In Brief

This article started out as a bit of an argument. Jerry Liguori and Brian Sullivan, in a previous article in *Birding*, presented evidence against the conventional wisdom that gray Northern Harriers are necessarily older males. Peter Pyle subsequently questioned some of Liguori and Sullivan's assumptions. Now Pyle shows how both parties' viewpoints may be correct, an insight made possible by factoring in behavioral and ecological aspects of the Northern Harrier's natural history. Pyle's present contribution also highlights the danger of circular reasoning—in field birding, in biology more broadly, and indeed in much of life.

How old is this male Northern Harrier? It doesn't fit neatly into a box; instead, this bird is intermediate, showing some of the browns of juvenile (first-cycle) males, but also some of the grays of older adult males and some females. But we're getting ahead of ourselves. First, a foundational question: *Why* do harriers (and other birds) show such variation? This article explores that question, and presents some answers. *Kern County, California; February 2002. Photo by © Bob Steele.*

Plumages of Second-basic and A Circular *Circus*?

Liguori and Sullivan (2013a, 2013b) have proposed that both second-cycle and older male Northern Harriers (*Circus cyaneus*) can show brown and gray morphs, whereas Pyle (2008, 2013a) has affirmed the more traditional view that **second-cycle** males have a distinctly browner plumage than older males. Often, during debates such as this, the answer involves a combination of the two views. In order to move the conversation forward, I pulled out specimen data on Northern Harriers that I had compiled during preparation of Pyle (2008), and performed additional examination of specimens at the Museum of Vertebrate Zoology (MVZ) and California Academy of Sciences (CAS).

I would now like to consider an alternate explanation, involving molt–plumage interactions, drawing from observations and insights of both Liguori and Sullivan and myself. I propose that an earlier prebasic molt leads to browner plumages in male Northern Harriers of all ages, and that this plumage is found more often in second-cycle birds due to the second prebasic molt's averaging earlier in the year than later prebasic molts.

Molt Timing, Pigments, and a Brief Detour for Murres

When a molt is early or late relative to the hormone cycle that signals pigment deposition, the resulting feathers may resemble those associated with earlier or later plumages (see summaries in Pyle 2008, Howell 2010). I have recently discussed this type of interaction in reference to dark-faced Common Murres in **basic** plumage during fall and winter off California (Pyle 2013b). In these murres, an earlier prebasic molt appears to produce darker basic feathering because hormone pigment signaling has not yet switched from dark for alternate plumage to white for basic plumage.

Interestingly, darker feathers appear to be produced on much of the body during such early prebasic molts, not just on the head where alternate feathering is typically limited; in extreme cases, this molt–plumage interaction may result in an entirely dark plumage (Fig. 1). Such birds could be "hypermelanistic" mutations or could represent dark morphs, as has been documented in many bird species, including the Northern Harrier (Howell et al. 1992, Liguori 2009, Miller et al. 2012); in the case of the Common

Fig. 1. A completely dark **Common Murre** (carrying a fish) is accompanied by three typical, alternate-plumage murres. The appearance of the dark bird may be the result of molt–plumage interactions after an early prebasic molt (Pyle 2013b). *14 kilometers southeast of the Farallon Islands, California; 24 July 2013. Photo by © Dru Devlin NOAA/ONMS/ACCESS.*

Older Male Northern Harriers

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Fig. 2 (a, b). Shown here are specimens of Northern Harriers at the Museum of Vertebrate Zoology (MVZ), Berkeley, California. From left to right (Fig. 2a, ventral; Fig. 2b, dorsal): MVZ 106749, a female in typical brown basic body plumage; MVZ 30324, a probable female showing intermediate gray and brown body plumage; MVZ 4080, a male showing brown basic body plumage; and MVZ 106748, a male showing gray basic body plumage. *Photos by © Peter Pyle.*

Murre, though, it might also result entirely from a molt–plumage interaction. In any case, darker feathering on the head and elsewhere was shown by a greater proportion of second-cycle basic-plumage murres than by older murres in basic plumage. I surmise that this is due to the second prebasic molt's averaging earlier in the season than later molts, a result of the fact that second-years do not breed and are "freed up" to molt earlier.

A Molt–Plumage Interaction in Harriers

I propose a similar molt–plumage interaction in male Northern Harriers. First, two facts of harrier natural history: Most if not all one-year-old males do not breed (Smith et al. 2011), and commencement of the second prebasic molt averages earlier (April) than the later prebasic molts (June) of older individuals that breed (Pyle 2008). I suggest that, as a consequence, most but not all second-cycle male Northern Harriers show browner plumage, while most but not all older birds show grayer plumage. Males with intermediate timing to the molt may produce intermediate gray and brown plumage.

Analysis of museum specimens

I examined 58 specimens of second-cycle or older male Northern Harriers at MVZ and CAS. I divided them into brown (18 specimens), intermediate (11), and gray (29) plumages based on the extent of brown wash to the breast and back: heavy, intermediate, or light/lacking, respectively (see Fig. 2). Of these, none had **retained** juvenile **secondaries** and could thus be confirmed as second-cycle; in my specimen notes from other museums, however, there were two confirmed second-cycle

birds with retained **juvenile** secondaries and brown plumage.

Five specimens of males at MVZ and CAS (and three at other museums) had retained basic secondaries and were thus older than second-cycle. Three of these showed intermediate plumage and five showed gray plumage. At MVZ and CAS, there were 17 males that showed **suspension limits,** indicating probable breeding the year before (Pyle 2005). None of these were brown, 3 were intermediate, and 14 were gray.

Two individuals (MVZ 14081 and 53078) were completing the second prebasic molt, with one or two outermost juvenile primaries retained, on 29 and 21 July, respectively. These were molting in brown second-basic breast feathers (Figs. 3a, 3b). Another bird (CAS 44510) was completing a third or later prebasic molt on 15 September, with two retained definitive basic (adult) outer primaries. This bird was molting from brown to gray breast and back feathers (Fig. 3c, 3d).

The importance of breeding ecology

Second-cycle birds may rarely retain juvenile feathers because they do not breed; freed from the metabolic constraints of breeding, they can molt earlier and more completely than breeders. They may average browner incoming second-basic feathers due to an earlier molt, according to the molt–plumage interactions described above. Older birds and breeders undergo later prebasic body molts and show grayer subsequent plumage on average. The specimen at CAS (#44510), molting later in the season and from brown to gray, shows that plumage may not be static with age (as would be the case for plumage morphs) but can vary from year to year. This bird may have been undergoing the third prebasic molt (see Pyle 2008); however, the relationship between molt timing and plumage color may be correlated with breeding status more than with age per se.

Therefore, some later-molting second-cycle birds may show grayer plumage, some earlier-molting older birds, perhaps failed breeders, may show browner plumage, and birds of both age classes with intermediate molt timing may show intermediate plumages. This explanation potentially supports the proposed theories of both Liguori and Sullivan (2013a,

2013b) and Pyle (2008, 2013a).

The problem of individual variation

Another potential clue to aging second-cycle male Northern Harriers is by the retention of juvenile under-wing coverts (Liguori and Sullivan 2013a). I was able to examine the under-wing coverts to varying degrees on the male specimens at MVZ and CAS, and noticed none with retained juvenile or basic coverts. However, the amount of dark in the coverts varied substantially, with some brown-plumage and intermediate-plumage males showing basic under-wing coverts with almost as much dark as found in juvenile feathers (see photos in Liguori and Sullivan 2013a). Gray-plumage males showed paler under-wing coverts on average, although some showed dark-centered coverts that had not been retained from a previous molt. We will need to better understand variation in second-cycle and **definitive** basic under-wing covert patterns before we can reliably apply it to aging male Northern Harriers.

A curious specimen and a note of caution

Finally, among the specimens was a larger individual (MVZ 30324) showing mixed brown and gray feathers (Fig. 2, second bird from left), similar in plumage to the individual shown in Fig. 3 of Liguori and

Fig. 3 (a, b, c, d). These specimens from the MVZ and the California Academy of Sciences (CAS), San Francisco, show some of the complexities involved in aging male harriers.

Fig. 3a: MVZ 53078, a male completing its second prebasic molt, replacing worn, brown, juvenile breast feathers with fresh, brown, second-basic breast feathers. Fig. 3b shows the same bird's yet-to-be molted juvenile outer primaries.

Fig. 3c: CAS 44510, a male completing its third or later prebasic molt, replacing worn, brown, basic breast feathers with fresh, gray, definitive basic breast feathers. Fig. 3d shows the same bird's yet-to-be molted definitive basic outer primaries. *Photos by © Peter Pyle.*

Sullivan (2013a), reported by those authors to be a male of at least four years of age. Although the specimen was labeled a male, it had a wing chord of 362 millimeters, indicating a small female; the label included no data on gonads, suggesting that it may have been (mis?)sexed based solely on plumage.

I continue to be curious about the bird in Fig. 3 of Liguori and Sullivan (2013a), in particular about what evidence there may be for its sex besides plumage (e.g., size and plumage of its mate?). I'm wary of the view that it couldn't be a female because then "there would be no way to distinguish males and females by plumage" (Liguori and Sullivan 2013b), as older females of many bird species have been documented to acquire male-like plumages as they age (Pyle 2008). Which reminds me of something about the generic epithet of the Northern Harrier...

According to Gruson (1972), Aristotle was struck by the circular flight style of the bird we today call the harrier. So he called it *Kirkos*, whence *Circus*. Well, maybe. But there's another sense in which the name *Circus* is apt. As those of us in the age and sex determination business have long known, a lot about bird ID is circular ("If it quacks like a duck..."—problem being, most ducks don't quack, and many birds that make quacking sounds aren't ducks). And as Liguori and Sullivan have suggested, just because it looks like a second-year male harrier doesn't necessarily mean it's a second-year male harrier...a veritable circular, er, *Circus*.

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Glossary

Basic (plumage). A complex but important term! As the name implies, this is a bird's "basic"—fundamental, reference, or baseline—plu-mage. In adult male Indigo Buntings, the brownish fall–winter plum-

age is the basic plumage; this plumage alternates annually with the stunning blue *alternate plumage*. All birds have a basic plumage, and many adult birds have only a basic plumage. In most birds, the basic plumage is grown in (molted, replaced) once per year. Often, a bird just molts from one basic plumage to the next, with little appreciable change in appearance (Wrentits are exemplary in this regard). In other instances, the acquisition of the basic plumage (whether from an alternate plumage as in tanagers or from a distinctively worn basic plumage as in starlings) can result in drastic changes in appearance.

Coverts. Feathers that cover something up—in particular, the shafts of other feathers. The under-tail coverts cover the underside of the tail, the ear coverts cover the ear, and the wing coverts protect the bones and muscles of the wing.

Definitive (basic). The (basic) plumage of a full-on adult. In many songbirds, this plumage is acquired within a year of hatching. In large gulls and raptors, definitive basic plumage isn't acquired for three, four, or more years. In albatrosses and frigatebirds, definitive plumage may not be acquired until the bird is more than a decade old.

Juvenile (plumage). The first full coat of feathers (the first plumage) in which a bird is capable of flight. (Assuming the species is capable of flight!)

Prebasic (molt). A key point in bird biology is that every plumage is preceded by a molt. The prefix "pre" signifies the upcoming plumage. So the prebasic molt is the molt that results in a basic plumage. Note that it is possible—indeed, common—for one basic plumage to be replaced, via the prebasic molt, by another basic plumage.

Retained. Feathers left over from a previous plumage. Even though the body plumage of a second-year bird may essentially resemble a third-year or even a thirteenth-year bird, it might show one or a few or even many retained juvenile flight feathers in the wing. Knowing how to recognize retained feathers can be extremely useful in aging and identifying birds.

Second-cycle. A plumage cycle runs from one basic plumage to the next. In general, adult plumage cycles run from the late summer or early fall of one year to the late summer or early fall of the next. If birds were humans, the second plumage cycle would be, roughly speaking, a one-year-old.

Secondaries. The powerful flight feathers of birds are referred to as primaries and secondaries (together, and to be technical about it, they are called

the remiges). The secondaries are the inner of these flight feathers, attached to the bird's ulna, closer to the body.

Suspension limits. Diurnal raptors and some other birds can begin molt of the flight feathers of their wings while they are incubating young, then suspend molt while feeding chicks, and then resume molt once the chicks have fledged. This strategy takes advantage of the slow period during incubation to get a few feathers replaced. Feathers replaced during incubation can be noticeably and contrastingly older-looking than those replaced after suspension. We call this contrast a "suspension limit," and it can help not only with aging the bird but also in determining its breeding status the previous year.

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Final Thoughts

Birding and field ornithology are best practiced holistically. Modern bird study depends on insights gleaned in the field, at the keyboard, in the lab, and—as much as ever—from museums. Here the author, with Carla Cicero, Staff Curator of Birds at the Museum of Vertebrate Zoology, ponders Sagebrush and Bell's sparrows in the museum's collection. Advances in the field identification of these lookalike sparrows have been made possible by the author's detailed examination of museum specimens: tinyurl.com/Pyle-Artemisiospiza. *Photo by © Beth Womack.*