations of the Caribbean Basin, but these may constitute a valid subspecies (*A. h. occidentalis*) based on the dominance of the white morph (rare elsewhere). If not recognizable, then these populations and those of *A. h. wardi* should be merged under the older name of *A. h. occidentalis.*

Methods

Several caveats apply to the museum specimens used in this study, the first being the dearth of properly labeled and prepared adult nesting season skins for studies of geographic variation among Great Blue Herons in North America. For example, I found no nesting season adult males from Delaware, Virginia, West Virginia, and Kentucky; only single males from Maryland, Tennessee, South Carolina, and Alabama; and only two from North Carolina! Secondly, many specimens lack information on gonad size, weight, and fat condition, making it difficult to ascertain whether such birds are likely nesting or are migrants. As a result, one must often assume that birds are nesting on the basis of collection localities and dates, which can be complicated by (a) regional differences in the timing of breeding activities and (b) the migration and other forms of dispersal in this species. For example, we know post-nesting southern populations (*A. h. wardi*) can be dispersing northward in the northeastern U.S. while northern birds (*A. h. herodias*) are in the process of nesting (Dickerman 2002). Whereas coloration and measurements do distinguish these subspecies, some specimens overlap or intergrade between the two. As a result, these may be either included in or excluded from nesting samples, thus introducing some degree of bias into the data. In any case, I have arbitrarily set the nesting season for most North American populations of this species as April to July, subject to modification based on specimens' gonadal condition, weight, fat levels, coloration, and measurements.

A second caveat with Great Blue Heron specimens is that the plumage coloration can be altered by a variety of factors, including wear, bleaching, molt stage, chemicals used to preserve or protect skins, mu-

seum age, and especially staining due to the leakage and oxidation of body fat. In addition, winter-taken specimens in the north may be under greater nutritional stress, so that they may produce less powder down to coat the feathers. This in turn would greatly affect feather color, as the powder-down coating produces a pale bloom that makes the plumage appear lighter. In fact, this same effect can be extreme when the plumage is washed and the powder-down is removed (Dickerman 2004).

For my final comparisons of plumage coloration in Great Blue Heron populations, I borrowed 26 adult skins taken throughout North America, representing all of the mainland forms. All were clean but unwashed specimens, taken as early in the nesting season and chronologically recently as possible. As I found no differences in plumage color between males and females, I combined the sexes for these comparisons. In addition, I measured 214 males and 189 females for the following characters: wing chord, tail length, exposed culmen, and tarsus length (all in mm). After a preliminary analysis, I have variously grouped these measurements by subspecies, area, and sometimes type specimens (Table 1). I then calculated the sample sizes, ranges, means, and standard deviations for the four mensural characters, as well as performing two-sample t-tests to determine the significances ($P = 0.05$) of differences. I did not analyze either plumage or mensural variation in other age classes, because sample sizes were too small for juveniles and nestlings. Immatures were not analyzed.

Results

As did Oberholser (1912), I find Great Blue Herons can be aggregated into three distinct North American nesting populations on the basis of plumage coloration, exclusive of the white-phased birds of the Caribbean Basin (*A. h. occidentalis).* More specifically, this variation involves the coloration of the upper-parts, neck, and wing feathers in adult birds, which ranges from pale to darker gray. The first of these aggregates consists of the moderately gray populations to which the name *A. h. herodias* can be applied. These nest in southern Canada west to interior southern British Columbia, then southward in the United States to eastern Washington, North Dakota, Wisconsin, Indiana, Maryland, and South Carolina. The second aggregate of paler populations in the southeastern, central, and western U.S. and Mexico that Oberholser (ibid.) assigned to four subspecies, of which the oldest name is *A. h. wardi* with *A. h. treganzai, A. h. hyperonca* and *A. h. sanctilucae* here considered synonyms. And the third is the darker gray *A. h. fannini,* whose range I have recommended be restricted to the coastal region of northwestern British Columbia and adjacent Alaska, specifically the Queen Charlotte Islands north to Prince William Sound (Dickerman 2004). However, as noted earlier, the slaty-black coloration of the holotype (Chapman 1901) is abnormally dark, apparently due to washing that removed the powder down coating and thus the paler bloom of the plumage (Dickerman 2004).

Oberholser (1912) further characterized nesting Great Blue Herons on the basis of measurements, which he particularly emphasized in allotting pale populations to four subspecies. Given this, I also assessed measurements in this species, in which males generally average larger than females in nesting populations (Table 1). For example, my overall samples reveal that males are 4.1% larger in wind chord, 3.5% in tail length, 6.5% in exposed culmen, and 6.5% in tarsus length (including only "typical populations of named forms, excluding *fannini* because of small sample size). However, the sexes overlap in all of these mensural characters, and t-tests often show the differences are not significant at the $P = 0.05$ level. Nonetheless, it is important to segregate the sexes when using measurements to allocate specimens to subspecies

and populations. As for the mensural characters themselves, I found the following:

Wing chord.—Nesting populations with the longest wings are 4.8% and 5.2% greater than those with the shortest in males and females, respectively. Means are smallest in *A. h. herodias,* generally becoming progressively larger through the populations of the interior western U.S., the Pacific Coast region, and Mexico to the southeastern U.S. (Table 1). However, a notable departure from this is that *A. h. occidentalis* has the wing chord intermediate, as opposed to being among the largest in the species. T-tests reveal that *A. h. herodias* averages significantly shorter in wing length than all but two other North American populations, the exceptions being males of *A. h. fannini* and *A. h. "treganzai."* By contrast, the latter is significantly shorter-winged than all but one of the *A. h. wardi* populations, that being the small Texas sample. All other populational differences in this character are insignificant, with clinal intergradation being smoother among females than males.

Tail length.—Nesting populations with the longest tails are 7.7% and 8.8% greater than those with the shortest in males and females, respectively. Means are smallest in *A. h. herodias* and become progressively and significantly larger in Texas/Florida populations of *A. h. wardi, A. h. "hyperonca" × A. h. fannini,* and *A. h. fannini* (Table 1). All other populational differences in this character are insignificant, with rather mosaic intergradation occurring among both males and females.

Exposed culmen.—Nesting populations with the longest culmens are 29.4% and 31.9% greater than those with the shortest in males and females, respectively. Means are smallest in *A. h. fannini* and then *A. h. "hyperonca" × A. h. fannini,* each of which has a significantly shorter culmen than all other populations of the species (Table 1). Elsewhere, males average smallest in *A. h. herodias,* which differ significantly from those with the longest culmens in Florida, Texas, and eastern Mexican *A. h. wardi* and *A. h. occidentalis.* However, these extremes intergrade circuitously through *A. h. "treganzai," A. h. "hyperonca"* and *A. h. "sanctilucae"* with a similar pattern of geographic variation, except that *A. h. occidentalis* has a significantly longer culmen than all but one *A. h. wardi* (*sensu latu*) population—that in eastern Mexico, which has a sample size of only one!

Tarsus length.—Nesting populations with the longest tarsi are 33.2% and 27.3% greater than those with the smallest in males and females, respectively. Means in males are shortest in *A. h. fannini* and then *A. h. "hyperonca" × A. h. fannini,* each of which has a significantly shorter tarsus than all other populations of the species (Table 1). The same is true with females, except that the means of those two populations are essentially identical. Elsewhere, males and females average smallest in *A. h. herodias* and *A. h. "hyperonca"* which differ significantly from those with the longest tarsi in Florida *A. h. wardi* and *A. h. occidentalis.* However, these extremes intergrade circuitously through *A. h. "treganzai," A. h. "sanctilucae"* and Texas/eastern Mexican populations of *A. h. wardi.*

Discussion and Conclusions

Based on these findings, I recommend recognizing three subspecies among North American nesting populations of the Great Blue Heron, excluding the white-plumaged *A. h. occidentalis* of the Carribbean Basin.

The first is *Ardea herodias herodias* L, with its moderately gray plumage and a nesting range as outlined above (see Results section). This the most highly migratory of the subspecies, with birds regularly moving southward into Central America and the Caribbean and as far as Belize, Panama, Colombia, Venezuela, Curacao, and the Dominican Republic (also eastward to Bermuda). In addition, lesser numbers move elsewhere, including northward to Hudson Bay, northern Quebec, Anticosti Island, and Newfoundland (plus as a vagrant to Green-

Table 1.—Measurements in millimeters of mostly nesting season adult Great Blue Herons (*Ardea herodias*) from North America, with number, range (mean), and standard deviation.

Population	n	Wing chord	n	Tail	n	Culmen	n	Tarsus
				Males				
herodias[1]	35	441–496 (470.0) *SD* 12.6	32	165–192 (177.4) *SD* 5.8	33	128–155 (144.1) *SD* 6.1	21	169–188 (179.8) *SD* 5.7
wardi								
Florida	28	470–533 (493.0) *SD* 13.8	22	171–195 (182.7) *SD* 5.6	27	140–172 (154.6) *SD* 8.5	28	180–223 (202.8) *SD* 14.6
Type *wardi*[2]		518		198		166		225
Texas	6	466–500 (485.5) *SD* 12.7	5	178–186 (182.8) *SD* (4.4)	6	148–165 (160.0) *SD* (6.9)	6	185–212 (199.0) *SD* (10.5)
Gulf Coast of Mexico	7	475–498 (489.7) *SD* 9.7	7	176–189 (181.6) *SD* 4.5	7	154–164 (159.1) *SD* 3.0	7	184–212 (193.6) *SD* 8.7
"*sanctilucae*" Baja California	19	460–502 (485.6) *SD* 11.6	19	160–191 (179.7) *SD* 8.6	20	139–158 (149.7) *SD* 5.5	16	173–200 (188.7) *SD* 7.9
"*treganzai*"[3]	28	434–495 (476.0) *SD* 14.6	24	165–188 (178.9) *SD* 6.8	28	133–161 (146.5) *SD* 8.0	14	167–198 (183.9) *SD* 9.4
"*hyperonca*" Central and Southern California	31	474–516 (491.8) *SD* 11.4	29	174–201 (187.2) *SD* 6.4	31	133–160 (147.9) *SD* 6.6	29	164–203 (178.9) *SD* 7.7
Type *hyperonca*[2]		500		193		156		195
fannini X "*hyperonca*"[4]	29	460–508 (484.9) *SD* 12.2	25	180–208 (190.3) *SD* 6.4	30	120–149 (132.6) *SD* 7.2	26	147–180 (162.0) *SD* 7.2
fannini, sensu strictu[5]	7	458–488 (474.0) *SD* 10.8	7	182–198 (189.6) *SD* 5.4	7	116–133 (124.8) *SD* 6.2	7	142–164 (152.6) *SD* 9.7
occidentalis	22	472–495 (480.1) *SD* 10.0	21	171–195 (182.5) *SD* 7.2	21	150–167 (159.7) *SD* 5.2	21	170–227 (201.2) *SD* 13.9
				Females				
herodias	35	431–480 (452.8) *SD* 9.2	34	161–188 (171.0) *SD* 6.0	32	124–145 (134.5) *SD* (5.0)	19	150–175 (166.5) *SD* 7.3

Table 1.—Continued.

Population	n	Wing chord	n	Tail	n	Culmen	n	Tarsus
wardi								
Florida	19	452–505 (476.2) *SD* 16.5	20	169–194 (178.4) *SD* 6.2	20	138–157 (144.0) *SD* 6.6	20	181–226 (193.8) *SD* 13.4
Texas	5	445–483 (470.6) *SD* 16.5	5	171–182 (177.2) *SD* 5.3	5	133–153 (142.6) *SD* 7.4	5	153–182 (170.4) *SD* 11.6
Gulf Coast of Mexico	1	465	1	171	1	157	1	182
"*sanctilucae*" Baja California	9	438–480 (461.2) *SD* 12.2	10	164–180 (173.0) *SD* 4.8	10	131–140 (138.1) *SD* 3.7	7	152–182 (170.8) *SD* 10.0
"*treganzai*"[3]	47	432–491 (459.3) *SD* 13.7	46	160–192 (175.7) *SD* 6.9	47	123–156 (139.3) *SD* 6.7	22	155–185 (168.6) *SD* 7.3
"*hyperonca*" Central, South California	29	450–485 (468.6) *SD* 10.3	26	168–190 (178.5) *SD* 5.7	30	123–152 (134.2) *SD* 7.2	28	152–184 (166.1) *SD* 7.2
fannini X *hyperonca*[4]	22	445–495 (463.5) *SD* 11.8	22	167–190 (180.0) *SD* 5.6	21	118–132 (125.9) *SD* 4.9	22	142–163 (152.6) *SD* 7.1
fannini, sensu strictu[5]	7	459–489 (467.8) *SD* 11.0	7	184–195 (186.8) *SD* 5.4	7	104–126 (117.4) *SD* 7.1	7	146–157 (151.8) *SD* 3.3
occidentalis	14	445–510 (466.4) *SD* 17.8	15	160–185 (172.8) *SD* 7.2	14	142–172 (154.0) *SD* 9.0	15	167–226 (192.9) *SD* 16.0

[1] Connecticut, Maine, Massachusetts, New York, Indiana, Wisconsin, Michigan, North Dakota, Maryland, Virginia, North Carolina, South Carolina.
[2] Measurements from Oberholser (1912).
[3] Idaho, Oregon, Utah, California, Arizona, New Mexico.
[4] Southern British Columbia and coastal Washington.
[5] Queen Charlotte Islands and coastal Alaska, north to Prince William Sound.

land), and west to California, Arizona, New Mexico, and Colorado. *A. h. adoxa* and *A. h. olgista* of Oberholser (1912) and *A. h. lessoni* Wagler were based on migrant *A. h. herodias*. Oberholser restricted the type locality of *A. lessoni* to the Valley of Mexico. However, there are no records of the species ever having nested in the Valley, and Payne (1979) was correct in just citing Mexico as the type locality. Hellmayr and Conover (1948) erroneously placed *A. h. olgista* in the synonomy of *A. h. hyperonca*. However, the wing chord of the type (433 mm) is far too short for that population and is even short for *A. h. herodias*! It is also darker, as in the nominate population.

The second subspecies recognized here is the pale *A. h. wardi,* which includes *A. h. "terganzai," A. h."hyperonca,"* and *A. h. "santilucae."* Payne (1979) wrote in a footnote (p.198) "The type of *wardi* was taken on 5 January 1881. It is not known whether this was a local breeding bird or a wintering bird from a more northern population." There is no doubt that it was from the local population. The type of *A. h. wardi* is a very large bird (Oberholser 1912, Table 1), larger in all measurements than any male *A. h. herodias,* and it has longer tail, culmen, and tarsus measurements than any other male *A. h. wardi.* Size is largest in the southeast (Table 1) and smallest in the Great Basin region (*A. h. "treganzai"*), and only extremes can be identified based on measurements (Dickerman 1992, 2002). Oberholser described *A. h. "hyperonca"* as the color of *A. h. herodias,* but larger. The type is from northern California and is somewhat intermediate towards *A. h. fannini* and indeed inseparable from *A. h. herodias* in color, but it is larger than the largest male of *A. h. fannini* or of *A. h. herodias* (Table 1). However, specimens from central California in the California Academy of Science and the Museum of Vertebrate Zoology labeled *A. h. hyperonca* are inseparable in color from a topotype of *A. h. treganzai,* from early nesting season specimens from southern New Mexico and south Texas, or from a midwinter specimen of *A. h. wardi* from Florida.

Contra Payne's comment on clinal variation in size in the east (1979), there are not enough nesting colony or even nesting season specimens yet available to fully document a cline. As mentioned earlier, there are no nesting season adult males from Delaware, Virginia, West Virginia or Kentucky; only single males from Maryland, Tennessee, South Carolina, and Alabama: and only two from North Carolina. Indeed the best clinal variation in size is on the west coast, with an increase in culmen and tarsal length from *A. h. fannini* in the north, through an intermediate population in southern British Colombia and Washington, to the long-billed, long- legged *A. h. "hyperonca"* population of California (Dickerman 2004).

A. h. wardi may be separated from *A. h. herodias* as follows:

1. Neck of *A. h. herodias* darker, colder "vinaceous" gray vs. "warmer," paler neck of *A. h. wardi*..
2. Chestnut of mid-ventral neck stripe is more extensive and darker in *A. h. herodias,* and usually extends to the area behind and below the eye, thus faintly outlining the white of the throat; in *A. h. wardi* the area behind and below the eye is always white; chestnut of mid-neck is reduced and paler.
3. Dorsum and wings are darker in *A. h. herodias* and paler in *A. h. wardi.*

The third subspecies recognized here is *A. h. fannini,* which differs from *A. h. herodias* in being darker gray in color and in having the exposed culmen and tarsus significantly shorter and tail longer (plus wing in males, Dickerman 2004). *A. h. fannini* differs in being notably much darker gray than *A. h. wardi* (sensu latu), and in having the exposed culmen and tarsus significantly shorter. In addition, males have significantly shorter wings than all *A. h. wardi* populations except *A. h. "treganzai"* on the interior western U.S. *A. h. fannini* seems to

differ from other Great Blue Herons in that it perforce fishes much of the time from rocks rather than wading, as do the other longer-legged subspecies. It appears to be largely resident within its nesting range (contra A.O.U. 1957), with the only extralimital specimen being an adult taken at Wainwright on the Arctic coast of Alaska (Brock 1959). I know of no specimens of *A. h. fannini* (as here defined) from south of the Queen Charlotte Islands. *A. h. fannini* intergrades southward with *A. h. "hyperonca"* and perhaps *A. h. "treganzai"* (both here = *A. h. wardi*) in southwestern British Columbia (including Vancouver Island) and western Washington (Dickerman 2004). For example, that population is paler gray as in *A. h. wardi* (sensu latu), but it is closer to *A. h. fannini* in the shorter exposed culmen, tarsus, and male wing chord.

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