40 BONAPARTE, CHARLES LUCIEN

It has also become a major market segment. These trends are all the more striking in view of the fact that participation in other popular outdoor activities involving wildlife, for example, hunting and fishing, is actually declining.

## Bonaparte, Charles Lucien (1803–1857)

A nephew of Napoleon I, the young Bonaparte tackled the description of the North American avifauna in his American Ornithology during an eight-year stay in America. He was well educated in science and is generally acknowledged to have been one of the foremost ornithologists of his time. His American reputation is eclipsed somewhat due to his appearance on the scene between the two giants of early American ornithology, WILSON and AUDUBON. He continued to study and write about birds and other zoological subjects on returning to Europe, but much of his later life was consumed by politics, especially the independence of Italy. Bonaparte's Gull (Larus philadelphia) nests in the boreal forests of Canada and Alaska, where, uncharacteristically for a gull, pairs build their nest of sticks in coniferous trees.

## **Brood Parasitism**

Describes the laying of one or more eggs by one bird in the nest of a "host" pair (often of a different species), which rears the chick or chicks, often at the expense of some or all of its own young.

INTRASPECIFIC BROOD PARASITISM. Laying eggs in the nests of neighboring members of the same species is now known to be a common practice among songbirds

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and certain other groups of birds, including grebes, waterfowl, gallinaceous birds, gulls, and pigeons. It tends to be especially prevalent when population density is high (e.g., in colonial species) and when good nest sites are scarce. In some cases, as many as a quarter (colonial swallows) to three-quarters or more (ducks) of nests have been found to contain the eggs of another pair. European Starling females actually prospect for host nests of their own species and remove an egg from the clutch before laying a replacement. Because such parasitic eggs are virtually identical to those of the host, they are usually accepted (unless the receiving female has not yet laid any of her own eggs), and the unrelated young are reared along with the host's own. This model has little or no detrimental effect on the host's reproductive success and gives the parasite's genes an additional survival option. It has been suggested that such parasitism within species may have been an early stage in the evolution of obligate brood parasitism described below.

FACULTATIVE (DISCRETIONARY) BROOD PARASITISM describes cases in which birds occasionally lay eggs in nests of different (usually closely related) species. Several duck species practice this casual form of parasitism, and the Redhead and Ruddy Duck are known to avail themselves of the alternative regularly. In the species studied, the parasite's eggs typically outnumbered the host's own in completed clutches, conferring a reproductive disadvantage on the foster parents. Some land birds also parasitize each other occasionally, especially in years when good food supplies permit high egg production.

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OBLIGATE BROOD PARASITISM refers to species that never build a nest of their own or care for their own eggs or young. It is characteristic of only about 1% of all bird species in 6 families worldwide, including one duck species; the majority of the 78 species of the Old World cuckoo family; 3 species of New World cuckoos; probably all 17 species of honeyguides; 5 of 6 cowbird species; one species of African weaver; and the whydahs and indigobirds in the genus *Vidua*.



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BEHAVIORAL VARIATIONS. Brood parasitism has evolved independently in the families noted above, and its practice varies significantly among them. The Black-headed Duck of South America will use virtually any nest it can find (including that of at least one raptor species), does not displace eggs or young from the host's nest, takes no food from the host parents, and becomes fully independent within two days of hatching; it has therefore been called "the most perfect of avian parasites" (Weller 1968). Even more "virtuous" perhaps is the Giant Cowbird, whose nestlings, according to Smith (1968), actually benefit their host oropendolas in some circumstances by removing botfly larvae from their step-siblings. All the other obligate brood parasites inflict some degree of harm on their hosts: (1) by removal of host eggs or young (by parent or nestling parasites); (2) by consuming food intended for a nest's rightful inhabitants; and/or (3) by taking up inordinate amounts of the parent birds' time and energy.

The response of the host also varies, from (I) complete obliviousness of the deception and sacrifice of its own young to the needs of the (often much larger) parasite; (2) rearing the parasite along with some of its own young; (3) evicting the parasitic egg; (4) covering over a parasitized nest with successive "floors"; or (5) abandonment of the parasitized nest.

IDENTITY CRISIS? How does a young cowbird or cuckoo know it is not a warbler and how to find an appropriate mate? In cuckoos and cowbirds, the answer lies at least partially in their genetically inherited ability to sing and to recognize and respond to the songs of their own species. The African indigobirds, by contrast,

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adopt much of their host's identity throughout their lives. In addition to mimicking the appearance and behaviors of the host nestlings—species of firefinches in the same (waxbill) family—both males and females learn the song of their host fathers and will mate only with indigobirds that sing or respond to the right firefinch song, including the correct local inflection (see SONG). On the one hand, this improves the odds of cuckolding the right host species and maintaining this remarkable identity bond. However, if an oddball female indigobird places eggs in the "wrong" waxbill nest and the hosts do not reject them, the misplaced young are programmed to learn the ways of their foster parents, and the foundation is laid for the evolution of a new species of indigobird (see INTELLIGENCE).

BROOD PARASITISM AND BIRD CONSERVATION. A potential catch-22 in the brood parasite model is that theoretically if the parasite is too "successful," it could put its hosts-and therefore itself-out of business. Where small isolated populations of birds coexist with generalist parasites, local extinctions can occur. Sadly, there are already examples of the worst-case scenario, created largely by human agency. Cowbird populations and distribution have expanded greatly due to habitat alteration and an increase in food sources. This has enabled Brown-headed, Shiny, and other cowbirds to reach hosts from which they were once barred by ecological barriers. Were it not for muscular efforts to control Brown-headed Cowbirds in and around the Huron-Manistee National Forest in northern Michigan, the world's only population of Kirtland's Warbler might have vanished forever decades ago. And the

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endemic Yellow-shouldered Blackbird of Puerto Rico faces a similar threat from the rapidly increasing Shiny Cowbird, a recent arrival over much of the Caribbean and southern Florida.

# Buzzard

In North America, this is a slang term for the New World vultures. Elsewhere in the English-speaking world it is the standard name for the relatively broad-winged, short-tailed raptors in the genus *Buteo* and similar forms. (In this Old World nomenclature, arising from the ancient traditions of falconry, our Red-tailed Hawk would have been properly called Red-tailed Buzzard and the term "hawk" would be reserved for the long-tailed raptors of the genus *Accipiter*.)



Turkey Vulture (*L*) and Common Buzzard For general queries contact webmaster@press.princeton.edu.

46 CACHING

**aching** Woodpeckers, tits, nuthatches, and members of the crow family (including jays, magpies, and nutcrackers) habitually store food. The degree to which it is retrieved by the storers apparently varies and has been thoroughly studied in only a few species. Eurasian Nutcrackers are known to recover a majority of the nuts they bury in caches in the ground for sustenance during the winter and to feed young in the spring. And the North American Clark's Nutcracker stores food in communal caches and displays an uncanny ability to relocate these sites even when they become obscured by heavy snow cover.

Canada (Gray) Jays are also prodigious cachers. Patient ornithologists have counted more than 1,000 caches



Canada Jay

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during a single 17-hour day. Fitted with exceptionally large salivary glands, the jays can make quantities of very sticky saliva with which they glue sundry morsels into tree crevices and other secure niches. The food items are stored within a prescribed radius from the sources, with the birds instinctively balancing the quality of the tidbit (i.e., its size or nutritional value), the distance it will have to travel to retrieve the cache, and the contingency of densely situated caches being robbed.

A key element of effective caching, of course, is retrieval: *Where the heck did I put that Cheese Doodle?* Retrieval success—essentially a function of memory—has been the subject of careful studies in a few species that demonstrated an extraordinary ability to remember not only where they stored some tidbit but what the tidbit was and how long ago it was cached. Clark's Nutcrackers, for example, can store more than 30,000 items in up to 2,500 locations over a season, in some cases traveling more than 15 miles, and are able to recover about two-thirds of them as much as 13 months later.

That many stored items go unrecovered is demonstrated, for example, by the sprouting of oak trees where jays were known to have buried acorns—adding seed dispersal to the benefits of avian caching.

## **Canopy Feeding**

A practice peculiar to several species of herons in which the wings are spread forward to shade the area of water in which a feeding bird is standing, presumably affording some advantage in catching prey. It has been suggested that the canopy acts as a trap of sorts, with fish attracted to a suddenly available patch of shade. It also

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seems plausible that the gesture may act as a simple sun shade for herons feeding in the open, where the glare off the water obstructs a clear view of activity below the surface. It is not clear to what extent either or both of these possibilities explain this distinctive behavior.

## Carson, Rachel (1907-1964)

That the general public, government agencies, and even corporate interests now understand the dangers of indiscriminate use of toxic chemicals in the environment can be attributed to a great extent to Rachel Carson and her consciousness-altering book *Silent Spring*. Though Carson focused her analysis on the effects of pesticides such as DDT, dieldrin, and heptachlor on birds, she made it clear that the outcomes were likely to be equally dire for human beings and for the Earth's biosphere as a whole.

The powerful impact of *Silent Spring*, which began even before it arrived in bookstores, resulted from the author's combination of scientific knowledge and a writing style that was both lyrical and accessible. For Carson, it was the writing that came first; she composed her first works at age 8 and was published by 10 (in *St. Nicholas Magazine*). And she began her college career as an English major before switching to biology.

Inspired by her reading as a teenager of Melville, Conrad, and R. L. Stevenson and her growing fascination with the ocean, she became an aquatic ecologist, earning her Masters with a thesis on the embryonic development of the excretory system of fishes. And her first full-length works, eventually to be known as the Sea Trilogy, celebrated the wonders of the marine en-

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vironment. The first of these, Under the Sea Wind (1941), was critically acclaimed but did not sell well initially. But her next book, *The Sea Around* Us (1951), was serialized in the New Yorker, abridged in the Readers' Digest, won the 1952 National Book Award for nonfiction, and remained on the New York Times best seller list for 86 weeks. This allowed her to quit her job as chief editor



of publications at the U.S. Fish and Wildlife Service and concentrate full time on her writing. In 1955 she published the *Edge of the Sea*, which was also well received.

Carson became interested in the effects of pesticides on the environment as early as 1945 but could not capture the interest of publishers in the subject in the postwar era, when an emerging chemical industry seemed to promise the miraculous eradication of life- and crop-threatening insect pests. But by the late 1950s—due to programs such as the federal Gypsy Moth Eradication Program, which employed blanket aerial spraying of pesticides, and to disturbing events such as the "cranberry scare," in which herbicides were linked to cancer—she was able to publish articles documenting bird deaths attributable to pesticides, and in 1962, she published *Silent Spring*.

The effect was explosive—in both directions. Carson's well-documented and eloquently described thesis that pesticides were actually "biocides" potentially

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affecting the well-being of nontarget organisms, including people, and that their residues accumulated in the environment captured the public's imagination immediately and was soon taken up by conservation organizations, government commissions, the president's Scientific Advisory Committee, even the Supreme Court. From industry, the outcry was equally vehement, though often less civil. Her scientific credentials were questioned because she was a marine biologist, not a biochemist. One industry chemist thundered that if we followed Carson's lead we would "return to the Dark Ages and the insects and diseases and vermin would once again inherit the earth." And another called her a "fanatic defender of the cult of the balance of nature." Ezra Taft Benson, a former U.S. Secretary of Agriculture, opined that because she was unmarried, despite being physically attractive, she was "probably a communist."

Given the widespread support of the public and much of the mainstream scientific community, Carson's arguments prevailed and can be seen as inspiring the founding of the Environmental Defense Fund in 1967 and the establishment of the Environmental Protection Agency in 1970. She is also credited with influencing the rise of eco-feminism and empowering many women scientists.

Carson's legacy contains many national and international honors, including the Presidential Medal of Freedom awarded by Jimmy Carter in 1980. Sadly, this and most of the other tributes were awarded posthumously. During her work on *Silent Spring*, she developed breast cancer and died of complications from the disease on April 14, 1964.

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# Chicken Hawk

Pejorative colloquial name used in the broadest sense to refer to any medium-sized to large hawk, any of which is presumed by the ignorant to ravage poultry yards habitually. The Northern Goshawk preys on grouse among other medium-sized birds, but it is a forest species unlikely to haunt barnyards. Smaller accipiters such as the Eurasian Sparrowhawk and Cooper's Hawk are more wide-ranging, know an easy kill when they see one, and might carry off a chick on occasion, but would hesitate to tackle an adult hen. In summary, the term has little basis in fact and has been one of many pretexts, especially pre-bird conservation laws, to kill raptors.

# **Climate Change**

There is no longer any credible doubt that the Earth's changing climate and its living inhabitants are now on a collision course. Even so, there are many who refuse to acknowledge this, either from self-interest or because of understandable denial, based on a lack of knowledge, a distrust of science, a willingness to listen to those who say it is all a hoax, and perhaps an underlying anxiety that it is all true.

Phenomena such as shrinking glaciers, rising sea levels, ocean acidification, temperature averages, and weather anomalies don't raise alarms for many people because they tend to happen gradually and are comfortably dismissed as natural fluctuation: "The climate has always changed!"

Just as the warning of a "silent spring" by Rachel Carson galvanized the public to demand the banning of DDT in 1972, it may be that birds may once again

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provide the most visible evidence that a new threat has arrived—and that it is not just birds that will suffer from its effects. For example:

- Shorebirds that depend on coastal beaches are already losing real estate for nesting and roosting due to sea level rise, and higher tides are flooding Saltmarsh Sparrows out of their nearby (and only) breeding habitat. Tern colonies on barrier islands, like human inhabitants of low-lying archipelagos, are beginning to sink under water.
- The warming and acidification of the ocean causes a loss of biological productivity due to a reduction in dissolved oxygen. We are already seeing local shifts and reductions in populations of sea ducks, alcids, and pelagic species such as shearwaters and stormpetrels due to a reduction in the crustaceans, mollusks, and fish on which they feed and changes in the life cycles of the planktonic organisms that support the marine ecosystem.
- It is now well documented that plants in the Northern Hemisphere are blooming earlier due to earlier and warmer springs. Over eons, long-distance migratory birds have timed their arrivals at key stops as they move northward to their nesting grounds, to coincide with the flowering of prominent tree species. These attract myriads of insects that the birds need as fuel to continue their migration. If the birds, which cannot foresee changes of the flowering cycle from their distant wintering grounds, arrive too late to catch the peak bloom and pollination period, they may lack the fitness to rear young successfully or fail to nest altogether.

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— The composition and microclimate of our forests are also changing with rising temperatures. Birds are extremely sensitive to changes in the structure of their habitats and the associated web of other organisms on which they depend. For example, as more humid forests in North America become drier they may cease to support a thick growth of understory shrubs that Wood Thrushes and other birds of the forest floor require for nesting cover.

In view of the many abundantly documented (and largely preventable) threats to birdlife—and human life—that we have visited upon the planet (see APOCALYPSE), and given that predictions for the effects of climate change are becoming more dire, not less, do we really want "let's wait and see" to be our motto going forward?

#### Cloaca

In birds, reptiles, amphibians, and many fish, the terminal enlargement of the digestive tract, through which solid wastes, urine, and the products of the reproductive system all pass prior to excretion, egg-laying, or copulation. In mammals, of course, the digestive passage is separate from the urinary and genital passages. The word derives from a Latin verb meaning "to cleanse," and the non-zoological meaning in English is sewer or toilet.

See also POOP, ETC. and SEX.

## **Colloquial Names of Birds**

People the world over have given names to conspicuous birds or those that have some significant impact on their daily lives. Cultures that use birds extensively for food or adornment tend to have a high degree of recognition

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of their region's birds and invent names to differentiate them. These colloquial or local names almost always refer to some distinctive plumage, voice, or behavioral characteristic. In this regard, in fact, they are often more relevant and almost invariably more imaginative and pleasing than standardized vernacular (common) names (see below).

Of course, a majority of standard English names for birds derive from colloquial stock, especially at the generic level, and are sometimes of ancient lineage. "Finch," for example, can be traced back at least 3,000 years to a similar word that echoes (quite recognizably) the sharp call of the Eurasian Chaffinch; other, seemingly distinctive names, such as "Merlin" can be traced back only so far before disappearing in a tangle of linguistic roots. The American Robin would doubtless have been called Red-breasted Thrush or the like had it not reminded British colonists of the Robin Redbreast (European Robin) of their homeland. "Anhinga" and "caracara" come to us virtually unchanged from classical Tupi, a now-extinct language of natives of the Amazon Basin. And a significant number of "official" common names have survived intact from their folk origins, for example, Wheatear (a corruption of "white arse," referring to their distinctive rump and tail pattern), and Bobolink (originally "Bob Lincoln," echoing its bubbly song). As in this last example, it was once common in Britain to personify common bird species, hence Maggie the Pie which became Magpie and Jack the Daw, shortened to Jackdaw.

Despite the fact that we have now constructed a reasonably standardized English nomenclature for our native (and other) avifauna(s), it should be remembered

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(probably with considerable gratitude) that the great majority of people have paid not the slightest attention. A few of us insist that this pointy-winged bird, flying erratically over fields and cities at dusk uttering a nasal call that sounds like *peent!* is a "Common Nighthawk." But those who know it (in some ways at least) as well as or better than most ornithologists do, know full well that it is a "bullbat," which, after all, is shorter and hardly less accurate than the "official" name.

The main objection raised against colloquial names, of course, is that they are confusing. One person's Black-bellied Plover is another's "gump" or "chucklehead" and still another's "too-lee-huk." But it is on scientific names that we depend for nomenclatural consistency, and the terrible ambiguity exemplified above can usually be relieved with a little conversation. Furthermore, it is absurd to claim that standard vernacular names are especially apt. Golden and Blacksmith Plovers are just as "black-bellied" as *Pluvialis squatarola* yet, alas, no one had the imagination to call the Blackbellied Plover instead "Silver Plover." The smorgasbord of regional flavors and the local humor contained in North American bird slang easily outweigh any fancied need to cleave rigidly to an ornithological Esperanto.

It is gladdening to think that someone out there may still know the Ruddy Duck as a biddy, blatherskite, butterball, blackjack, hobbler, broadbill, bluebill, daub duck, dipper, dapper, dopper, bullneck, bumblebee buzzer, butter bowl, chunk duck, deaf duck, dinky, dip-tail diver, goddamn, goose teal, greaser, broadbill dipper, creek coot, pond coot, dumb bird, goose wigeon, stiff-tailed wigeon coot, hardhead, toughhead,

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steelhead, sleepyhead, hardheaded broadbill, booby, murre, pintail, hickoryhead, leatherback, leather breeches, lightwood knot, little soldier, muskrat chick, noddy paddy, paddywhack, quill-tail coot, rook, spoonbill, gray teal, bumblebee coot, saltwater teal, shanty duck, shot pouch, spiketail, spatter, spoon-billed butterball, stiffy, stub-and-twist, water partridge, wiretail, and who knows what else. This is a mere 60-odd names; the naturalist John K. Terres has noted that there are at least 132 "common" names for the Northern Flicker.

Needless to say, it is impossible to give more than a sample of such names here. The names below were selected by the author for their historical, anthropological, ornithological, or etymological interest—or because they made him laugh.

*Arsefoot:* Refers to the loons and grebes, all of which have their legs situated at their extreme tail end, a useful adaptation for swimming and diving, which, however, makes moving on land awkward at best.

*Burgomaster:* Seamen's name for the Glaucous Gull, which tends to have a well-filled figure and a proprietary bearing. The name derives from the Germanic term for a chief magistrate, for example, a mayor.

*Butcherbird:* Northern and Loggerhead Shrikes, both of which kill large insects, small mammals, and birds and then hang the "meat" in the crotch of a branch or impale it on a thorn.

*Callithumpian Duck:* Long-tailed Duck (until recently Oldsquaw); a callithumpian band is an amateur musical group that characteristically produces an odd assortment of notes at random; the same may be said of flocks of Long-tailed Ducks.

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*Doughbird* (or doebird): Though Thomas Nuttall and many shorebird shooters came to regard this name as generic for many of the larger, longer-billed sandpipers, it originally referred specifically to the Eskimo Curlew, "for it was so fat when it reached us in the fall that its breast would often burst open when it fell to the ground, and the thick layer of fat was so soft that it felt like a ball of dough." (Bent, 1929)

*Erne:* An old Anglo-Saxon name for the White-tailed Eagle, perpetuated in modern usage in the Scandinavian words for eagle (ørn or örn); well known to workers of crossword puzzles.

*Jiddyhawk:* Seamen's name for the species of jaegers; this is a laundered version of a name that refers to jaegers' alleged habit of eating excrement expelled by terns and other birds that they harass. The Latin genus and family names of the jaegers (*Stercorarius*, Stercorariidae) also mean "eaters of excrement."

*Mother Carey's Chickens:* Seamen's name for the stormpetrels, particularly European, Wilson's, and Leach's.

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Speculation that this widespread nickname is associated with the Virgin Mary (i.e., *mater cara* or *mater caritas*) seems at odds with the usual superstitions about "carey chicks," which describe them as tormented souls of lost sailors or cruel ship's officers or even avian demons keeping watch over the drowned. It is more likely a socalled noa name, that is, a name used to avoid calling an evil spirit by its right name and thus attracting it.

Peabody Bird: White-throated Sparrow, one song of which is often verbalized by residents of the United States as "Old Sam Peabody-Peabody"; Canadian ears hear "Oh, sweet Canada, Canada, Canada."

*Preacher:* Two-way pejorative name for the Red-eyed Vireo, which is noted for its monotonous, endlessly repeated song.

*Shitepoke:* Laundered version of a name applied to several species of herons, referring to their habit of defecating conspicuously and often copiously when flushed.

*Smutty-nosed Coot:* Hunters of North Atlantic waterfowl call all of the scoters "coots." This variation refers to the fatty orange knob at the base of the bill of the male Black Scoter.

*Tickle-arse:* Seamen's name for the Black-legged Kittiwake; the name is a contraction of "tickle-your-arsewith-a-feather" and is inspired by the giggle-like calls of this northern gull; "kittiwake" and "tickle-arse" are also onomatopoeic for this species' titter.

*Timberdoodle:* One of many folk names for the American Woodcock, an upland shorebird that nests in woodlands but performs dramatic aerial displays over adjacent open areas. Other names include bogsucker, hokumpoke, twitter pate, and bumblebee chicken.

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*Wobble:* Seamen's name for the Great Auk, perhaps describing its penguin-like gait? Not to be confused with "wobbla," the collective name in New England for the members of the family Parulidae, for example, "a wobbla wave at Mount Awbun (Auburn) Cemetery."

## **Convergence (Convergent evolution)**

The development of similar traits in unrelated groups of organisms due to adaptation to similar living conditions. In a broad context, the development of the forearm into a wing in both birds and bats is an example. In birds, a number of uncanny look-alikes from different families have evolved in this manner. Two striking examples are the superficial resemblance between some members of the Northern Hemisphere auk family (Alcidae) and the phylogenetically distant penguins and diving-petrels of southern oceans. Other examples include the New World hummingbirds and Old World sunbirds and the nuthatches (Northern Hemisphere), Nuthatch Vanga (Madagascar), and sittellas (Australasia), all unrelated.

# Coues, Elliott (1842–1899)

One of the foremost—and easily the most interesting of the American ornithologists of the late nineteenth century. Coues was born in New Hampshire, graduated from the college and medical school of what is now Georgetown University in Washington, D.C., and almost immediately began a writing career that eventually included almost 1,000 works, several of them major volumes. He was the most eminent of the army surgeons who collected specimens for Spencer BAIRD while on duty in the western states and became secretary and

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naturalist of the U.S.-Canadian Border Commission, out of which experience came two of his own ornithological works, *Birds of the Northwest* and *Birds of the Colorado Valley*. He also published extensively on western mammals. As secretary and naturalist for the Geological and Geographical Survey of the Territories, Coues added papers on the history of the exploration of the American West to his extensive bibliography. He was a founder of the American Ornithologists' Union (now renamed the American Ornithological Society), and his 1882 *Check-list of North American Birds* was the basis for the AOU publication of the same name, the first edition of which appeared shortly thereafter.

What set Coues apart from the other brilliant naturalists of his time was his personality, which has been described as "electrifying." He was physically handsome and had a highly developed sense of humor, boundless energy, and a greater than average taste for the eccentric. The most notable example of this last characteristic was his passionate conversion late in his life to the cult of the infamous "spiritualist" charlatan Madame Blavatsky, whose séances were also attended by such worthies as Thomas Edison, John Ruskin, and William James. Coues took to spiritualism with the same zest he brought to his other interests but was eventually banished from the movement for publishing the details of a Blavatskian hoax. Coues has remained unchallenged as the best writer among American ornithologists, and much of what was in his personality is evident in the eloquent, witty, and opinionated introductory chapters to his Key to North American Birds. Besides being a landmark in American ornithology, this volume contains a fine

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evocation of what being a nineteenth-century naturalist was like, from how to clean your collecting gun ("elbow grease"), to the wisdom (none) of taking "stimulation" when afield, to the perils of skinning a putrid bird (festering sores), to the excesses of the overzealous "splitters" who dominated taxonomic theory in Coues' time. Until the 1980s, the Greater Pewee (*Contopus pertinax*) was known as Coues's Flycatcher. Given his distinguished ornithological career, the loss of his eponym seems a pity.

## Crepuscular

In general usage, refers to twilight. But in the context of animal behavior, the term means active in low levels of light, especially at dusk but also before dawn. No



Woodcock courtship display For general queries contact webmaster@press.princeton.edu.

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bird species is exclusively crepuscular, but some species of owls, swifts, and nightjars are especially active or conspicuous in the twilight hours just after sunset and around first light. Some shorebirds (e.g., woodcock and snipe species) and songbirds (e.g., Henslow's Sparrow) are especially active at these hours, especially in the context of courtship. The skimmers, which feed best in calm water, typically take advantage of the low wind levels characteristic of dawn and dusk and are therefore largely crepuscular in their feeding habits. Many mammals and insects, and some reptiles are also crepuscular.

# In the broadest sense, any innate, stylized visual signal made by a bird, the function of which is to trigger or "release" appropriate behavior in the intended object of the signal. The most conspicuous examples of avian display are complex, prolonged rituals in a sexual or defensive context. These frequently involve the actual "display" of some prominent plumage or other physical characteristic, but the gestures involved often give no hint of the intended outcome—at least to a human witness. All birds engage in some form of display, though there is much variation in both size of repertoire and intricacy of ritual.

COURTSHIP (SEXUAL) DISPLAYS. When courtship displays are performed by males alone, they serve not only to attract the attention of unmated females, but also as "no trespassing" signs to other males. The displays of most ducks, shorebirds, hummingbirds, and passerines are dominated by the males. While he engages in some form of plumage display, accompanied

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Male frigatebird inflating red throat sac to attract females

by sound effects and/or movements, the female typically remains composed, sometimes appearing completely indifferent, even impatient, and may express her reaction with "displacement" activities such as feeding or preening. Or she may respond with ritualized gestures of submission alternating with solicitation. For one elaborate form of this kind of display, see LEK.

Many waterbird species in which the sexes look alike—for example, loons, grebes, tubenoses, pelican relatives, gulls, and terns—perform courtship displays in which both members of a pair are equally active. Some large grebes, for example, engage in tandem "races," and gannets face off in a mirror-image "greeting" ceremony.

The often bizarre and elaborate antics of birds engaged in sexual display are among the most fascinating and entertaining aspects of birdlife. Virtually every avian attribute and external anatomical feature—plumage, bill, legs, eyes, voice, flight—is active in one ritual or another, and not a few adaptations apparently function

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solely in display. Egrets, for example, acquire exquisite, erectile head and back plumes (historically called "aigrettes"); many alcids develop decorative facial tufts and colorful bill sheaths; and the colors of the so-called soft parts (bill, legs, fleshy eye rings, and facial skin) intensify greatly, though often very briefly, in a wide range of species during courtship.

FLIGHT DISPLAYS are a class of mating/pair bonding ritual that takes many forms, for example:

- Volplaning. In this display, a bird or pair of birds glide down from a height with wings held outstretched and motionless. Red-billed Tropicbird pairs volplane one above the other with the upper bird's wings held down and the lower bird's up so that they almost touch; courting terns often volplane (sometimes in groups); and some sandpipers volplane down from song flights. Perhaps the most readily seen volplaning displays are those of many common species of pigeons and doves over their long breeding seasons.
- *Butterflying.* Many plovers and sandpipers incorporate a very distinctive slow, shallow wingbeat in their flight displays, as do male Vermilion Flycatchers and American Goldfinches.
- Hovering. This replaces a tall singing perch for many open country species, for example, larks, pipits, longspurs, and many tundra-breeding shorebirds. The singer may hover hundreds of feet in the air while delivering a full-throated aria.
- Plummeting. Woodcock and snipe descend from the top of their aerial displays in erratic swoops, making characteristic mechanical sounds (see SONG) as they do so. Common Nighthawks plummet and "pull-For general queries contact webmaster@press.princeton.edu.

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out" abruptly after gaining speed, making a distinctive noise with their wings as they arc upward.

- *Sky Dances.* Male hummingbirds describe patterns in the air characteristic of their species in front of their mates, calling and in a few cases also making feather noises.
- Aerobatics. Perhaps the most dramatic of aerial displays are the stunt maneuvers performed by most species of hawks and eagles. A familiar variation is a series of continuous undulations. Some species fold their wings and plummet from as high as 1,000 feet before pulling out sharply and rising to repeat the dive. Vying for most remarkable stunt is the "tumbling" of some eagle pairs. In the North American Bald Eagle, the male flies above the female. She then turns on her back and presents her talons, which the male grasps in his. Then they fall down through space in a tumbling roll, releasing each other in good time. Many species of hawk also lock talons during courtship displays, falling earthward in helicopter-fashion, like some enormous maple samara.

DANCING. Pairs and sometimes small groups of albatrosses, cranes, some pelican relatives, and many gulls and shorebirds engage in more or less conspicuous, formalized, earthbound displays. These involve a great diversity of actions, including "bill fencing," gaping (to show the bright color of the mouth lining), wing posturing, "curtseying," pointing, stretching, and presentations of food or nesting material. Owing to their size and the exaggerated and intricate choreography of many of their movements, the albatrosses and cranes are especially renowned as "dancers."

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WATER DISPLAYS. The courtship displays of loons, grebes, and waterfowl are essentially aquatic dances. Loons and grebes with legs placed near the end of their bodies are capable of rising nearly erect from the surface and paddling furiously across their breeding lake in this vertical posture; pairs do this in tandem as one act in the courtship ritual. The goldeneyes execute a distinctive combination of head and neck motions involving "inflating" the head feathers until the head is nearly spherical, stretching the neck forward, and then tossing the head violently over the back ("head throwing"); in one version, this is accompanied by splashing, which exposes the bright orange legs and feet; other ducks have their own balletic moves.

THREAT DISPLAYS. Faced with territorial intruders of their own or other species, most if not all birds assume characteristic defensive postures, whether to intimidate rivals or protect themselves and their young. The tendency to erect body feathers with the effect of making the potential victim seem larger or otherwise more impressive is a common ploy. Blue-footed Boobies, for example, create an imposing presence by raising the head and neck feathers, making them bristle like porcupine quills. Nestling hawks and owls and cornered adults will often spread their wings and display their talons as well as raising their feathers as a means of intimidating attackers.

Possibly the most impressive achievement in the evolution of threat performances is the so-called snake display enacted by species of titmice. When their hole nest is invaded, the sitting bird gapes wide, hissing and swaying in a serpentlike manner and finally "strikes" upward, simultaneously hitting the nest wall with its wings.

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Of course, when threat displays fail, a counterattack is sometimes mobilized—as anyone who has ever wandered into a tern colony or ventured too near a skua's or goshawk's nest during the breeding season can attest.

DISTRACTION DISPLAYS. This type of display by nesting adults diverts the attention of predators from eggs or young. It is most highly evolved among open-country ground nesters, but it has been observed in some form in most bird families. The basic effect, performed with greater or lesser verisimilitude by different species, is of an injured or ill bird, flopping helplessly on the ground (away from the nest) while crying out in faux anguish. This "broken wing act" performed by many sandpipers and plovers is a remarkably convincing bit of avian pathos.

## Diving

A significant proportion of the world's living birds habitually dive in water. This includes the penguins, loons, grebes, some tubenoses, some pelicans, tropicbirds, boobies and gannets, cormorants, anhingas, coots, sungrebes, terns, alcids, some raptors, about 60% of duck species, some kingfishers—and one songbird family (see Dippers, below). And other swimming birds such as shearwaters and gulls will dive occasionally for various reasons explained below. The behavior is mainly a means of obtaining food but can also be effective in eluding predators. Some characteristics of and statistics about diving birds are as follows:

FOOT POWER. When progressing normally at the surface, diving birds paddle with alternating strokes. But birds that use foot power while diving push with both feet at once.

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WING POWER. Wings modified for diving are surprisingly common among birds, since most adaptations of these limbs are related to flight. The most extreme example is the penguins, whose forelimbs have become flippers—useless for flying in the air but perfectly adapted for "flying" underwater. Of all birds, penguins are by far the most at home in the water. They are as agile as any marine mammal (or more so) and can swim underwater faster than many birds can fly-Gentoo penguins at up to 22 miles per hour. The alcids-petite penguin lookalikes of the Northern Hemisphere—have wings that are also strongly adapted for use underwater. Though fully feathered and capable of flight in living alcid species, their forelimbs are notably narrow and flipperlike when extended. Some shearwaters and petrels also use their rather narrow wings to "fly" under water in pursuit of prey in ocean waters; some of these "tubenose" species regularly dive 100-200 feet deep in this manner.

LIGHT HEAVYWEIGHTS. Birds that habitually dive should ideally both be buoyant and have a high specific gravity. This seemingly contradictory condition is achieved in most divers by a combination of anatomical specialization and behavior. Birds' body cavities are lined with a system of air sacs that fill the spaces between the other organs and can be inflated and deflated as the lungs are by inhaling and exhaling. These air sacs even penetrate many bones so that even a bird's skeleton is partially air filled. The buoyancy thus achieved is of course an advantage in flight, and, when combined with the air-trapping capacity of PLUMAGE, also makes birds natural floaters.

When it comes to diving, however, buoyancy becomes a liability, working against a bird's efforts to pen-

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etrate water, which becomes ever denser with increasing depth. Species that plunge into the water from the air depend partly on gravity to counteract their natural "floatability," and those that dive from the surface and pursue prey once submerged push themselves under using their legs and feet—and in some cases their wings (see above).

More subtle is the ability of many waterbirds to compress their plumage, squeezing trapped air out and raising their specific gravity. It is this trick that allows the grebes to sink like a submarine apparently without exerting any effort. The plumage of cormorants and anhingas is relatively porous and fills with water readily; this makes for efficient diving but also explains the amount of time these birds spend drying out with their wings spread. In preparing for a dive, birds also expel air from their lungs and air sacs, further reducing buoyancy.

OUCH? Anyone who has watched a gannet plummet head first into the sea from high in the air is likely to wonder how the impact can be sustained time after time without resulting in a broken neck or at least a bad headache. In its practical way, evolution has given gannets and boobies unusually powerful neck muscles, a thickened and strongly supported skull, and air sacs lying under the skin of the head, which act as a kind of crash helmet. The eyes of diving birds are also modified to enable them to see prey underwater (see VISION).

And the nostril openings of pelicans, cormorants, and gannets and boobies are either closed at birth or become so by adulthood, and breathing is done through openings at the corners of the gape, another adaption to underwater life.

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HOW DEEP AND HOW LONG? The farther down a bird dives, the harder and slower the going, and therefore there is some correlation between the depth of a dive and its duration. However, long dives are not necessarily deep dives: one Western Grebe submerged for 63 seconds in  $5\frac{1}{2}$  feet of water.

The majority of diving birds are not deep or long divers; most species rarely exceed 10 feet or stay under more than 10–20 seconds. Even the deep divers, such as the loons, grebes, sea ducks, shearwaters, and alcids rarely approach their full diving potential. The recordholding Common Loon (see below) usually dives to a depth not exceeding 35 feet and takes less than a minute (sometime much less) to resurface. Also, birds under duress (e.g., chased or wounded) will typically stay submerged much longer than normal.

RECORD DIVES. The Emperor Penguin can reach at least 1,754 feet (534 meters) below the surface and stay under for at least 16 minutes, currently the world record. The Common Loon and the Long-tailed Duck are tied at dives of 180–225 feet and perhaps slightly deeper, both having been trapped in fishing nets set at these depths. Though their average dives are much shorter (see above), these birds are apparently little taxed by dives lasting 3 minutes, and the loon has survived forcible submersion for 15 minutes. These follow only the Emperor Penguin as world records.

DIPPERS (5 species in genus *Cinclus*) are the only songbirds that habitually swim and are quintessentially birds of fast-moving streams and rivers. They superficially resemble large (6-inch), stocky wrens with their compact form, short wings, frequently "cocked-up"