Mottled Duck Hybridization

By Tony Leukering and Bill Pranty

Mottled Duck is locally fairly common in the southeast United States on the Coastal Plain from Texas to South Carolina, with isolated outposts in northern Louisiana, southern Arkansas, southeastern Oklahoma, and south-central Kansas. The species' range extends south from Texas to central Tamaulipas (around Tampico), with some records to central Veracruz. Mottled Ducks also have wandered north of Texas as far as North Dakota (Robbins *et al.* 2010). Two subspecies have been recognized, although due to similar appearance often merged: nominate *fulvigula*, an isolated race endemic to peninsular Florida that occurs from Alachua County south, utilizing primarily freshwater habitats; and *maculosa* in coastal Alabama west around the Gulf of Mexico to Northern Tamaulipas, which favors coastal marshes and inland-prairie wetlands (A.O.U. 1957, Baldassarre 2014). The population of coastal South Carolina and Georgia (and possibly accounting for many of the North Carolina records) was introduced into southern South Carolina from both subspecies (Bielefeld *et al.* 2010).

The Mottled Duck's range has little overlap with the southern part of Mallard's "wild" breeding range, but feral populations of "park" Mallards essentially overlap it completely. Hybridization with Mallard is widespread, and one study showed that 11% of Florida birds judged to be Mottled Ducks based on appearance had mixed genetic ("hybrid") composition, with these "hybrids" accounting for as much as 24% of ducks at one sampled locality (Williams *et al.* 2005). This phenomenon is considered to be the primary driving force behind Mottled Duck population decline there (FWC 2014). Hybridization and genetic swamping facilitated by the introduction of Mallards into the ranges of other endemic members of the Mallard complex (e. g., Hawaiian Duck) has been shown to be the cause of endangerment of those species (Rhymer *et al.* 1994; Rhymer and Simberloff 1996).

Hybridization of Mallards has been identified as a serious threat to Florida's Mottled Duck population for more than 20 years (Moorman and Gray 1994) but no meaningful action by state and federal biologists has been taken to control numbers of feral Mallards (Pranty 2011 pg. 66, contra Eggeman 2002). In fact, hybridization seems to be increasing considerably (B. Pranty pers. obs.). In some areas, Mallard x Mottled Duck hybrids (colloquially "Muddled Ducks") now greatly outnumber Mottled Ducks. In December 2010, Christmas Bird Counts at St. Petersburg (Pinellas County) and Aripeka–Bayport (Hernando and Pasco counties) totaled 470 and 158 Mallard x Mottled Duck hybrids, respectively, compared to just 190 and 85 Mottled Ducks, respectively (Pranty 2011). Because so little has been published on the occurrence of Mallard x Mottled Duck hybrids, most eBirders probably are unaware that many "Mottled Ducks" that they observe and report to eBird may, in fact, be Mallard x Mottled Duck hybrids.

The two subspecies of Mottled Duck, despite minor differences in appearance, are relatively distinct genetically (Lavretsky *et al.* 2014). Based on this study, the two are more genetically different than the trio of other members of the North American Mallard complex—American Black Duck, Mexican Duck, and Mallard—are from each other. While this and previous published efforts might result in a split of Mottled Duck into two species, the importance to this essay is that the two populations might respond differently to the presence of feral populations of Mallard. This potential difference between the taxa appears to be supported by eBird data on the occurrence of Mallard x Mottled Duck hybrids (Fig. 1), with eBird records showing very few occurrences of this hybrid combination outside Florida. Granted, at least some of that difference may be due to heightened awareness of hybrids among eBirders in Florida compared to those outside the state where Mottled Duck is less of a conservation concern. The extreme magnitude of the difference in reporting hybrids convinces us that much of the pattern is real. Of additional interest in this map is the concentration of occurrence in northeastern-most Florida, where Mottled Duck is not of regular occurrence.

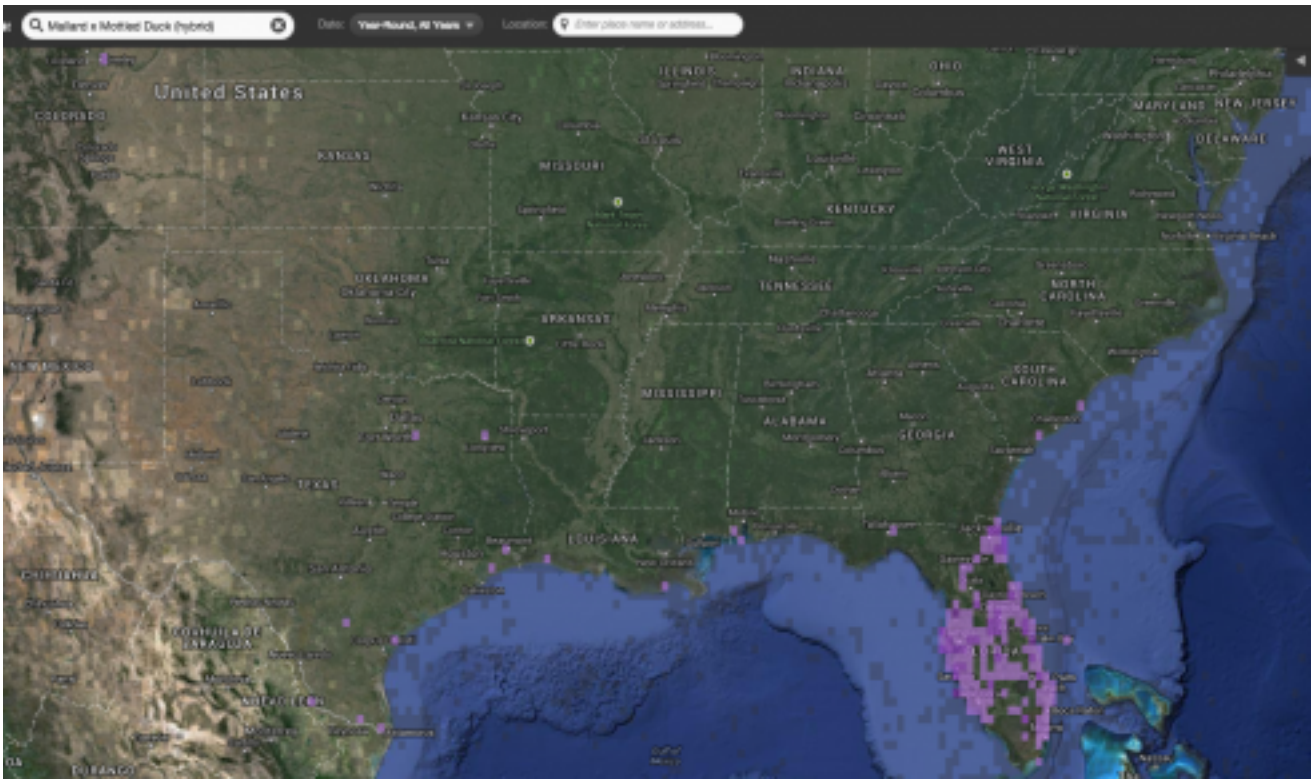

Figure 1. All-time distribution of Mallard x Mottled Duck hybrids across all eBird data.

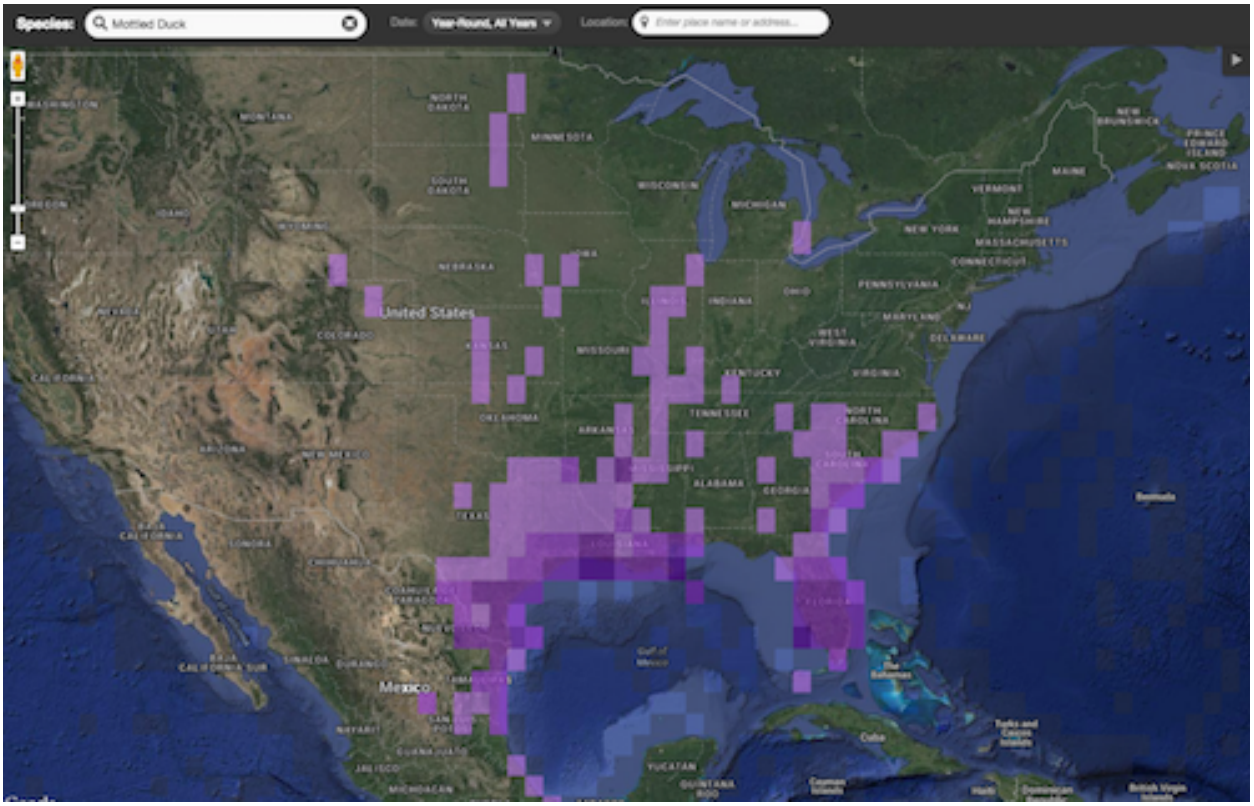

Figure 2. All-time distribution of Mottled Ducks across all eBird data.

Quiz time – How many Mottled Ducks are present in Figures 3-12? The solution is presented later in this essay.

Figure 3. Lake Villa Park, Largo, Pinellas Co., FL; 2 March. © Tony Leukering

Figure 4. Donegan Park, Largo, Pinellas Co., FL; 19 November. © Tony Leukering

Figure 5. Sarasota Celery Fields Preserve, Sarasota Co., FL; 8 October. © Bill Pranty.

Figure 6. Donegan Park, Largo, Pinellas Co., FL; 19 November. © Tony Leukering

Figure 7. Arlington Park, Sarasota, Sarasota Co., FL; 15 June. © Bill Pranty.

Figure 8. Veteran's Memorial Park, Hudson, Pasco Co., FL; 29 January. © Bill Pranty.

Figure 9. Taylor Park, Largo, Pinellas Co., FL; 4 February. © Tony Leukering

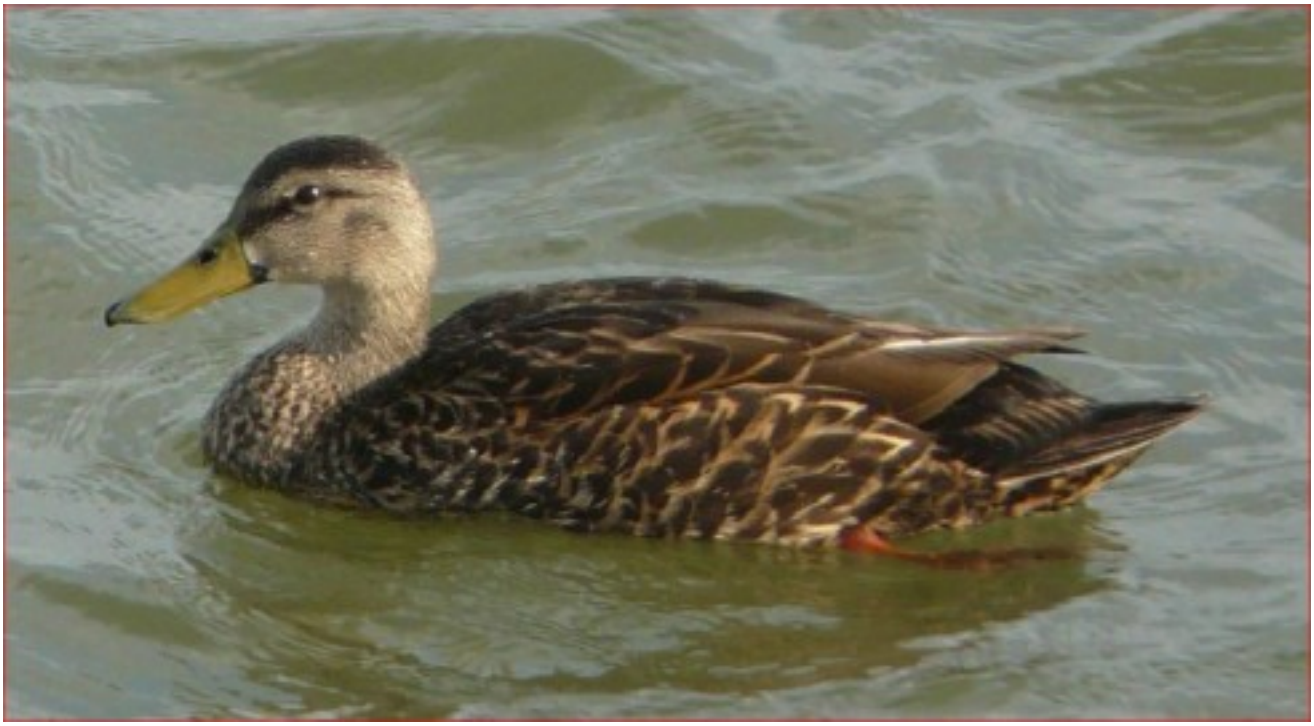

Figure 10. Fort Clinch State Park, Nassau Co., FL; 23 April. © Bill Pranty.

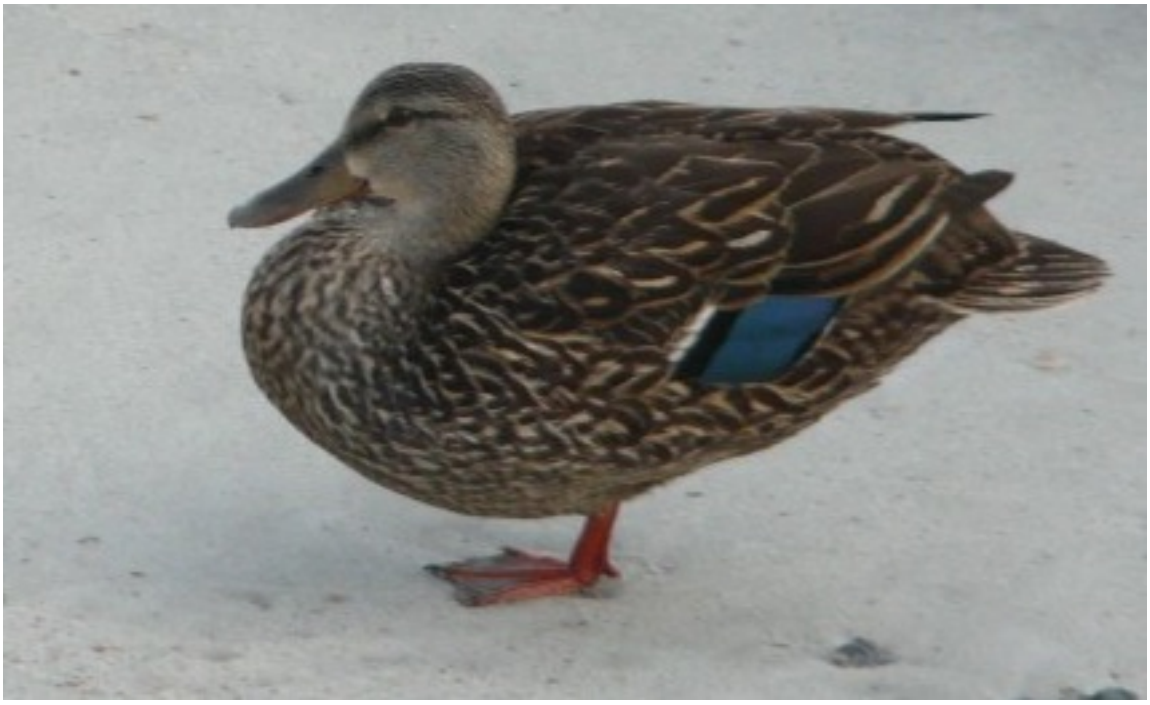

Figure 11. Fort Clinch State Park, Nassau Co., FL; 23 April. © Bill Pranty.

Figure 12. Lake Zephyr Park, Zephyrhills, Pasco Co., FL; 26 December. © Bill Pranty.

Quiz answer: zero! See below for details on why!

Mottled Ducks and Mallard x Mottled Duck hybrids

The primary reason for writing this essay is to encourage those eBirders living in or visiting Mottled Duck range, particularly in Florida, to take a closer look at all apparent Mottled Ducks, specifically to study them with the possibility of mixed parentage in mind. We also strongly encourage eBirders to use the "Mallard/Mottled Duck" entry wherever and whenever superb views of possible Mottled Ducks are **not** obtained; close looks are required to determine whether mixed plumage characters are present in such birds [Note that slash options in eBird always include the hybrid between the two species as well as either parent species]. We also encourage eBird reviewers in the appropriate regions to incorporate that same entry into relevant filters with numerical limits at least as large as those allowed for Mottled Duck. In urbanized areas of Florida, those limits should probably be larger than those for Mottled Duck, much larger in areas such as the Tampa Bay/Sarasota area, where hybrid Mallard x Mottled Ducks are common and Mottled Ducks uncommon at best. Finally, we encourage those same reviewers to consider "zeroing" the filter for Mottled Duck in places like Pinellas County, Florida, where the species has become quite rare, if not accidental, probably due to a combination of lack of native habitat and the genetic swamping of the species by feral Mallards.

Caveat: we understand that the parentage of any individual bird depicted in this essay is uncertain, as we cannot know its actual parentage, though that parentage is much less uncertain for some than for others. Of particular uncertainty is how Mallard-like "pure" Mottled Duck females can be; our understanding of the appearance of female Mottled Duck may be overly restrictive. However, all characters that we use to describe female Mottled Ducks are well-entrenched in the identification literature; whether they incorporate the entire variation in appearance is uncertain. Additionally, the two subspecies of Mottled Ducks differ in a few characters, especially the extent of fine, dark streaking on the head (less in the Florida subspecies), the overall darkness of the body plumage (lighter in the Florida subspecies) and extent of internal markings therein (more extensive in Florida subspecies), the color of the speculum (less purple in the Florida subspecies), and extent of white borders above and below the speculum (more white in the Florida subspecies). With the expansion of the introduced population that has spread nearly throughout coastal Georgia, Florida populations of Mottled Duck are faced with another source of potential genetic swamping if or when that population of mixed Mottled Duck ancestry meets native *fulvigula* in northern Florida. End caveat.

Despite the similarity to Mottled Duck of many of the individual ducks presented in the ten quiz photographs, all of the birds are Mallard x Mottled Duck hybrids (with one possible exception), some more subtly so than others. Most of these images were taken in the great Tampa Bay/Sarasota metropolitan area, a region that is extensively developed, with little in the way of native non-marine aquatic habitats. Most local aquatic habitats are man-made or strongly man-influenced and host large numbers of feral Mallards, both natural-looking and of obvious domestic strains, none of which are native to Florida as a breeding species. While this area is not necessarily representative of the rest of peninsular Florida, it does provide an example of how urban populations of Mallards contribute to the genetic swamping of native Mottled Duck populations. In fact, in a non-rigorous assay of a large number of the water bodies in Pinellas County (home of St. Petersburg, Clearwater, and Largo and which is >98% developed) in 2013 and 2014, Leukering was able to find just one "pure" Mottled Duck. That one Mottled Duck compared to counts of 29 Mallards (nearly all of obvious domestic origin), 50 Mallard x Mottled Duck hybrids, and eight birds that he reported to eBird using the "Mallard/Mottled Duck" category, as they did not provide good-enough views to differentiate between Mottled Duck and hybrids.

Identification

Mottled Ducks are differentiated from Mallards by a suite of plumage characters (i.e. field marks), delineated below. Assaying as many characters as possible will enable more-accurate identification, something to which all of us eBirders should strive. Though much subtler than in Mallards, the sexes of Mottled Ducks are still readily distinguished, with the most definitive feature being bill color. Males sport bright yellow to orange-yellow bills, dull yellow, olive-yellow, yellow-orange, or orange in females, with or without a blackish saddle similar to that of female Mallard. Note that the depiction of bill color in females in most field guides does not illustrate the gamut of color described here. In the below character descriptions, *italics* are used to indicate features that are particularly useful in determining hybrids that look otherwise like Mottled Ducks. Finally, the below descriptions are focused on Florida birds, where the problem of Mallard x Mottled Duck hybrids appears much more severe. Take this fact into account when considering possible hybrids in the range of *maculosa*. Finally, in the western part of Mottled Duck range, hybrids with Mexican Duck (currently considered a Mallard subspecies by eBird) are apparently fairly common. With the strong similarity between Mexican and Mottled ducks, sussing hybrids would be even trickier.

Superciliary: Mottled Ducks sport buffy superciliaries that are the same color tone as that of the cheeks with little or no darker streaking; males may be more likely to exhibit streaking here. The superciliaries of many Mallards and *some Mallard x Mottled Duck hybrids are noticeably paler, whiter than the cheeks, and often sport darker streaking*.

Eyeline: The eyelines of Mottled Duck are typically isolated on the face from the dark of the crown and nape; that is, there is an obvious and fairly wide gap between the posterior end of the eyeline and the nape. Those of Mallards and many hybrids continue across the rear end of the superciliary to meet – or nearly so – the darker color of the nape. This difference is well seen in Figure 5.

Cheeks: Mottled Ducks have cheeks buffy (often fairly bright) with very little or no darker streaking in females and little to some in males; those of female Mallards (and males in alternate plumage, the so-called "eclipse" plumage) are gray-brown with extensive, fine darker streaking. In hybrids, the background color of the cheeks is quite variable, ranging from a similar buff of Mottled Duck to a gray-brown like that of Mallard*. Streaking across the cheeks, a Mallard trait, seems to be a dominant feature expressed in nearly all birds of mixed parentage*. Because mixed-ancestor Mottled Ducks from the introduced population may be occurring in northeastern-most Florida, individuals there sporting both a strong buffy ground color to the check and extensive darker streaking might not be expressing the cheek streaking trait of Mallard, but rather that typical of *maculosa* Mottled Ducks. Thus, particular caution at assigning individual ducks to particular categories is strongly advised; the "Mallard/Mottled Duck" category should, perhaps, be the default entry in that area.

Gape spot: Mottled Ducks all sport a distinct black spot or patch at the posterior end of the gape (at the bottom of the base of the bill). *Mallards lack this spot, as do a large percentage of hybrids, but some hybrids have a well-defined gape spot*. Note that the gape spot in *maculosa* is typically less-distinct than in *fulvigula*, such that intermediate gape spots may not be due to the presence of Mallard genes. Again, using multiple field marks – preferably >3 – is more likely to produce a correct identification of a putative Mottled Duck than is relying on just one or two.

Bill color: While some male Mottled Ducks sport brighter, more-orangey bills than do male Mallards, many have bills indistinguishable from those of male Mallards. Many female Mottled Ducks have bills of color and pattern indistinguishable from those of female Mallards, many have bills much yellower than those of Mallards. Unfortunately, hybrid females seem to sport the entire gamut of bill colors found in the two parental species, though nearly all show the dark saddle.

Chest: Both sexes of Mottled Duck have warm, dark brown chests (those of females are typically somewhat paler than those of males) with extensive blackish markings, and with the color tone not contrasting appreciably from that of the upper sides. Alternate-plumaged male Mallards have a distinct reddish tone to the chest that contrasts at least somewhat with the cooler color tones of the upper sides. Male hybrids often (usually?) exhibit some of this reddish aspect on the chest.

Tertials: Mottled Ducks exhibit dark brown tertials, often/usually with buff to rufous fringes, while Mallards sport gray (males) or gray-brown (females) tertials. Hybrids express seemingly the gamut of coloration inherent in both parental species. However, a "Mottled Duck" with tertials contrastingly grayish is almost certainly of mixed parentage.

Tail coverts: The uppertail coverts of Mottled Ducks are dark with paler fringes that range (depending upon sex and wear) from bright rufous in males and fresh plumage to dull buff in females and worn plumage, with the width of those fringes being wider on females than on males. Female Mallards have similar uppertail coverts to those of female Mottled Ducks, though are a bit paler on some. Male Mallards, however, sport solidly black uppertail coverts. The undertail coverts of Mottled Ducks are similar to their uppertail coverts. Female Mallards, however, have their palest body plumage here, sporting whitish feathers with dark spotting/streaking; male Mallards have solidly black undertail coverts. *Black in the tail coverts of male Mallards seems to be a dominant character, and a female "Mottled Duck" with whitish undertail coverts is almost certainly the result of mixed parentage*.

Tail: Mottled Duck tails are dark brown, often slightly paler (particularly the outer two or three pairs of rectrices) than the tail coverts, with blackish markings, and with individual feathers (particularly the outer few pairs) often edged paler (buff to rufous). Male Mallard tails are mostly white with black central rectrices that are strongly recurved. Female Mallards have rectrices a mix of medium brown and whitish, with the proportion of white declining from the outermost rectrix inward, with the result that their tails look brown-centered and white-edged. *Obvious white or whitish in the tail is often the single character expressed in hybrids that is most noticeable and most quickly damning when looking at a putative Mottled Duck. Additionally, the curled aspect to the central rectrices in male Mallards seems to be a strongly dominant trait that is expressed in most males of mixed parentage to greater or lesser extent (see Figures 3, 5, 8, and 12). This last is also true of Mallard hybrids with both American Black Duck and Mexican Duck*.

Speculum [the "metallic" patch on the secondaries, often visible on the folded wing]: The speculum of Mottled Duck is a deep metallic blue (bluer in *fulvigula*; more purple in *maculosa*) bordered above and below by blackish. The blue color is intermediate between the paler blue of Mallard and the purplish-blue of American Black Duck, with this color extending across more secondaries in males than in females. The color, however, is typically not useful in field conditions to differentiate Mallards and Mottled Ducks, in part due to its iridescent nature. The string of white tips bordering the speculum in front and behind, however, can be quite useful. In Mottled Duck, the tips of the greater coverts (which create the leading edge bar) are very narrowly white, though some individuals sport no white here (these may be mostly males). The tips of the secondaries (which create the trailing bar) are a bit more extensively white than those of the greater coverts, though they can be so narrow on some birds as to not be detectable in many field conditions. Mallards exhibit wide and obvious white tips to both greater coverts and secondaries. Most importantly, the white tips to the secondaries are of the same width as the posterior black border of the speculum; on Mottled Duck, the white tips are obviously narrower than the posterior black speculum border. *A putative Mottled Duck with wide white tips to either or both of the greater coverts and secondaries is almost certainly of mixed parentage.*

These identification characters can be seen in the below pure Mottled Duck examples.

Pure Mottled Duck examples

Figure 13. Male (left) and female pure Mottled Ducks, Palm Beach County, Florida, 16 January. © Chris Wood.

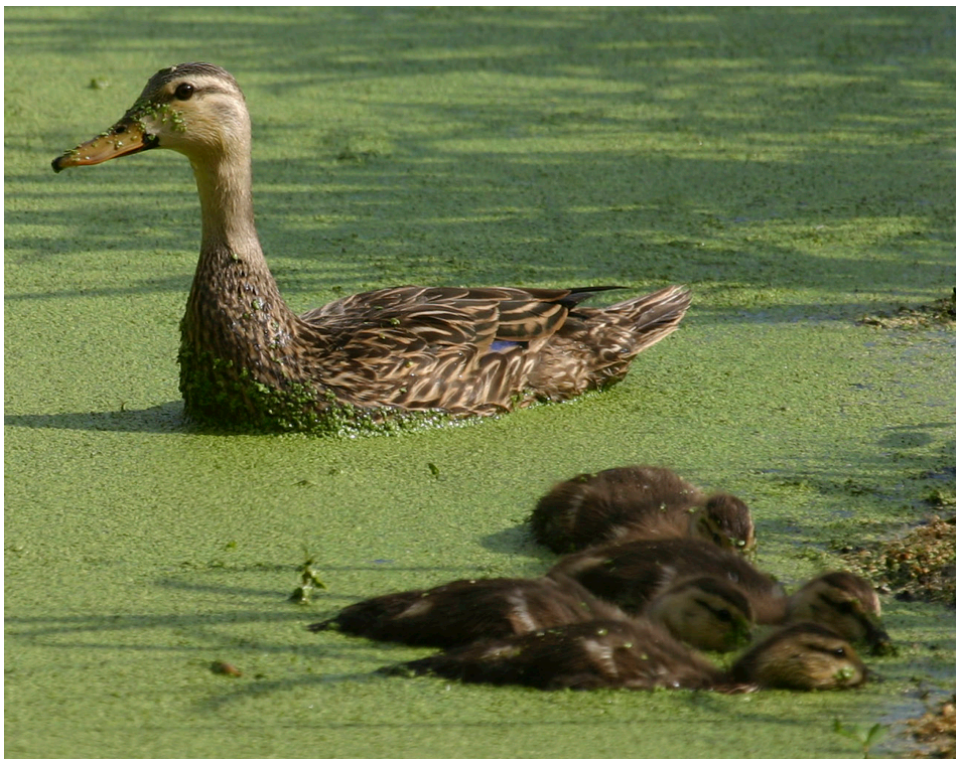

Figure 14. Female Mottled Duck with brood, Palm Beach County, Florida, 24 April. © Chris Wood.

Figure 15. Mottled Duck in flight, Harn's Marsh, Florida, 13 March. © Brian Sullivan.

Figure 16. Mottled Duck , Harn's Marsh, Florida, 13 March. © Brian Sullivan.

Discussion of illustrated hybrid examples

Figure 3. Male and female Mallard x Mottled Duck hybrids. Lake Villa Park, Largo, Pinellas Co., FL; 2 March. © Tony Leukering. This male has the slightly orangey bill of many male Mottled Ducks, as well as that species's typical gape spot and buffy cheek. However, it sports some green on the back of the head and its central rectrices are black and curl upward a bit. Closer scrutiny reveals dark streaking on the cheek that is more extensive than in Mottled Ducks, at least in Florida. The rich chestnut breast is especially noticeable and unlike pure Mottled Duck. The female's bill is typical of both Mallard and Mottled Duck, while the cheek is buff and mostly unstreaked, suggesting Mottled Duck. However, the superciliary is slightly whiter than the cheek and is also nearly cut off at the back end by the long eyeline; the cheek streaking also seems too extensive for a pure Mottled Duck. While the tail is, perhaps, a bit too pale for a Mottled Duck, the undertail coverts certainly are (note how the ground color of the undertail coverts is obviously whiter/paler than the uppertail coverts). This female also lacks the Mottled Duck gape spot.

Figure 4. Male and female Mallard x Mottled Ducks, Donegan Park, Largo, Pinellas Co., FL; 19 November. © Tony Leukering. It is hard to tell why the left male is not simply a Mallard, but the near-lack of green on the head provides a solid clue, as does the brown on head and sides. However, a male Mallard that is delayed molting out of alternate plumage may well match this bird's appearance, though such a lengthy delay is quite rare. The other male (front center) sports an obviously white tail, extensively black undertail coverts, a reddish aspect to the chest, and some green on the head. However, the bird's very dark tertials and the flank feathering — dark feathers with pale internal markings vs. pale feathers with dark markings – are Mottled Duck features. The females are more problematic, as we cannot see them that well, but both sport gray-brown cheeks with extensive darker streaking and what is probably too much white in the tail. Additionally, the flank feathering, at least on the right-hand bird, is Mottled Duck-like.

Figure 5. Sarasota Celery Fields Preserve, Sarasota Co., FL; 8 October. © Bill Pranty. The female (right) closely resembles a Mottled Duck, with the gape spot, dark tail, and narrow white trailing edge to the secondaries, but note the extensive streaking in the cheek and superciliary; this individual is one of the most Mottled Duck-like of the birds presented in this essay. The male (left) also resembles Mottled Duck, but note the streaked cheek, paleness in the tail, and, especially, the undertail coverts, and the slightly recurved central rectrices.

Figure 6. Male and female Mallard x Mottled Ducks, Donegan Park, Largo, Pinellas Co., FL; 19 November. © Tony Leukering. The female's head pattern looks reasonable for Mottled Duck at first glance, but she lacks the Mottled Duck gape spot and shows what may be too much dark streaking in the cheek. Additionally, the left side of the tail looks too whitish for Mottled Duck. The male mostly lacks the gape spot of Mottled Duck and the head is too gray. However, the most obvious features pointing away from an identification of Mottled Duck is the white tail and solidly black uppertail and undertail coverts.

Figure 7. Male Mallard x Mottled Duck hybrids, Arlington Park, Sarasota, Sarasota Co., FL; 15 June. © Bill Pranty. Both ducks show minimal gape spots, extensive streaking on the cheeks, and much white in the tail.

Figure 8. Male and female Mallard x Mottled Ducks, Veteran's Memorial Park, Hudson, Pasco Co., FL; 29 January. © Bill Pranty. Again, both of these ducks strongly resemble Mottled Ducks. The male (top bird) shows a reddish wash to the breast, paleness in the tail and subtly recurved central tail feathers; the male's cheek might be a bit too streaked for Mottled Duck (though see the caveat about that feature, above). The female shows a minimal gape spot, very long dark eyeline, and a very pale tail.

Figure 9. Male (right) and female Mallard x Mottled Ducks, Taylor Park, Largo, Pinellas Co., FL; 4 February. © Tony Leukering. This male's head pattern and coloration are probably outside the ranges of these characters in Mottled Duck, and the bird's gape spot is on the small side. More-obvious indicators of mixed ancestry include its chest being slightly redder than the upper sides and the very wide tips to the greater secondary coverts, which are greatly outside the range of male Mottled Duck, being at least as wide as the upper black boundary of the speculum. The female's heavily streaked cheek and contrastingly pale superciliary should immediately cause concern when considering Mottled Duck as an identification. Additionally, we can see that at least one greater covert is widely tipped in white (despite the narrow tips to the secondaries on the same bird). However, the overall body coloration is too dark for a pure Mallard.

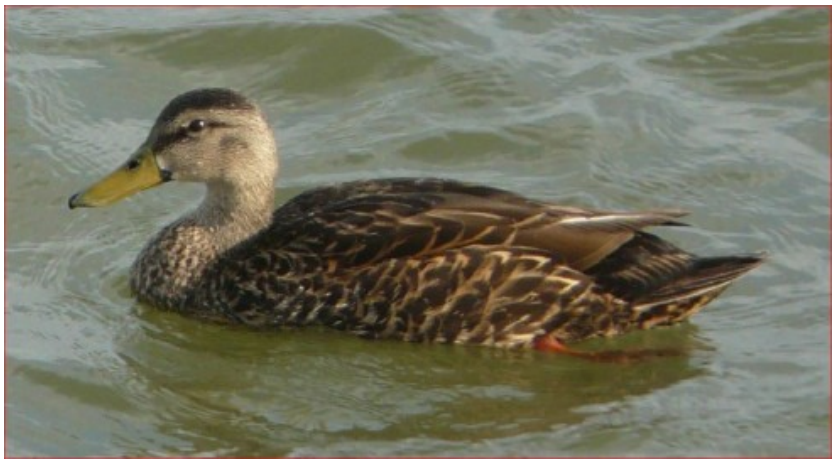

Figure 10. Male Mallard x Mottled Duck, Fort Clinch State Park, Nassau Co., FL; 23 April. © Bill Pranty. The site of this photo, on the opposite side of the St. Mary's River from Georgia, is outside the normal range of Mottled Ducks in Florida. In this view, the duck looks "good" for Mottled Duck except for the lightly (but wholly) streaked cheek that lacks the buffier tone of Mottled Duck. Additionally, the white outer edge to the outermost rectrix is of concern, but as late in the plumage cycle as April, that feather may simply be worn and bleached enough to appear white-edged, a facet that should be considered in spring and summer. Finally, this individual may actually represent the typical appearance of the mongrel Mottled Ducks (intergrades between *A. f. fulvigula* and *A. f. maculosa*) in the introduced population of the species in South Carolina and Georgia. This bird provides an excellent example of the reason that we recommend extensive use of the "Mallard/Mottled Duck" entry in eBird.

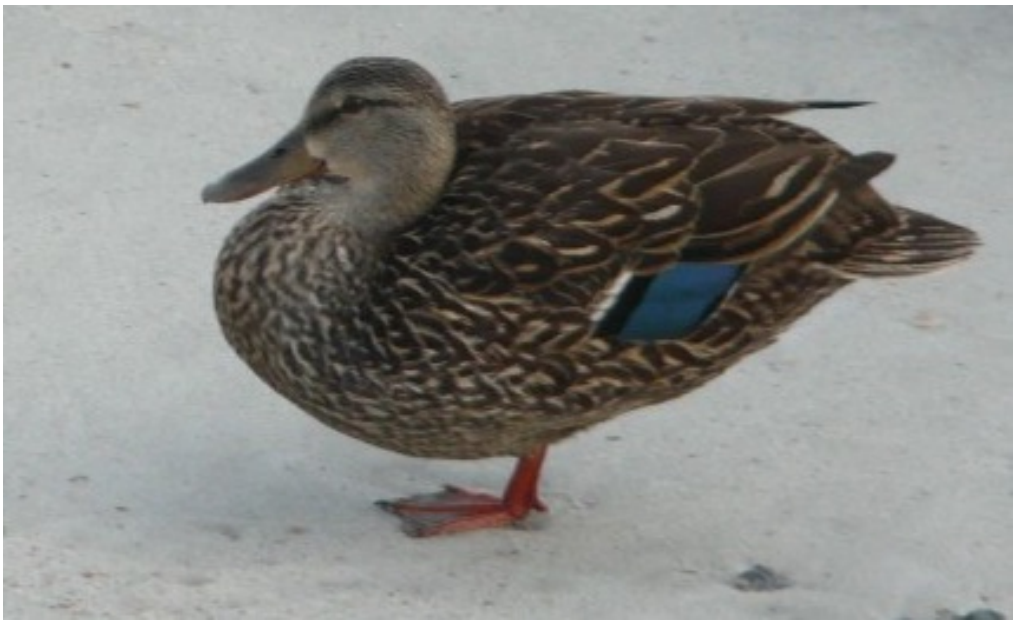

Figure 11. Female Mallard x Mottled Duck hybrid, Fort Clinch State Park, Nassau Co., FL; 23 April. © Bill Pranty. This is the presumed mate of the above duck, both occurring well outside the range of Mottled Ducks in Florida. Characters that suggest a hybrid include the extensively streaked cheek, the lack of a gape spot, and the wide tips to the greater coverts. Additionally, the tail is too dark for a pure Mallard but may show a bit too much white for Mottled Duck, but see the Figure 10 caption. Finally, while the bird in Figure 10 may well be a "pure" Mottled Duck, but of mixed subspecies ancestry, this bird's lack of a gape spot and its extensive eyeline strongly suggests the presence in its genome of Mallard genes.

Figure 12. Male Mallard x Mottled Duck hybrid, Lake Zephyr Park, Zephyrhills, Pasco Co., FL; 26 December. © Bill Pranty. This male strongly resembles a Mottled Duck but note the minimal gape spot, extensively streaked cheek, the hint of a rusty chest, and recurved central tail feathers.

Acknowledgments

We thank Louis R. Bevier and Steven G. Mlodinow for critical review of a previous draft of the manuscript. Ian Davies and Marshall Iliff from Team eBird provided edits as well.

Literature Cited (all websites accessed December 2014)

Baldassarre, G. 2014. Ducks, Geese, and Swans of North America, vol. 1. Johns Hopkins Univ. Press, Baltimore, MD.

Barry, J. H., C. D. Cox, and A. Jaramillo. 2006. Ducks, geese, and swans. *In* Complete Birds of North America. National Geographic Society, Washington, D.C.

Bielefeld, R. R., M. G. Brasher, T. E. Moorman, and P. N. Gray. Mottled Duck *Anas fulvigula*. The Birds of North America Online (A. Poole, ed.). Cornell Lab of Ornithology, Ithaca <bna.birds.cornell.edu/bna/species/081>.

Eggeman, D. R. 2002. Mottled Duck vs. Mallard. Florida Forest Steward 9:3 <sfrc.ufl.edu/Extension/FFSnl/ffsnl93.htm#duck>.

FWC [Florida Fish and Wildlife Conservation Commission]. 2014. The problem – hybridization. <http://myfwc.com/wildlifehabitats/managed/waterfowl/hybridization/>

Lavretsky, P., B. E. Hernández-Baños, and J. L. Peters. 2014. Rapid radiation and hybridization contribute to weak differentiation and hinder phylogenetic inferences in the New World Mallard complex (*Anas* spp.). Auk: Ornithological Advances 131:524-538.

Moorman, T. E., and P. N. Gray. 1994. Mottled Duck *Anas fulvigula*. *In* The Birds of North America, Number 81 (A. Poole and F. Gill, eds.). The Academy of Natural Sciences, Philadelphia; and the American Ornithologists' Union, Washington, D.C.

Pranty, B. 2011. Florida [111th Christmas Bird Count summary]. American Birds 65:64–66 <birds.audubon.org/sites/default/files/documents/ab_111_61-69_n._carolina_s._carolina_georgia_florida_ohio_west_virginia_kentucky_tennessee.pdf>.

Robbins, M.B., P. McKenzie, and B. Jacobs. 2010. A review of Mottled Duck (*Anas fulvigula*) reports in the North American interior, with comments on historical records of dark *Anas* ducks. North American Birds 64:518-522.

Rhymer JM, Williams MJ, and Braun MJ (1994) Mitochondrial analysis of gene flow between New Zealand mallards (*Anas platyrhynchos*) and grey ducks (*A. superciliosa*). Auk 111:970–978.

Rhymer JM, and Simberloff D (1996) Extinction by hybridization and introgression. Annu. Rev. Ecol. Syst. 27:83–109.