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Corvus corax

FRENCH:
Grand Corbeau
SPANISH:
Cuervo cumún,
Cuervo grande
ALEUT:
Tulugak

Common Raven

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This large, black, majestic bird is geographically and ecologically one of the most widespread naturally occurring birds in the world. It is distributed throughout major portions of North America, Europe, Asia, and North Africa, and in all terrestrial biomes except tropical rain forests. Historically in North America, it lived on the Great Plains in association with American bison (*Bison bison*) and wolves (*Canis lupus*). It still lives in wilderness areas throughout much of the continent, is reestablishing its former distribution in forests of the east, and is even moving into urban areas in parts of its range—adapting to human presence much as it also associates with other top carnivores. In some parts of its range, ravens are considered pests whose populations are rapidly expanding, and programs have been implemented to reduce population sizes. In other parts of its range, populations have declined so drastically that reintroduction programs have been implemented.

The Birds of North America

Life Histories for the 21st Century

The largest-bodied of all passerines, this raven is widely known for being a scavenger on animal carcasses and human garbage. It is also a predator, hunting rodents in fields, pulling nestlings out of nests, and taking food from conspecifics and heterospecifics. Its diet includes large numbers of arthropods, including scorpions and grasshoppers, and sometimes large amounts of seeds and grains.

Year-round

Figure 1.
Distribution of the Common Raven in North and Central America. This species often wanders during the nonbreeding season to areas just outside of this range. It also breeds in the Palearctic. See text for details.

Often considered a pest because individuals eat agricultural products (e.g., peck eyes from newborn lambs) and damage human-made objects (e.g., peel identification labels off toxic waste drums), the Common Raven has also been implicated as a causative factor in the declines of several threatened and endangered species including desert tortoise (*Gopherus agassizii*), California Condor (*Gymnogyps californianus*), Marbled Murrelet (*Brachyramphus marmoratus*), and Least Tern (*Sterna antillarum*).

This species has long been a part of the folklore of many cultures. Native Americans of the Northwest revere ravens as being the creator of earth, moon, sun, and stars, but also regard it a trickster and cheater. Poets and authors of Western cultures have often used the raven to symbolize death, danger, and wisdom. It is difficult to imagine any other bird being associated with so much myth, mystery, and misinformation. Nonetheless, despite more than 1,400 research reports and articles on this bird in the scientific literature, there are many gaps in our expanding knowledge of this fascinating species.

DISTINGUISHING CHARACTERISTICS

Very large corvid. Adult length up to 69 cm, mass 689–1,625 g. In adults plumage entirely glossy black with relatively long pointed wings (wing chord 35–46 cm), wedge-shaped tail, throat with elongated feathers commonly referred to as "hackles," and large, chisel-like bill (culmen length 59–86 mm, culmen height 21–30 mm, culmen width 15–31 mm). Sexes similar in appearance although female smaller than male in some characteristics (see Measurements, below). Sexes distinguishable only using regression or discriminant function analyses (Bruggers 1988, Knittle 1992). No seasonal variation in adult plumage. Immatures similar to adults except remiges and rectrices become dull brownish through their first winter and heavily worn by their second calendar year compared with adults. Immatures obtain glossy black flight feathers, which fade little or not at all, by their second Prebasic molt (Heinrich 1994a).

Common Raven similar to other all black North American members of the genus *Corvus* in coloration and general structure. Best distinguished by larger size, wedge-shaped tail, more massive bill, well-developed throat hackles, sometimes low and hoarse voice, and tendency to soar and glide rather than flap its wings continually in flight; wings appear longer and more tapered toward tip ("hand"). Tends to be found solitary or in pairs more often than other *Corvus*, but in many areas seen foraging or roosting in flocks or groups of several hundred to several thousand individuals. Unlike American Crow (*Corvus brachyrhynchos*), does not flick wings. Common Raven most similar to Chihuahuan Raven (*C. cryptoleucus*), which overlaps Common Raven's range in Colorado, Kansas, Oklahoma, Arizona, New Mexico, Texas, and n. Mexico. Common Raven distinguished by larger size (only possible in direct comparison), longer, heavier, and less blunt-tipped bill, longer tail; rictal bristles rarely cover more than half of bill (rarely less than half on Chihuahuan Raven); voice hoarser and lower in pitch; base of neck feathers pale gray (whitish in Chihuahuan Raven), but this visible only when feathers are blown by wind or when a bird is preening (Howell and Webb 1995).

DISTRIBUTION

THE AMERICAS

Figure 1. Alaska and Canada: Resident from the Brooks Range south throughout Alaska (including Aleutian Is. and Alaska Peninsula; Am. Ornithol. Union 1998), and from s. Elsemere I. and Prince Patrick I. south throughout Canada including most offshore islands (Godfrey 1986), but excluding eastern half of s. Alberta (Semenchuk 1992), southern third of Saskatchewan (Smith 1996), sw. Manitoba (Godfrey 1986), and areas south of the Canadian Shield in s. Ontario (Blomme 1987).

Western U.S.: Resident throughout w. U.S. from Pacific coast east to nw. and s.-central Montana (Bergeron et al. 1992), e.-central Wyoming (Oakleaf et al. 1992), e.-central Colorado (Winn 1998), extreme w. Oklahoma (Cimarron Co.), ne. and central New Mexico (Hubbard 1978), and throughout central and s. Trans Pecos and Edwards Plateau region of Texas (Texas Breeding Bird Atlas Project unpubl.). In California, largely absent from Central Valley, portions of central coast, and cultivated valleys of southeast (Small 1994). Locally absent from nw. Colorado and s.-central Wyoming and locally elsewhere within range.

Eastern U.S.: Resident throughout all but western portion of n. Minnesota (Janssen 1987), n. Wisconsin, n. Michigan (south to northern Lower Peninsula), the Adirondack Mtn. and Catskill Mtn. regions of e. New York (Peterson 1988), and from Canadian border south to s. Maine, se. New Hampshire, w. Massachusetts, and nw. Connecticut (Bevier 1994, Am. Ornithol. Union 1998). Also resident locally in sw.-central New York (Peterson 1988), and in Appalachian and Allegheny Mtns. from extreme nw. New Jersey, west through Pennsylvania, and south through w. Maryland, W. Virginia, e. West Virginia, extreme se. Kentucky, extreme e. Ten-

nessee, westernmost N. Carolina, extreme nw. South Carolina, and extreme n. Georgia (Am. Ornithol. Union 1998).

Mexico and Central America: resident in Mexico throughout Baja California, Isla Clarión, on Pacific slope from Sonora south to Nayarit, and in the interior and on adjacent slopes from n. Sonora, Chihuahua, and Coahuila south to e. Oaxaca. Also resident from w.-central Chiapas, Mexico east through s.-central Guatemala, and from s. Honduras east to nw. Nicaragua (Howell and Webb 1995).

Although resident throughout breeding range, often wanders to areas just outside of breeding range during winter. Casually wanders south through Great Plains, to southern shores of Great Lakes, and to lower elevations in Atlantic coastal states (Am. Ornithol. Union 1998).

OUTSIDE THE AMERICAS

Resident through most of Holarctic region from n. Europe (including Greenland and Iceland) through Siberia, south through central and w. China, south and west to n. Africa, and north through much of Europe (Cramp and Perrins 1994).

HISTORICAL CHANGES

By early 1900s, populations dropped well below previous levels in much of eastern North America. Previously along the coast south to N. Carolina, but now along coast only north from Maine and has retreated to relatively isolated areas in the Appalachians (Hooper 1973). Early in the twentieth century, extirpated from Alabama; now endangered in Tennessee. Before 1875, common on prairies south to S. Dakota, but disappeared probably from shooting, poisons, baited traps, and disappearance of bison (Houston 1977, Rea 1986). Second half of 1990s has witnessed populations increasing in most areas and species reclaiming parts of its previous range. As early as 1956, Sprunt (1956) reported ravens were returning to s. Appalachians, which he attributed to protection afforded by establishment of Great Smokey Mountains National Park. In some parts of the West, populations increased by 500 to 7,600% from 1968 to 1992 (Boarman and Berry 1995). Breeding Bird Survey data show increases occurring over most of range (http://www.mbr-pwrc.usgs.gov/bbs/htm96/trn626/tr4860.html). See Demography and populations: population status, below.

FOSSIL HISTORY

Fossil ravens from Pleistocene found from many sites throughout much of the range of the species (ne. Mexico, Am. Ornithol. Union 1957, Brodkorb 1978).

SYSTEMATICS

GEOGRAPHIC VARIATION

Comparing mitochondrial DNA (mtDNA) of Common Ravens from Maine and California showed moderate differentiation (4.2% uncorrected divergence in control region sequences; Tarr and Fleischer 1999). New genetic work based on wider geographical sampling shows a deep genetic split between Common Raven populations in w. U.S. and populations from throughout the rest of their range in the Old and New World. These 2 groups are about 3% divergent in mtDNA (cytochrome-*b* gene sequence), suggesting an old geographic split between the 2 groups (K. E. Omland, W. I. Boarman, R. C. Fleischer unpubl. data).

Size varies clinally with trend from largest in north to smallest in south within North America (possibly averaging larger in wing and tail in Central America, however). Although populations said to show broad range of individual variation, further study is required based on analysis accounting for age and sex (Rea 1983, 1986). Variation throughout range, including Old World, involves intensity of gloss, color of feather-bases, length of throat feathers, size (wing, tail, weight), relative length of tarsus, and relative length and depth of bill (Cramp and Perrins 1994).

SUBSPECIES

Four subspecies recognized in North America following Rea (1986), who based differences on measurements of wing, tail, tarsus, bill length and depth, and body mass. This classification differs from that presented by Am. Ornithol. Union (1957) in recognizing a Siberian-Alaskan population (*kamtschaticus*) as distinct within North America from *principalis*, and extending the range of the southwesternmost subspecies (*clarionensis*) to n. California. Another 6 subspecies occur across Eurasia. Differences between taxa slight; identification complicated by similarity in color, uncertain degree of local variation in size, and paucity of data on dispersal and migration (Willett 1941). Taxonomic revision needed; ranges and characters below tentative. Also see measurements given in Rea 1986 and Pyle 1997.

C. c. kamtschaticus Dybowski, 1883: Resident from ne. Siberia eastward through Aleutian Is. to Chignik, Alaska Peninsula, and northeast to Cape Newenham, Alaska (not on Pribilof Is. except as vagrant). Heavier bodied (adult about 1,460 g) with heavier limbs, tarsus longer and thicker, bill and skull slightly more massive than other northern Nearctic taxon, *principalis*. Other described races included under this name are *behringianus* and *grebnitskii*. Some populations ascribed to *kamtschaticus* are

synonymized under *tibetanus* of central Asia and other populations under *principalis* depending on taxonomic authority.

C. c. principalis Ridgway, 1887: Resident from n. Alaska across Canada to n. Greenland south to central British Columbia, central Saskatchewan, n. Wisconsin, and through Appalachian Mtns. to n. Georgia. Large race but slightly smaller (3 females 1,235–1,272 g) and with less massive limbs, skull, and bill than *kamtschaticus*. Birds of Alaskan tundra approach *kamtschaticus*.

C. c. sinuatus Wagler, 1829: Resident in w. North America from se. British Columbia and Montana south through the Great Plains and Great Basin (east of California) and mainland Mexico to Nicaragua; one specimen from Death Valley, CA (Rea 1986). Intergrades with *principalis* in central-s. British Columbia, Washington, and Oregon. Intermediate with shorter wing and tail, slenderer and shorter bill, smaller feet and skull; mass adults and immatures 855.5–987 g. Southernmost populations (s. Mexico, but chiefly Guatemala south) may average larger than northern *sinuatus* and have been named *C. c. richardsoni* Miller and Griscom, 1925.

C. c. clarionensis Rothschild and Hartert, 1902: Resident from n. California south through Baja California and on Clarion I. in Revillagigedo Is., Mexico. Occurs east in Mojave Desert to s. Nevada and w. Arizona. See Oberholser 1918 and Willet 1941 regarding range to n. California. Smallest race in North America; shorter wing and tail, thinner bill, and smaller skull than *sinuatus*; mass of adults and immatures 770.8–950 g.

Old World taxa include the following 6 races (Cramp and Perrins 1994): *C. c. corax* Linnaeus, 1758, Europe and Asia (intergrading with *kamtschaticus* between Yenisey and Lena basins); *C. c. hispanus* Hartert and Kleinschmidt, 1901, Iberian peninsula and Balearic Is. (grades into nominate *corax* on Sardinia and perhaps Corsica and Sicily); *C. c. laurencei* Hume, 1873, se. Europe and Balkans to nw. India (former name "*subcorax*"); *C. c. tibetanus* Hodgson, 1849, central Asia from Tien Shan and Pamir-Alay Mtns., Himalayas, and Tibet; *C. c. tingitanus* Irby, 1874, n. Africa; *C. c. canariensis* Hartert and Kleinschmidt, 1901, Canary Is.

RELATED SPECIES

In North America, Chihuahuan Raven is probably most closely related (Goodwin 1976, Jollie 1978). In fact, recent genetic data suggest that w. U.S. Common Ravens may be more closely related to the Chihuahuan Raven than they are to Common Ravens from Alaska, Minnesota and the Old World (K. E. Omland, W. I. Boarman, R. C. Fleischer, unpubl. data). Brown-necked Raven (*C. ruficollis*) of North Africa and Middle East sometimes con-

sidered conspecific with Common Raven (Vaurie 1954, Goodwin 1976, Jollie 1978). Systematic relationships based on molecular characters have not been worked out for all *Corvus* (but see Cibois and Pasquet 1999).

MIGRATION

In most areas a year-round resident; no evidence of migration from radio-tagged or marked populations in North America and Iceland (Mahringer 1970, Dorn 1972, Coldwell 1972, Stiehl 1978, Skarphedinsson et al. 1990, Engel and Young 1992a, Heinrich et al. 1994, WIB), nevertheless at edges of distribution (e.g., North and South Dakota, n. Iowa, and central Wisconsin), categorized as a fall or winter visitor (Rea 1986). In many areas, breeders probably remain throughout the year, while in other areas may temporarily abandon territory for ≤6 wk after the breeding season, during times of food shortage, or for regular daily feeding or drinking forays (Dorn 1972, WIB, BH).

Numerous reports of groups of primarily juveniles, ranging from fewer than a dozen birds to thousands (Mahringer 1970, Dorn 1972, Stiehl 1978, Kochert et al. 1983, Marzluff and Heinrich 1991, Heinrich et al. 1994). Almost nothing known about the source or destination of these groups that are sporadically sighted, although it is known that group membership is transitory (Heinrich 1989, Heinrich et al. 1994, but see Dorn 1972) and that genetic relatedness among individuals within flocks is no greater than it is among flocks (Heinrich and Marzluff 1995, Parker et al. 1994). Some may be migrating or dispersing birds, but local roost shifts and flights to and from food bonanzas by birds from a roost would also result in group flights unrelated to dispersal (Marzluff et al. 1996). Finally, group migration and dispersal could in many cases be combined with local movements to and from roosts that are formed for various durations during dispersal and/or migration. At present, no long-range or long-term studies are available to distinguish between the various alternatives.

HABITAT

Broad range of habitats: boreal, conifer, and deciduous forests; tundra; prairies and grasslands; isolated settlements, towns, and cities (including Los Angeles, CA, and Chicago, IL); deserts; sea coasts and islands; agricultural fields; Arctic ice floes; and the highest mountains. Prefers heavily contoured landscape (e.g., cliffs), which provides thermals for long-distance foraging; and also areas

with cliffs, trees, or human structures necessary for nesting. See also Breeding: nest site, below.

In the Canadian Arctic, occurs in large numbers in human settlements (BH). In other portions of its range, particularly in the deserts of the Southwest, also occurs near humans—in significantly greater numbers at landfills, agricultural fields, and along highways than in open desert (Knight and Kawashima 1993, Knight et al. 1993, WIB). In other areas, particularly forests of the ne. and e. U.S., prefers wilderness and often avoids areas with human activities. In many parts of range, often found scavenging for roadkills along highways (Austin 1971, Bruggers 1988, Farrell 1989, Knight and Kawashima 1993), but shuns roads in ne. U.S, where it is replaced by American Crow as scavengers along highways.

FOOD HABITS

FEEDING
   Main foods taken. Commonly associated with carrion, but not limited to scavenging. A generalist omnivore eating live meat, eggs, insects, grains, fruit, garbage, and carrion.
   Microhabitat for foraging. Individuals generally hunt in flight or while walking on the ground, but no quantitative data available. Generally feed anywhere food is present, probably most often on the ground but can and do catch birds and insects in flight. Few quantitative data on microhabitat for foraging. In Oregon, proportion of reptile remains in pellets was significantly higher in sagebrush habitat near roads than in other habitats, and ravens nesting near roads had more variable diets (Stiehl and Trautwein 1991). Seasonal change in food availability probably results in seasonal patterns in raven distribution and foods eaten (Dorn 1972, Stiehl 1978, Boarman 1993). Nesting ravens in e. Mojave Desert of California spent 75% of foraging time within 400 m of the nest, but at least once per day individuals flew several kilometers out of sight, probably to obtain water (Sherman 1993, pers. comm.).
   Food capture and consumption. Adapts well to different and changing environments, probably because of the variety of ways it finds food. Follows wolves and cougars to scavenge on leftovers (Pearse 1938, Mech 1970). Follows harvesting machinery to catch insects and rodents (Stiehl 1978, Young and Engel 1988) and systematically searches roads and highways for roadkills, particularly in early morning (Farrell 1989). Captives used olfaction to locate ground fish over short distances (Harriman and Berger 1986). No experiments to test ability to detect food by smell from longer distances in the wild, but

in Maine individuals did not dig up meat buried under snow nor a cow carcass hidden in thick brush (BH).

Uses a variety of methods to attack and acquire food once it is found. Has attacked Rock Doves (*Columbia livia*) and an eider (*Somateria* sp.) in flight (Maser 1975, Jefferson 1989, Watts et al. 1991); known to pull adult Rock Dove and Northern Flicker (*Colaptes auratus*) out of their nests (Eells 1980, Marr and Knight 1982). In one case, a pair of ravens dropped straight down into flock of several hundred roosting Black-legged Kittiwakes (*Rissa tridactyla*) and the ravens attacked, killed, and partially consumed a kittiwake (Parmelee and Parmelee 1988). In another possibly coordinated attack, one raven attacked a cat, causing it to drop a mouse from its mouth, then a second raven that was out of sight carried away the mouse (Zirrer 1945).

Feeding in crowds (we refer throughout to groups of birds as "crowds" because they lack the tight cohesion and consistency of membership typical of standard flocks; Heinrich et al. 1994, *cf*. Dorn 1972) often aids food capture: most ravens patrolling a kittiwake colony did so alone (87% of 625 observations), 9% were in pairs, and 4% were in groups of ≥3 (up to 20), but larger groups were more successful at finding and eating kittiwake eggs (Montevecchi 1979). Ravens, particularly juveniles, at new carcasses often exhibit a fear-like response. They land several meters from food, stop frequently to examine it, make sudden vertical leaps, sometimes with wings, slowly approach and leap, peck at the food, then sometimes fly away (Heinrich 1988c, Marzluff and Heinrich 1991). Often they do not approach and consume the food until other birds are in the area (Heinrich 1988c, Marzluff and McKinley 1993). Juveniles also wait for others before approaching a carcass, perhaps because larger groups are more effective at overwhelming and inhibiting aggression by more aggressive adults (Heinrich 1988b, Heinrich and Marzluff 1995). Fear of certain foods may be innate; naive captive juveniles readily approach smooth, round objects of various sizes, but ignore long, thin objects; small animals are rapidly approached and eaten, but large dead animals instill greater hesitancy (Heinrich et al. 1995).

Unable to open carcasses of ungulates and even those of smaller animals such as raccoons (*Procyon lotor*) or canids. In an experiment where ravens were offered unopened rabbit and deer carcasses, they ate more often at the smaller (rabbit) carcasses (Marzluff and McKinley 1993). They rely on carnivores and other scavengers for access to these larger sources of food. Even the fresh skin of gray squirrels (*Sciurus carolinensis*) is too tough for them to rip, although they may skin an entire squirrel by

turning it inside out through the mouth (BH). Western toads (*Bufo boreas*) were eviscerated and the skin from many limbs peeled off before the limb was removed (Olson 1989).

The upper bill has a slight hook at the end, which is useful in ripping off pieces of meat. The lower bill is pointed and sharp. Ravens use their lower bill, slightly opened, to hammer into solid objects such as frozen meat. Two ravens pecked long grooves into frozen suet to acquire larger pieces of fat (BH). Ravens eat juvenile desert tortoises by pulling off head or limbs (40%) or pecking holes through the soft carapace (46%) or plastron (13%; n = 341; WIB). They pry objects apart, for example, to reach food in crevices, by inserting the bill and opening it. To eat large eggs, they first punch hole into them with the lower mandible, then knock off more chips around the hole, and finally reach in to pull out the contents. They usually carry chicken whole in the bill between upper and lower mandibles. Ravens knock pistachios out of trees, remove the hulls and shells, then eat the remaining endocarp (Salmon et al. 1986).

Single or paired birds at a carcass often lay pieces of meat aside into a pile as each is ripped off, then depart after picking up the whole pile (BH). Birds in crowds never lay food aside, and store all food in their sublingual pouch before departing.

DIET

Major food items. Diverse diet includes arthropods (even scorpions), amphibians, reptiles, birds (adults, chicks, and eggs), small mammals, carrion, grains, buds, and berries. Diet varies considerably within and among individuals, depending in large part on spatial or temporal distribution of food; e.g., in Wyoming (Engel and Young 1989), feeds on a variety of foods in summer, such as nestling birds, garbage, insects from meadows and cow dung, and insects disturbed by grazing cattle. In winter, switches to garbage and carrion (Dorn 1972), moving out of areas without active garbage dumps. In W. Virginia, mammals were the predominate food item during winter, with birds becoming more prevalent in spring (Harlow et al. 1975). In Oregon, relies heavily on insects, particularly grasshoppers, in summer, barley in early winter, and cow placentas (will also peck at eyes and noses of newborn calves) in late winter, fish (carp carcasses) in early spring, and bird eggs in late spring (Stiehl 1976, Littlefield 1986). In California, 89% of ravens observed foraging were eating wild animals in the open desert in spring versus 5% in fall (McKernan 1992a, McKernan 1992b).

Quantitative analysis. Analysis of pellets, stomach contents, and prey remains beneath nests has demonstrated that mammals tend to be most important source of food followed by insects and birds, but the relative proportions of each prey type vary greatly among studies, sites, and season. In Oregon, 41% of the contents of 1,413 pellets collected in spring and summer were of mammals, 38% were of birds or their eggs, and 21% composed of insects, fish, vegetable matter, and reptiles (Stiehl and Trautwein 1991). Insects were the most heavily represented in stomachs analyzed from Utah (Knowlton 1943) and a close second to mammals in those from Oregon (Nelson 1934). Grains were most heavily represented in pellets of ravens in Idaho year-round (69% dry weight), with mammals representing 13%, invertebrates 7%, and birds 1% (Engel and Young 1989).

Diet breadth has commonly been assessed by analyses of the undigested remains in regurgitated pellets (e.g., Temple 1974, Engel and Young 1989, Camp et al. 1993). Although these studies show what has been regurgitated, they do not show how much nor do they indicate what has been eaten that is not regurgitated. For example, one mouse would leave hard parts detectable in a pellet whereas hundreds of pounds of meat from a moose (*Alces americana*), consumed without ingestion of hair or bones, would be undetectable. In California, the remains of desert tortoises were found in pellets beneath 2 out of 19 nests, but entire shells of tortoises were found beneath 5 of those nests (Camp et al. 1993, R. Knight pers. comm.).

Impacts on prey populations. Over a 10-yr period in California, ravens took 1.2% of 5,708 eggs of the endangered Least Tern (Avery et al. 1993). Ravens primarily take juvenile desert tortoises, a threatened species, with carapace length ranging in size from 32 to 105 mm ± 19.94 SD (mean = 67.1, n = 341, WIB); the level of predation may be sufficient to prevent recruitment in declining populations (Congdon et al. 1993). In Oregon, 14% (95/674) of Greater Sandhill Crane (*Grus canadensis*) nests were depredated by ravens from 1966 to 1981 (Littlefield 1986). In Arizona, 37% of 282 Pinyon Jay (*Gymnorhinus cyanocephalus*) nests were depredated by either ravens or American Crows (Marzluff 1988). Ravens preyed on breeding western toads at 3 of 15 breeding aggregations, eating >20% of the breeders at one aggregation in California (Olson 1989). Ravens and American Crows ate so many eggs at several Herring Gull (*Larus argentatus*) and Ring-billed Gull (*L. delawarensis*) colonies that they may have been responsible for complete failure of three colonies (Ewins 1991). Predation by ravens is thought to explain the high degree of nesting synchrony in Common Murres (*Uria aalge*; Murphy and Schauer 1996). In a Thick-billed Murre (*U. lomvia*) colony, ravens were responsible for <10% of the breeding failures (Gaston et al. 1985).

FOOD SELECTION AND STORAGE

Food selection. When young ravens leave the nest, they examine and manipulate with their bills almost all new objects they encounter (i.e., neophilia; Heinrich 1995a). At first, these objects consist primarily of leaves, sticks, pine cones, pebbles, etc. After gaining familiarity with these common objects, the birds ignore them and pick at previously unencountered objects, some of which may be edible and are subsequently sought out. By being open to a wide range of objects initially, the birds in effect "cast a wide net" to come in contact with whatever the environment has to offer. Learning then focuses their attention on the most remunerative items available. After 4–5 mo post-fledging, individuals are less inclined to manipulative or exploratory play, although in captivity this behavior persists, albeit at a diminished level, even in older birds, especially when they are hungry (Heinrich 1995a). This neophilia may account for their well-known behavior to contact shiny objects such as coins and jewelry, objects they generally do not encounter often enough to become habituated to them.

In addition to neophilia, the birds also show neophobia (i.e., fear of novel objects; Heinrich 1988c, Heinrich et al. 1995), which becomes more pronounced with age as neophilia declines. In general, young birds just out of the nest (who follow their parents) are not fearful, but if they do not encounter live or dead animals during this following period, they later become fearful of both. Birds several months old are very fearful of animal carcasses that they have not previously seen, though still attracted to them through neophilia. However, they learn through experience not to fear what may later become important food items.

Food storage. Like other corvids, ravens cache food (Stiehl 1978, Gaston et al. 1985, Heinrich 1988c, Kilham 1988). In n. Quebec, 69 of 84 (82%) Thick-billed Murre eggs and chicks taken early in the breeding season were cached in moss within 1 km of the murre colony (Gaston et al. 1985). Young Common Ravens begin to cache inedible as well as edible objects in apparent play when only days out of the nest by walking with them ≤1 m and shoving them into crevices or cracks. Older birds may fly several kilometers from a carcass to cache meat, and food caches (generally on the ground) are covered with material collected from nearby (leaves, earth, grass, snow; Heinrich 1988c, Kilham 1988). The more conspecifics present, the farther will birds fly to cache in secrecy (Heinrich and Pepper 1998).

Ravens store a variety of food and at all seasons, e.g., bones (Turcek and Kelso 1968), pine nutlets (N. F. Reimers in Turcek and Kelso 1968), bread (Simmons 1970), bird eggs and chicks (Gaston et al.

1985), and meat scraps (WIB, BH). The food-caching response, however, is related to apparent perceptions of an ephemeral food supply and to the presence of competitors for food. Thus, at least in an aviary, they do not cache when food is continuously available (Heinrich and Pepper 1998, BH). If birds are allowed to go hungry, however, they store food when again fed (Gwinner 1965). Each cache is at a different location and generally consists of one billful or gular-pouchful of food; however, some single loads may be cached at several locations (Heinrich 1988c). Memory for cache-sites has not been investigated in detail, but it shows evidence of decline after about 2 wk (Heinrich and Pepper 1998). Ravens remember the locations not only of their own caches, but also of those at which they observe others caching food (Heinrich and Pepper 1998). However, when caching prized food items, they attempt to evade others. In contrast, "play" caching of inedible items or items of low value is often done in the presence of others. Some of the stored meat may be used to feed young, although little is known on this topic. At one nest, the young were fed both fresh deer meat and some meat that was semidried, apparently stored (BH).

NUTRITION AND ENERGETICS

Few data; 750 kg of meat (cattle carcasses) was eaten by 300–500 ravens over 10 winter days in Maine (Heinrich 1994b). Captive ravens experienced an average loss in mass of 45 g/d (3.5% body weight) when deprived of food but regained this in <5 h of feeding (Heinrich 1994b). Using estimates of daily energy expenditure for passerines, "group energy requirements" was estimated at 721 kcal/d (group = 2 individuals; Shank 1986). Ravens need approximately 309 kcal of gross energy each day from food (Temple 1974); 684 pellets collected in Alaska represented 118,656 kcal of gross energy intake. The hunted animal remains in those pellets represented 60,893 kcal, or 51% of energy intake (Temple 1974).

METABOLISM AND TEMPERATURE REGULATION

Able to live in winter in Arctic temperatures near at least −50°C; in southwestern deserts tolerates summer temperatures regularly >45°C. Such tolerance is probably a result of two abilities: (1) increased metabolism allowing individuals to adapt to cold climates and (2) high heat loss (through eyes, bill, and legs; BH) allowing tolerance to hot climates. The metabolic rate for summer-acclimatized resting ravens is 8.40 kcal/h (Schwan and Williams 1978). Heart beat increased from 250 to 350 beats/min as ambient temperature decreased; respiratory rate remained constant with temperature change (13–25 breaths/min, except up to 52

at 40°C), and there was little difference in response between seasons (Veghte 1975).

DRINKING, PELLET-CASTING, AND DEFECATION

No quantitative studies. Drinks water from various sources; once per day in the Mojave Desert, radio-tagged ravens flew several kilometers in a straight line from their nests, probably to drink from cattle or irrigation troughs (M. Sherman pers. comm.).

Regurgitates pellets approximately 2 mm × 60 mm in size, 1.6–2.8 g (mean = 2.8 g, n = 1,413; Stiehl and Trautwein 1991), composed of indigestible materials such as skeletal remains, fur, and feathers (Temple 1974, Harlow et al. 1975). Pellet appearance can be highly variable. In the Mojave Desert, they often look similar to most raptor pellets, but tend to be lighter in color and flakier in consistency, contain less or no hair and more vegetable matter or soil (WIB), and are found beneath nests, perches, and night roosts. In Maine, some pellets consist mostly of cherry pits; mountain cranberry or mountain ash skins and seeds; feathers; or deer, flying squirrel, or rodent hair; a few were all white from quartz gravel, and near a landfill some contained only plastic; 1 consisted completely of a handkerchief (BH).

SOUNDS

VOCALIZATIONS

Common Ravens can make a wide array of sounds. Recent evidence suggests that there are local dialects and individual-specific calls so that the total vocal repertoire may be virtually limitless (Enggist-Dueblin and Pfister 1997). Characterization of the calls is difficult because of high variability and extensive intergradation among these diverse sounds (Brown 1974, Conner 1985, Bruggers 1988). Wide ranges of calls are often given in any one apparent context. There are also innumerable anecdotal descriptions of the calls, but such verbal descriptions almost invariably differ from one culture and from one person to the next. Numerous attempts at elucidating the calls with sonograms have been made and descriptions are available (Dorn 1972, Brown 1974, Conner 1985, Heinrich 1988a, 1989c, Heinrich and Marzluff 1991, Heinrich et al. 1995). Nevertheless, the meaning or function of most calls of this species is not clearly known.

Most calls are a series of harmonic bands. Carrier frequency is typically weak, with second harmonic the strongest. Amplitude decreases progressively from third, fourth, and succeeding harmonics. Most calls range from 0.4 to 8.0 kHz with a carrier frequency of 0.5–2.0 kHz (Dorn 1972, Brown 1974).

The softest calls are mostly used when birds are near each other (Brown 1974).

Development. Little known. Begging of nestlings develops into the Yell Call (Fig. 2A), which, in the e. U.S., functions to attract other juveniles to food bonanzas (Heinrich and Marzluff 1991, Heinrich and Marzluff 1995, cf. Marzluff and McKinley 1993). In spite of a large variety of vocalizations, there is enough similarity in vocal repertoires across continents and with congeners to suggest a significant innate component in vocal development (Conner 1985).

Vocal array. Approximately 15–33 specific categories of acoustically and structurally similar vocalizations have been catalogued for the species (Brown 1974, Conner 1985, Bruggers 1988). The variance in number of categories is indicative of the complexity of vocalizations. Here we describe the most common and distinctive vocalizations; refer to the above referenced papers for detailed analyses.

BEGGING. The begging calls of young nestlings are high-pitched and faint and become loud, deeper, and rasping by the time the birds fledge. The young continue to beg from their parents after they leave the nest, and the hungry birds may then be heard for 1–2 km. The pitch and volume of the beg varies with hunger and among individuals. In adults, the beg loses its discordant rasping quality and becomes more pure-pitched. It is then given by the adult female near the nest. Some birds in captivity continue to give the juvenile beg to at least 2.5 yr of age in response to their keeper's bringing food (BH). In the wild during their first summer, the presence of an adult with food elicits the begging calls, and it then attracts other nearby juveniles (BH). Later on in the winter juveniles may beg in the presence of food itself. This food-indicating or short-range recruitment call (Yell; Fig. 2A) is given by hungry birds unable or unwilling to get visible food, and it is inhibited by social superiors (Heinrich 1988a, Heinrich and Marzluff 1991, Heinrich et al. 1993). Yell consists of 2–3 harmonics at 1.8, 2.5, and 3.5 kHz above carrier at 0.8 kHz. It is "given singly or in irregular sequences"; in Maine, Yells are produced after 4–6 birds first arrive at a carcass, but not when large groups are present (Heinrich 1988a). Most individuals that give Yells are hungry, dominant, nonbreeders (Heinrich and Marzluff 1991). Small groups (1–5 birds) arrive within 1 min after playback of Yells, provided they were already within about 0.5 km, but the Yells did not attract birds when broadcast at random spots in the forest (Heinrich 1988a).

VOCAL PLAY. From BH, unpublished. Young birds, from a week before fledging to at least 4 mo after fledging, may engage in monologues that last for many minutes to ≥1 h. This behavior occurs in some
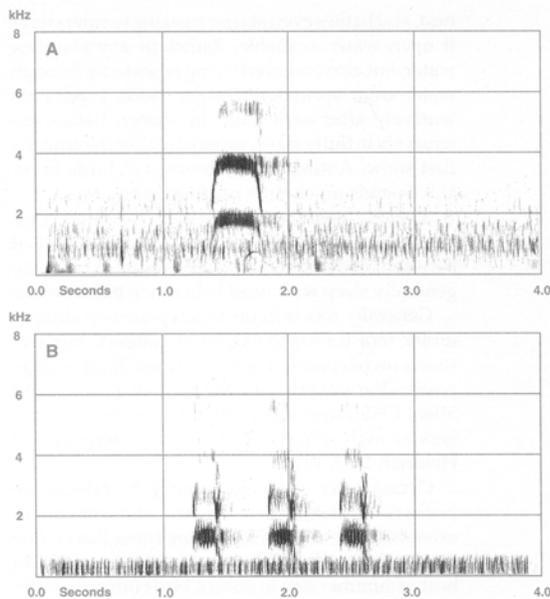
Figure 2. Vocalizations of the Common Raven. A. Yell Call by juvenile. B. Demonstration call by an adult. Recorded in Maine by BH.

individuals as early as 1 wk before they leave the nest and is especially common in the first few months after leaving the nest. Typically, the bird goes through a repertoire of sounds similar to babbling and gurgling with rapid changes of pitch and volume from whisper to high volume. Also observed in older birds that have been maintained as a group in an aviary, immediately after they were released. It occurs then both in the released birds and in single birds remaining in their previous enclosure. The song includes elements of many of the birds' other calls.

Predatory Alarms. Birds in crowds at no time give an alarm call when a human disturbs their feeding at a carcass. However, they give at least 2 kinds of alarm calls when disturbed by humans at the nest. One is a deep, long, raspy grating sound that is also given by aviary birds when they confront for the first time an animal or other unknown object. The second is a rapid series of short high-pitched *keck-keck-keck* calls, which is sometimes given by aviary birds when a raptor flies over (BH).

Demonstrative Calls. Demonstrative calls (Fig. 2B), universally diagnostic of the raven, are loud and can generally be heard for 1–2 km. They are given in the apparent context of advertising one's location or territory occupancy, because they are especially elicited when other ravens are giving

similar calls in the distance yet they do not attract these others. Typically these calls, always given in a series of several identical repeats, are given in the morning, especially in or before the breeding season by the resident adults, or in pairs in an aviary. The most common call is a long (about 1 s) undulating call with an upward inflection. Birds appear to give this call spontaneously after scanning into the distance. Another is a ripping-rasping *rrock, rrock, rrock* or *calk calk calk calk* call most commonly given as a response to other ravens flying over or one calling in the distance, almost always in series of 3–4. Both calls are given by males and females. Presumably these calls function as territorial advertisement calls that keep others away. Also called Deep-Croak (Bruggers 1988), "gro"-Laute and general Kontaktlaute (Gwinner 1964), *Koww* and *Kowah* (Brown 1974), *Cawlup* and *Caw* (Dorn 1972, Conner 1985), *Croake* (Bent 1946), *quork* (Heinrich 1988a), and *Crroak* (Harlow et al. 1975).

Knocking. Ravens give a rapid percussion-like type of call that sounds like a woodpecker drumming or a stick thrust in a spinning bicycle wheel. Typically about a second long, it consists of a dozen or so notes with the final "percussion" of a lower pitch than the first, and it is commonly followed with a bill snap. A second knocking call consists of just 2 knocks in rapid succession, and a third call is of 3 knocks. The knocking calls are given only by females, and at any time of year after about the first year of life. In a captive group, only the dominant females knocked. When the dominants were removed, the subordinate female began knocking (BH). There appears to be geographic variation in this call (BH).

Comfort Sounds. A variety of soft quiet calls given by nestlings after they have been fed, and in pairs when they are next to each other, especially during allopreening.

Chase Calls. Short, choppy, high-pitched calls given in birds being chased during trespass into domains of adult residents.

Mimicry. Given the great variety of calls ravens make, it is easy to assume some of them are mimics of other sounds. For example, the knocking sounds of European ravens were first described as mimics of the mating calls of the European White Stork (*Ciconia ciconia*). A doglike whine would appear to mimic a dog, yet aviary birds who have never been in contact with a whining dog perform a doglike whine. In 5 yr of observing birds in the wild and birds raised with others of their kind in captivity, no unambiguous voice mimicry has ever been observed (BH, *cf.* E. Gwinner in Bruggers 1988). However, birds reared in isolation can be taught to mimic a variety of sounds, including to say "nevermore" (Heinrich 1989).

Social context. In a contextual analysis of raven communication, calls were shown to indicate more about what was not going to happen next than they did about what was going to happen next. Vocalizations also tended to inhibit behaviors of receivers rather than elicit behaviors (Bruggers 1988). In captive ravens, the presence of superiors suppressed all calling, but when the dominant one was removed, the next dominant bird would begin calling. See Vocal array, above, for more on social context.

NONVOCAL SOUNDS

The sex-specific displays of both males and females and some agonistic interactions between males often incorporate bill snapping. *Wissh* and *wheeewhoo* sounds generated by the wings sometimes accompany aerial displays (Brown 1974).

BEHAVIOR

LOCOMOTION

Walking, hopping, climbing. Normally walks on ground, rarely hops.

Flight. Liquid, even wing-beats when on long-distance travel. May circle and soar with immobile wings. When sighting something on the ground, characteristically slows down by rapid "back-pedaling" of wings. In general, flight is more erratic and consists of more soaring than that of American Crow, with which it is most easily confused.

Dives and rolls by tucking both wings in; dives and turns by tucking one wing in; turns loops and accelerates with short choppy wingbeats. Aerobatic rolls have been seen in as many as 16% of observations of individual flying birds (Van Vuren 1984). Sometimes makes half-rolls onto back (95% of recorded rolls), occasionally makes full rolls (3%) and double rolls (1%). Aerobatic rolls may serve a socialization function (dominance or courtship display) but are performed throughout the year by solitary individuals and by birds in large flocks and small groups (Dorn 1972, Van Vuren 1984). Observed flying upside down for as far as 1 km (Evershed 1930, Tåning 1931).

SELF-MAINTENANCE

Preening, head-scratching, stretching, bathing, anting, etc. Preens at all times of year. Scratches head by bringing one foot up between wing and body. Stretches by rising on one leg and extending opposite wing and foot, simultaneously clenching the wing in its foot. Tendency to bathe is not related to presence of dirt or temperature, but to other birds also bathing and time since last bathed (BH). Bathes vigorously in water several days out of the nest, and bathes even at near freezing temperatures if open water available. Bathes in any standing water, but also observed flying repeatedly through water from sprinklers (Jaeger 1963). Preens extensively after each bath. In winter, bathes extensively in fluffy snow, especially after the winter's first snow. Anting never observed in birds in ne. U.S. Spends much time panting on hot days.

Sleeping, roosting, sunbathing. Nestlings commonly sleep with head held back and tucked between feather tracts on back. Adults in captivity generally sleep with head held down but forward.

Generally roosts in protected places on cliffs or under roof (in captivity), or in conifers, but also roosts on telephone poles and wires, high-tension power-line towers, and the ground (Young and Stiehl 1981, Engel 1988). Often roosts in large numbers at night (Engel et al. 1992, Cotterman and Heinrich 1993, WIB).

Occasionally observed sunning by raising the feathers on head, neck, breast, and rump and extending one or both legs. Sometimes lies on one side and extends the upper wing (Dorn 1972). In heat of summer day in desert, birds often partially lower both wings and pant, presumably to cool off (WIB).

Daily time budget. Adults, subadults, and juveniles spend >45% of their time year-round resting or perching (Engel and Young 1992b, Knight et al. 1993, Sherman 1993, Knight 1994). Perches on power-line towers, telephone poles, trees, sign posts, and the ground. Tends to feed most in the morning and afternoon and rest or fly more at mid-day, although pattern varies some among seasons (Engel and Young 1992b, McKernan 1992b, Sherman 1993). Night feeding unknown, but occasional changes in roost sites within a night occur (Engel et al. 1992, Cotterman and Heinrich 1993). Seasonal differences in time budget expected to reflect changes in resource availability, weather conditions, and breeding activity, but no data to test these hypotheses.

AGONISTIC BEHAVIOR

Physical interactions. Members of a territorial pair may chase conspecific intruders for several kilometers or, if the intruders remain in the area because of food, for many minutes, and social soaring may ensue. Fights can become extremely vicious, involving grabbing, pecking, and biting, and have even been known to result in death (Craighead 1979). If many intruders are present, chasing eventually ceases. Agonistic interactions at food may also involve grappling with the feet, accompanied by loud vocalizations (Marzluff and Heinrich 1991). In birds that have developed a dominance hierarchy at a carcass, the physical interactions subside, and birds that have been

Figure 3. Common Ravens engaged in agonistic posturing. Photo by BH.

together in captivity for several weeks still signal their dominance but physical interactions are much reduced.

Communicative interactions. THREAT DISPLAYS. Agonistic behavior against intruders begins with loud calls, progresses to approach flight then escort flight, followed by vocal and/or postural threats, chases, and ultimately direct attack (Bruggers 1988). The highest level of dominance is displayed by slowly walking highly erect with bill pointed upward, fluffing out throat hackles and feather tracts above legs fluffed to create "pant"-like appearance, elevating "ear" tufts, and flashing white nictitating membranes (Fig. 3; Gwinner 1964, Jollie 1976, Heinrich 1988b, 1988c, Heinrich 1989). Wings are spread slightly at the shoulders. Both males and females engage in this behavior, but it is more pronounced in males. In captivity this display is given especially by dominant males when they are introduced to a group of other birds, and it is reciprocated by the most dominant male of that group. A grappling fight commonly ensues. Typical defense in flight is to extend feet and roll on side or back while approaching opponent. Following a settlement of the dominance dispute, these displays are rarely used, except in apparent self-aggrandizement to females (BH).

When feeding at carcasses, the dominant bird occupies the top of the carcass as well as favorite perches (in the aviary; Heinrich 1994b). The dominant may fly or hop to an occupied perch, as though the subordinate were not there, prompting the subordinate to leave. During these encounters dominants show sleeked-back head feathers, and they commonly spread their wings slightly at the shoulder so that the wing-tips cross over the tail, rather than lying parallel to it. Some interactions occur involving pecking, pulling tail or wing, and jumping on top of each other, usually lasting 1–2 s (Heinrich 1988c).

APPEASEMENT DISPLAYS. Subordinate birds pull their head in to their shoulders, rather than holding it up, and they fluff out their head feathers. If attacked, they duck down lower, fluff out their head feathers more, give appeasement calls, and sometimes roll onto their sides (Heinrich 1989, Heinrich et al. 1993). In a second subordinate display, the bird crouches, sleeks head feathers, rapidly vibrates tail, and droops wings (Jollie 1976, Heinrich 1988c). This "copulatory" display is also given by both males and females and is often given as a greeting (BH).

SPACING

Territoriality. Nature and extent of territory variable; in coastal California, where nest sites are fairly abundant and food resources are plentiful, defends relatively small (median = 5.1 km², $n = 5$)

territories (Linz et al. 1992). In many other areas, domains are larger (e.g., in Minnesota, 40.5 km^2 ± 10.2 SD, n = 9; Bruggers 1988), probably with active defense against adult intruders by single birds or very small groups (2–3 birds) only near the nest (Dorn 1972). Territorial defense is strongest during the breeding season but may also occur outside the breeding season (Knittle 1992).

On the open Arctic tundra, nests may be tens or hundreds of kilometers apart because nest sites (such as cliffs, Distant Early Warning radar towers, etc.) are limiting. In other areas, where nesting structures are in superabundance, neighboring raven nests have been reported within 300 m of one another (Steenhof et al. 1993, Dorn 1972). In a human-dominated landscape in the Mojave Desert of California, one pair of active nests were 70 m apart and others as close as 200 m (G. C. Goodlett pers. comm.).

Little information on establishment of territory. Maintenance involves threat displays described above. Defense is usually only against individual adults and small groups. Territory holders often stay out of sight in presence of flocks (Dorn 1972), perhaps to avoid intraspecific nest predation.

Interspecific aggression near nest shown toward some species, probably nest predators, e.g., American Crows, Red-tailed Hawks (*Buteo jamaicensis*), Prairie Falcons (*Falco mexicanus*), Gyrfalcons (*F. rusticolus*), but no evidence of true interspecific territoriality beyond immediate vicinity of nest.

Breeding pairs are thought to occupy and defend territories throughout the whole year, but no evidence that they defend boundaries during winter (e.g., Dorn 1972). At times, they do stray widely in search of food. The resident pairs from several territories may feed at the same carcass located near one nest site, provided they are camouflaged or shielded amongst crowds of vagrant juveniles (BH). Pairs commonly arrive from afar flying very high. In the Mojave Desert they often feed at landfills or other sites, sometimes with many other ravens, but often return to the vicinity of their nest to roost during the day and night (WIB).

Groups of ravens in captivity establish linear dominance hierarchies. In these hierarchies, the lowest ranking birds rarely interact with the highest. Most interactions are between birds of near-equal status, especially the high-ranking birds. Physical interactions are most intense when high-ranking birds first meet. Physical interactions soon subside, but dominance is still displayed by frequency of (numerous) vocalizations, body posture, and feeding and perching postures (as mentioned above). In aviary, friend or mate of dominant bird feeds near dominant and is shielded from aggression of others (BH).

Individual distance. In captivity, members of a pair commonly perch within a centimeter of each other, although huddling has not been observed. In communal roosts, birds may perch in direct contact with each other (WIB).

SEXUAL BEHAVIOR

Mating system. Apparently monogamous, but no data from studies with marked birds, no paternity studies; 5 observations of extra-pair copulations (Marzluff et al. 1995).

Pair bond. Dominance or Self-aggrandizing Display of male (Gwinner 1964, Heinrich 1988a) may also be a sexual display. Additionally, male generally holds more erect posture near female. In direct display to female, also fluffs out head, bows to female while spreading wings and tail, flashes white nictitating membranes, makes gurgling or choking sounds, and snaps bill. Aerodynamic flights, including dives and rolls, could serve to attract mate, but role not known (Brown 1974). Female displays fuzzy fluffed-out head, while making knocking calls and flaring the tail and spreading the wings. Both female and male displays given all year long, and by paired juveniles at least 2 yr before first nesting. Males are extremely vigilant during the breeding season, especially during the egg-laying phase, but function of vigilance is uncertain.

Two captive males formed a pair bond for 2 yr, during which they both built a nest and allopreened each other, even in the presence of females. Much fighting occurred during the "egg-laying" period, but this did not break up the pair (BH).

Not much of a display associated with copulation. Male edges up to female performing Gurgling and Choking displays, female crouches, vibrating wings, and male mounts (Gwinner 1964, BH). Sometimes Precopulatory Display includes allopreening and jumping immediately prior to copulation, and Postcopulatory Display involves aerobatic flights and a "musical, vibrating call" (Wilmore 1977).

DURATION AND MAINTENANCE OF PAIR BOND. Members of marked territorial pairs generally stayed together year-round, usually roosting near each other at night (WIB). In captivity, members of a pair frequently preen each other. Solicit preening by holding still and bowing head to be preened on back of head, or holding head back to be preened on throat. Birds often also hold each other's partly open bill and sometimes each other's foot.

Allopreening also occurs in temporary juvenile pairs. Among groups of nonbreeding birds in captivity, preening partnerships develop. These are seldom monogamous, but clear favorites are shown. Partner leaves if released, but not in mated adult pair. In feeding crowds, arriving birds also

commonly come in twos. Apparent pairs also observed in play flights of wandering juveniles. Preening and apparent temporary pairing at all times of year.

Extra-pair copulations. Observed at 5 separate nests in Idaho, immediately after male left female at nest, suggesting nest was under surveillance (Marzluff et al. 1995). No DNA fingerprinting data are available to confirm.

SOCIAL AND INTERSPECIFIC BEHAVIOR

Degree of sociality. Usually either solitary or in pairs; pairs stay together year-round (Jollie 1976). Occasionally trios (of unknown relationships) may associate loosely throughout the year (Dorn 1972) including at the nest (BH). Nonbreeders are solitary, but gregarious at carcasses and other concentrated food sources, and they sleep in communal roosts where they recruit each other to food bonanzas (Heinrich 1988b, Marzluff et al. 1996). "Aerial assemblies" develop where considerable aerial displaying is often performed (Dorn 1972).

Often forages in crowds, particularly juveniles and nonbreeders (Dorn 1972, Stiehl 1976, 1978, Jollie 1976). Individuals within feeding (and hence roosting) crowds are not more closely related than are individuals from among flocks (Heinrich et al. 1994, Parker et al. 1994, Heinrich and Marzluff 1995). Crowds form throughout the year, probably depending on seasonality of different food resources. Juveniles may form feeding crowds to overwhelm defensive adults at concentrated food sources (Heinrich 1989, Marzluff and Heinrich 1991) and in Maine use a characteristic Yell Call to attract others before eating. Not all crowds form to exploit food sources (Brown 1974).

Communal nocturnal roosts often form, generally in trees or on telephone poles and high-tension power-line towers, near food; size and duration of such roosts may be related to size of the carcass or other food source. In Maine, when winter food consists mainly of deer carcasses, roosts may number 50–100 birds and last ≤1 wk (Heinrich 1988b, Marzluff et al. 1996). In w. North America, where grain is a primary food, roosts may include >2,000 birds, can last months or years, and can be >21 km from the food source (Engel and Young 1989a, Watts et al. 1991, Engel et al. 1992, Littlefield and Ivey 1994). Roosts are occupied mainly in fall and winter (Dorn 1972, Temple 1974, Harlow et al. 1975, Stiehl 1981, Watts et al. 1991), but use of roosts at other times of the year is not uncommon (Brown 1974, Engel et al. 1992, Littlefield and Ivey 1994). Watts et al. (1991) found a positive correlation ($r = 0.88$, $p < 0.001$, df = 125) between windchill factor and number of ravens at a winter roost on the Hudson Bay in Churchill, Manitoba.

Birds typically collect at a nearby staging area (up to 1 km away), then depart for the roost site in groups around sunset (Cushing 1941, Stiehl 1981, Young and Engel 1988, Engel et al. 1992), but time of arrival may be affected by weather conditions (Young and Engel 1988). Departure from the roost site is generally near dawn and the entire roost may leave as a group, often after a group soaring display (Stiehl 1978, Cotterman and Heinrich 1983, Young and Engel 1988, Engel et al. 1992, Marzluff et al. 1996). Other times birds depart solitarily or in pairs (Stiehl 1976). More typically, however, birds may wander and move from one roost to another (Young and Engel 1988, Engel et al. 1992, Heinrich et al. 1994).

Roosts serve as information centers for food, and naive strangers are readily accepted into roosts and led to the food bonanzas used by that roost (Heinrich and Marzluff 1995, Marzluff et al. 1996). Although they likely contain individuals that know each other, they are more likely gregarious collections of birds joining the group to have access to food. The degree of sociality may vary with the durability of the food supply. In captivity, birds out of any one roost or feeding group that have been kept together for a month or more gradually reduce their aggression toward each other but become aggressive toward some strangers (BH). Solitary or paired adults may not join communal roosts and often roost at or near their nests, even outside of breeding season (Engel et al. 1992, WIB).

Members of flocks in captivity have killed conspecifics recently introduced to the flocks (M. W. Schwan cited in Brown 1974, BH).

Play. Diverse and complex, often involving inventive and learning behaviors: sliding down inclines on belly, lying on side grappling sticks, dropping and catching objects while in flight, hanging upside down by one or two feet, snow "bathing," giving vocal monologues, caching inedible items, playing "tug-of-war" or "king-of-the-hill" with other ravens, pecking predators on tail (Dorn 1972, Ficken 1977, Heinrich and Smolker 1998). All of these behaviors may have some ultimate function, perhaps relating to food acquisition and handling or mate attraction, but they are most common in young birds for whom the immediate function is often not evident.

Nonpredatory interspecific interactions. Interspecific interactions vary with experience. Ravens follow wolves and feed in their presence at their kills. They feed in the near presence of coyotes (*Canis latrans*) in Yellowstone and California (BH, WIB). They will eat from carcasses killed by Golden Eagle (*Aquila chrysaetos*), appearing at half of all rabbits killed by eagles (Marzluff and McKinley 1993). Anecdotal evidence suggests ravens may

even purposefully attract wolves and hunters to moose and caribou, presumably because they cannot kill and open large prey (Heinrich 1989). They feed at carcasses and landfills with coyotes but are clearly cautious of and subordinate to the canines (Dorn 1972, WIB). They have been observed fighting with a Canada Goose (*Branta canadensis*) over a piece of bread (Jefferson 1989).

Ravens are known to approach canids and large predatory birds on the ground from behind and yank on their tails. Tame fledglings engage in this behavior toward both cats and dogs. If a bird avoids a dog when pecking the dog's tail, it will become increasingly bolder and eventually attempt to peck it on the nose (BH). The exploratory behavior may be a mechanism of assessing the reactions and capabilities of animals that may be encountered later at food.

In Maine, ravens usually ignore Turkey Vultures (*Cathartes aura*) both in the air and while feeding next to them. Not seen to attack crows, but neither American Crows nor Blue Jays (*Cyanocitta cristata*) feed in the presence of ravens. But in Virginia and Nova Scotia, foraging ravens were dominant over American Crows; 1 raven would displace 3–11 feeding crows (Erskine 1968, Harlow et al. 1975). In Maine, however, crows chase ravens, but reverse rarely seen. Ravens not seen to mob owls, showed mildly aggressive behavior to Northern Goshawk (*Accipiter gentilis*) loitering near a feeding aggregation (Williamson and Rausch 1956, BH), but ignore Broad-winged Hawk (*Buteo platypterus*). Very aggressive toward Golden Eagles in w. U.S. and Alaska, except at food. Will tolerate presence of Red-tailed Hawks, Ferruginous Hawks (*B. regalis*), Prairie Falcons, and Golden Eagles in or very near night roost, but ravens usually keep their distance (Young and Engel 1988, Engel et al. 1992). Generally tolerant toward Peregrine Falcons and Gyrfalcons nesting nearby, sometimes as close as 12 m away, although the falcons sometimes chase them (Harlow 1922, Jones 1935, Murray 1949, White and Cade 1971, Smith and Murphy 1973). Ravens may nest near falcons to eat remains left by the falcons (White and Cade 1971). Finally, raven nests have been taken over by Great Horned Owls (*Bubo virginianus*), Red-tailed Hawks, Gyrfalcons, and Prairie Falcons (Wolfe 1929, White and Cade 1971, Smith and Murphy 1973, Smith and Murphy 1982, Steenhof et al. 1987). Gyrfalcons may depend on ravens for nesting structures (White and Cade 1971).

PREDATION

Kinds of predators. Predation of eggs unrecorded; predation at other stages rarely observed. Possible predators on nestlings include hawks, other Common Ravens, owls, and martens (*Martes amer-*icana). Likely predation of young by Great Horned Owl in Maine (BH). Golden Eagles may have destroyed and eaten "contents" of 2 nests in Idaho (Steenhof et al. 1987). In Wyoming and Maine, all nests that were near areas frequented by flocks of nonbreeding ravens failed and predation was suspected (Dorn 1972, BH). Peregrine Falcon (*Falco peregrinus*) seen swooping at just-fledged young in Vermont, but attending adult successfully defended the young (BH). Fledglings killed by Golden Eagle, maybe Great Horned Owl, and coyote in Idaho (Young and Engel 1988). Likely predation of adult ravens at food by a coyote (BH) and Golden Eagle or Great Horned Owl in Idaho (Young and Engel 1988). In Greenland, freshly eaten raven (age unreported) remains were found beneath a Gyrfalcon nest (Jenkins 1978).

Response to predators. Vigorously chased Golden Eagle and Gyrfalcon until at least 3–4 km away from nest with young in Alaska (BH). A group of ravens in Maine flew only mildly at, then ignored, a Bald Eagle (*Haliaeetus leucocephalus*) in Maine. Ravens readily attack Turkey Vultures, Golden Eagles, large hawks, and American Crows near the nest (Harlow 1922, Dorn 1972, Smith and Murphy 1973, Jollie 1976, Williams 1980, Dawson 1982, McNair 1988).

Captive ravens flush from food in response to aerial predators (Marzluff and Heinrich 1991). Sentinel ravens have been reported giving "alarm" calls (Farrell 1989), but BH has never observed this in his many stealthy approaches to feeding crowds of ravens.

Birds usually sneak away quietly when humans approach a nest with eggs (Dorn 1972, WIB). When humans approach nest with nestlings, one of the adults commonly gives rapid high-pitched *kek-kek-kek*-like calls, usually while flying with shallow wingbeats and with head feathers fluffed out. When an intruder climbs tree or cliff to a nest, one or both of the parents may disappear, be heard only from a distance, or come in close, but they rarely dive at or attack. When they do attack, adult makes deep long rasping calls and commonly pecks branches; may snap off twigs (Dorn 1972, Heinrich 1988d), or dislodge rocks (Janes 1976) from above. Much variation in response among individuals, less within individuals (Dorn 1972, Hooper 1977). In Washington, weak nest defense is associated with presumably high levels of persecution by humans (Knight 1984).

Individuals are wary of new food, particularly unknown species of carrion; may take several days before they approach a new food item, doing so with much caution and often jumping back (Avery et al. 1993). May respond in this way for fear that carcass is actually a sleeping predator. Ravens would not enter a garbage pit at a landfill (Conner et al. 1975) until sentinel American Crows were in

position and other crows were feeding in pit. They flushed when sentinel crows intensified "caws," became alert when Blue Jays in nearby woods gave alarm calls, and flushed when ravens overhead gave alarm calls (Conner et al. 1975).
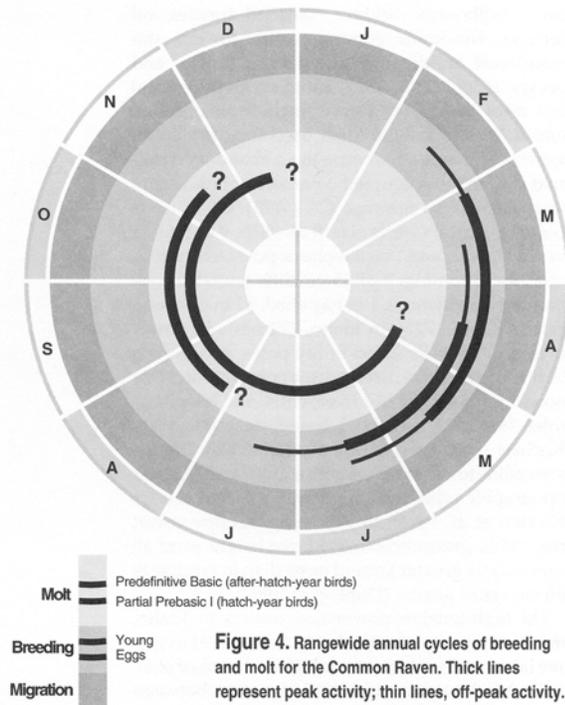
BREEDING

PHENOLOGY

Pair formation. No information on when pairs form. Considerable displaying, possibly courtship, occurs in flocks throughout the year, with greatest intensity in fall and winter (Jan and Feb; Dorn 1972, Conner et al. 1976, Heinrich 1989). Established pairs often stay together throughout the year (WIB), but no data (e.g., from long-term marking studies) to test the often-cited contention that ravens mate for life. In captivity, pairs may assemble within flocks in their first winter and stay together until they breed at 3 yr of age. Although pairs probably spend time on their territory throughout the year (*cf.* Dorn 1972), territorial occupation and defense becomes more apparent in late winter and early spring.

Nest-building. Nest construction or repair of old nest begins when territorial occupation becomes apparent or shortly thereafter, generally late Jan to mid-Apr. In Wyoming, one pair took 9 d; in Great Britain, average is 2–3 wk (Ratcliffe 1997). In Pennsylvania, egg-laying began 3–7 d after nest was completed (Harlow 1922).

First/only brood per season. Figure 4. Egg-laying dates vary considerably, but geographic pattern is unclear. Laying begins anytime between mid-Feb and late May, although most clutches are begun between early Mar and mid-Apr. Cold winters may delay breeding by a couple of weeks (Griffee 1937). Little synchrony in laying dates within populations (WIB) and considerable variation among years (Harlow 1922, Avery et al. 1993). In Wyoming, nests were begun earlier during a year with considerably less snowfall (Dunk et al. 1997). In Oregon, nests closer to roads begin earlier than those of pairs that depend more on scavenging from hunter's camps and raiding waterfowl nests (Stiehl 1976). Few accurate data on hatching dates, but in most areas hatching, which is asynchronous (Hooper et al. 1975, Coombs 1978, WIB), likely occurs between early Apr and mid-May. Fledging typically occurs between mid-May and mid-Jun and juveniles stay on their natal territories for 1–6 wk or longer, probably depending on food resources.

Second/later brood(s). No second broods; may renest after failure in some areas (not in ne. U.S., BH). Three records of fall nesting in Great Britain,

Figure 4. Rangewide annual cycles of breeding and molt for the Common Raven. Thick lines represent peak activity; thin lines, off-peak activity.

but no information on prior breeding activities at those nests. One nest had a near fledgling in early Jan and 3 young chicks 3 mo later (Mearns and Mearns 1989).

NEST SITE

Selection process. No information. Nest sites are often used in consecutive or sequential years (see Nest, below) for many years (Tufts 1916). Possible individual preference for nesting substrate (e.g., some always nest in trees even when cliffs are available, and vice versa), but no data (Harlow 1922, Jollie 1976).

Microhabitat/site characteristics. Microhabitat highly variable. Nests in many microhabitats including sea cliffs, rock quarries, woodlots, isolated trees, rural and urban areas, along heavily traveled highways, and in remote wilderness—almost anywhere there are sufficient food resources and adequate substrate. May avoid nesting in wooded areas along river bottoms in Washington (Bowles and Decker 1930). In Wyoming, prefers forest edges and isolated stands of trees over forest interiors (Dunk et al. 1997) and tends to avoid areas with heavy human foot traffic (Dorn 1972).

Substrate highly variable. Typically nests in or on cliffs and trees, but also power-line towers, telephone

poles, billboards, bridges, railroad trestles, oil derricks, windmills, communication towers, and abandoned buildings (Harlow 1922, Bowles and Decker 1930, McBee 1937, Knight 1984). Unusual nest sites in Mojave Desert include abandoned automobiles, a satellite dish used for deep space communications, a barbecue in an abandoned railroad car, and an occupied commercial building in downtown Palm Springs, CA (WIB). Of 29 nests found in coastal California, 18 on cliffs, 9 in trees, 1 on power pole, and 1 on telephone pole (Avery et al. 1991). In Wyoming, 2 of 35 on cliffs (suitable rock faces are rare in area), 1 in hay shed, 32 in trees of 5 species (Dorn 1972). In Idaho, 272 nests in power towers, 17 on cliffs, 15 on utility poles, and 1 on an "artificial platform"; used power poles significantly more than expected and trees, cliffs, and telephone poles less than expected based on availability (Kochert et al. 1984, Steenhof et al. 1993). Prefers power-line towers in areas with significantly greater topographic relief than randomly selected towers (Kochert et al. 1984). In Wyoming, canopy cover, tree width, ground cover, and tree height were all significantly greater around nests than in randomly selected sites nearby (Dunk et al. 1997).

On high-tension power-line towers in Idaho, prefers tower types with sturdy design and extensive latticework (Kochert et al. 1984, Steenhof et al. 1987). Most pairs nested inside junction between top crossbar and legs of tower; none on specially made raptor nesting structures (Steenhof et al. 1993). Lattice towers probably provide more shade, greater cooling from wind, and security (anchoring) against strong winds (Knight and Kawashima 1993). Power-line towers may enhance success by providing cooler conditions in the desert environment (Steenhof et al. 1993).

Nest heights vary considerably; depend on height of nesting substrates in area. Typical cliff nests are on ledges; potholes; cracks; or caves 5–20 m high, two-thirds of the way up steep cliffs 8–30 m high; tend to avoid eastern exposure; usually have an overhang providing good cover. Tree nests vary in height from 3–21 m high in trees 5–30 m high. Nests are usually close to the top, in a crotch, but with some canopy covering the nest. An insufficient number of measurements are available to characterize sites of nests on nonnatural substrates.

NEST

Construction and composition. Details of nest-building process not well known. Female apparently does most construction; male assists by bringing sticks to the nest (Harlow 1922, Jones 1935, Stiehl 1985) or performing some of the construction (Gwinner 1964, BH). For the base, large sticks about 0.9 m long, ranging in diameter from 3 to 25 mm are broken from living plants or taken from old nests, but rarely taken from large numbers of sticks that have dropped on ground beneath a nest. Ravens are not choosy about species of plant used, and sometimes they use bones and wire in base. Sticks are loosely placed on platform or wedged into crotch of tree, then woven into a rough basket. A cup is woven from smaller branches and twigs of many species of plants. Bottom of cup is sometimes lined with mud, sheep's wool (2.3 kg found in one nest; Johnson 1899), fur from many species of mammals, shredded bark, grasses, and sometimes rags or paper. An unpleasant odor often permeates the nest (Job 1898, Murray 1949). Nest took 9 d to build in Wyoming (Dorn 1972).

Dimensions. Vary in part with size of platform on which nest is built (Stiehl 1978). Often asymmetrically shaped. Base measures 40–153 cm diameter by 20–61 cm high. Cup measures 22–30 cm diameter by 13–15 cm deep.

Microclimate. Cliff nests usually under rock overhang, and tree nests tend to be high but below canopy. Nests in power-line towers are usually exposed to the elements.

Maintenance and reuse. No long-term studies to determine if the same birds return to the same nest site, but circumstantial evidence suggests they do. First, although nests in trees and power-line towers sometimes do not survive the winter, they are often reused or rebuilt on the same or nearby structure, and sometimes on the same spot. In Idaho, 48 of 72 (67%) nests present in one year were still present and reused in the next, and 74 of 81 (91%) birds nested in the same nest or tower, or within two towers of a previous year's nest (Steenhof et al. 1987). Nest sites of some identified individuals are 12 km apart in different years (Hooper et al. 1975), although usually the birds tend to nest within 0.5 km of previous nest in successive years, before switching back to the original site. Many territories have multiple nest sites, with remains of previously used nests often present for years. Sometimes birds alternate between sites from year to year. Switching nest sites between years does not appear to be related to success of nest, but may relate to condition of the prior year's nest (Stiehl 1978, Steenhof et al. 1987).

Nonbreeding nests. In Oregon, males sometimes "guarded nest" from a nearby shallow (5 cm) platform of large sticks (Stiehl 1978). In California, two areas, one on a water tank and 1 in several Joshua trees (*Yucca brevifolia*), had 5–20 small, poorly constructed raven nest-like structures (no other corvids occur in the area). Some of these structures in Oregon and California may have been prior years' nests or false starts.

EGGS

Shape. Ovate, elongate-ovate, cylindrical-ovate (Bent 1946).

Size. Mean 44.0–52.3 mm by 30.7–36.2 mm. Mean egg size may be largest in *C. c. principalis* from Alaska (51.2×34.6 mm; n = 4 clutches), intermediate in *C. c. prinipalis* from e. North America (48.4 × 32.8 mm; n = 18 clutches) and *C. c. sinuatus* from w. North America (48.3×32.4 mm; n = 22 clutches), and smallest in *C. c. sinuatus* from w. Mexico (47.2×32.0; n = 20 clutches); but the differences may not be statistically significant (L. Kiff pers. comm.). The observation that there may be clinal variation in egg size needs substantiation (Harlow 1922, Ratcliffe 1997).

Mass. No data for North America. Mean = 30 g (no variance estimate provided) in Great Britain (Ratcliffe 1997).

Color. Variable. Ground color of greens, olive, to pale blue and blue. Variously blotched, dashed, mottled, lightly scrawled, smeared, splotched, spotted, streaked, and striped with dark brown to drab brown, greenish brown, olive brown, lavender, or purplish. Some without markings. Females lay similarly patterned and sized eggs year after year (Harlow 1922).

Surface texture. Smooth.

Eggshell thickness. Not reported.

Clutch size. Average clutch size in North America = 5.4 ± 0.42 SD (range = 3–7, n = 7 study areas). See Demography and populations: measures of breeding activity, below.

Egg-laying. In Wyoming, egg-laying begins 5–6 d after nest completion (Dorn 1972). In the Pacific Northwest, after a 2-d break following laying of the first egg (Stiehl 1978), subsequent eggs laid every 24 h (Bowles and Decker 1930, Stiehl 1978, Stiehl 1985). Parental attendance and copulation most frequent at time of laying of first egg. Five extra-pair copulations observed; defense of female by male was not always successful, intruder usually entered when male was absent, and the female did not always fight off the cuckolder (Marzluff and McKinley 1993, Marzluff et al. 1995).

Clutches are replaced within 2–3 wk if lost early in the season (Harlow 1922, McBee 1937, Stiehl 1978, 1985). In Idaho, replacement clutches had significantly fewer eggs (5.6 vs. 4.9) and were not always successful (Marzluff et al. 1995). Occasional third clutches recorded (Dickey 1915). Fledging success of nests having eggs removed experimentally (n = 4) was not significantly lower in the following year compared to success of control nests (Marzluff et al. 1995).

INCUBATION

Onset of broodiness and incubation. May begin incubating with laying of first or second egg (Stiehl 1978, Stiehl 1985) or may just cover, but not incubate, for first few days (Gwinner 1965).

Incubation patches. Common practice is to sex by presence of incubation patch in females, but no data on presence or absence in known males.

Incubation period. Usually incubates only at night until all eggs are laid, but in snowy weather will sit on nest all day leaving only briefly to feed (Harlow 1922). Incubation period 20–25 d (Harlow 1922, Dorn 1972, Stiehl 1976); in Oregon, average is 20.9 d ± 1.16 SD (n = 36; Stiehl 1985).

Parental behavior. Female generally does most of incubating (Gwinner 1965, Dorn 1972, Steenhof and Kochert 1982; but see Tyrrell 1945 and Conner et al. 1976), although no intensive studies have been conducted with marked wild birds. In aviary, male sometimes incubated in the first week (BH). Male often stands guard while female incubates, feeds female, and incubates in cold, stormy weather when female leaves to feed (Harlow 1922, Jones 1935, Stiehl 1978). Female assists in intra- and interspecific nest defense; leaves nest for about 10 min twice / 10-h period early in incubation, and up to five times / 8 h late in incubation (Stiehl 1978, 1985).

Hardiness of eggs. No data.

HATCHING

Preliminary events. No data.

Shell breaking and emergence. Eggs hatch asynchronously, presumably beginning with first egg laid (Hooper et al. 1975, Conner et al. 1976, Stiehl 1978); generally ≤1 d apart (Dorn 1972). Often 1 egg fails to hatch (Stiehl 1985).

Parental assistance and disposal of eggshells. Adults may eat unhatched eggs (Stiehl 1985, BH). No data on disposal of eggshells.

YOUNG BIRDS

Condition at hatching. At hatching, chicks are orange to pink, unfeathered or covered very sparsely with gray down, and sightless (Dorn 1972, Stiehl 1978, Conner 1988, WIB, BH). Nestlings have pale blue irides, which change to gray within 2 mo. Hard palate, soft palate, tongue, and mouth lining are all deep pink to red (Kerttu 1973). Respond to parents call on first day (BH). Do not respond to observer's calls until 3 d of age (Stiehl 1978).

Growth and development. Look like "grotesque gargoyles" (Tyrrell 1945), with small patches of gray down on otherwise featherless body; in Virginia, 7 cm long when about 4 d old. At 1 wk still naked and 11 to 12 cm long. By 2 wk, crouch and remain silent when approached; pink and covered with black down, feather sheaths for rectrices 1 cm long, eyes with smoke-gray irides beginning to open between days 12 and 14; body length 20 cm.

Figure 5. Adult Common Raven at its nest with young. Photo by BH.

On day 18, 1-cm-long flight feathers extended from 2-cm-long shafts. At 3 wk, down well grown, wing and tail feathers present, unable to stand up. At 4 wk young are covered with contour feathers, and they sometimes respond defensively and move about nest. At wk 5, young fully feathered, exercising wing muscles, and becoming very active. At 5–7 wk, they leave nest but stay nearby for a few days (Tyrrell 1945, Conner et al. 1976, Stiehl 1978, Williams 1980, Stiehl 1985, Conner 1988). Young give harsh, crow-like *cawr* from nest and out of nest until about 6 mo old (Harlow 1922; see Sounds: vocalizations, above). Analysis of growth in 6 chicks (2 wild, 4 captive) in New England showed slow increase from about 25 g at day 1 to 268 g ± 87.7 SD at day 9, followed by a greater increase to 1,093 g ± 95.7 SD at day 24 (BH). Growth leveled off by day 30 (mean 1,179 g ± 148.4 SD) followed by a decline, but measurement becomes unreliable after 30 d because of birds' activity.

In Oregon, 7 of 214 young had abnormalities of the feet or bill. Five from one nest had gross foot abnormalities that prevented perching or eating; none fledged. Two young from different nests had malformed beaks and died around day 20–25 (Stiehl 1985).

PARENTAL CARE
Brooding. In Tennessee, both parents brood nearly continuously during first few days after hatching (Williams 1980). At two nests in Idaho, adults at nest an average of 100.3 min/d ± 158.3 SD (range = 8.4–421.6, n = 6 d), and time reduced drastically from beginning to end of nestling period.

Very little brooding after day 25–28; 30 min at nest on day fledging began. Visits lasted an average of 114 s, but 152 of 314 lasted <15 s. No relationship between nest attentiveness and temperature or rain. Female made 58% of visits and 72% of the maintenance visits, and did all of the brooding. Adults visited nest 64.2 times/d ± 23.4 SD (range = 36–102, n = 10 d; Steenhof and Kochert 1982).

Feeding. Both parents feed young; in n. Canada, male did most feeding of nestlings and mate during chicks' first 2 wk (Bruemmer 1984; see also Harlow 1922, Dorn 1972, Stiehl 1976, McNair 1988).

In Tennessee, adults fed nestlings of undetermined age 5 times in 35 min (Williams 1980). At one nest in Wyoming, food was brought once in 1.5 h at 1 wk old (Dorn 1972). In Vermont, parent usually brings enough food each visit for 2–3 young chicks or 1 older chick (BH).

In Idaho (Steenhof and Kochert 1982), feeding visits made by pairs 50.9 times/d ± 13.7 SD (range = 35–72, n = 2 pairs), and did not vary much through season; no apparent relationship between feeding frequency and time of day or nestling age. Number of feeding visits/nestling/d did not differ between 2 nests (14 visits/young/d at nest with 4 chicks, and 13 visits/young/d at nest with 3 young). No significant difference in apportionment of food among individual young. Male and female made equal number of feeding visits during first 15 d, then male made 32% after female stopped brooding, except on day of fledging, when male made 67%.

Nest sanitation. In Maine, parents of wild birds ate the feces of week-old chicks (BH); captive parents swallow feces of very young chicks (Gwinner 1965). Medium-aged young (2–3 wk old) defecate on rim of nest (Dorn 1972) or parents carry feces away (BH). Older chicks shoot runny feces over edge of nest (BH). Overall, in Idaho, parents cleaned nests on 34% of visits (Steenhof and Kochert 1982). As a result, nest and ground beneath are often heavily fouled with feces and food remains (Dorn 1972).

Carrying of young. None reported.

COOPERATIVE BREEDING
Observations of trios throughout the year, including breeding season, are not uncommon, but social relationships and interactions are rarely observed (e.g., Zirrer 1945, WIB, BH). In Oregon, 3 nests each with 3 adults of unknown identity (Stiehl 1976); in Minnesota, a juvenile from the previous year's brood stayed at the nest, guarded young when parents were foraging, and was fed by parents (Bruggers 1988).

BROOD PARASITISM
None reported, but sometimes accepted chicken eggs, which were white or painted red or green,

placed in nest (BH). Also accepted strange feathered young after first being aggressive towards them (BH).

FLEDGLING STAGE

Departure from nest. Leave nest at 4–7 wk of age when contour feathers lack visible sheaths and can fly short distances (Harlow 1922, Hooper 1977, Stiehl 1985, Conner 1988,). At a cliff nest in Wales (Warren 1955), young (several days before departure) rested or strutted on nest or cliff ledge preening, stretching wings and legs, and flapping wings excitedly. One bird did a short "tumbling drop" while flapping its wings for 1 m over a 60-cm drop. On its first flight, one bird stepped to the ledge calmly, exercised a short bit, took to wing, and both parents from a distance immediately joined the bird on semicircular flight, 300–400 m over the ocean. The bird flew steadily and well, but bounced on the landing. Two more fledged on the same day, one the next, and the last 2 d after the first. All birds fledged within 48–53 h of each other. By the fourth day after departure, the birds were flying well, and were flying all over the small island by day 5.

Association with parents. In Pennsylvania, unmarked young and adults stayed near nest for 1 wk before leaving the area family (Harlow 1922). In Virginia, unmarked juveniles reportedly stayed with parents through the winter (Jones 1933). In Oregon, unmarked fledglings stayed within 200 m of nest for up to 6 wk, being fed by parents regurgitating into gape or onto ground. At 4–5 wk after departure from nest, young began accompanying adults on farther flights. However, late nesters stayed very near nest for only 5–7 d and started following adults up to 500–800 m after about 10–14 d postfledging. Differences between fledglings from early and late nests were related to seasonal changes in food preference or availability (Stiehl 1985).

IMMATURE STAGE

Generally young become independent of parents by Jul or Aug, at which time immatures often join others at communal nocturnal roosts, sometimes with siblings (Dorn 1972, Knittle 1992, Marzluff and McKinley 1993, *cf.* Jones 1933).

DEMOGRAPHY AND POPULATIONS

MEASURES OF BREEDING ACTIVITY

Age at first breeding. No data from marked wild birds. Probably does not breed until age 2–4 yr (Jollie 1976). In captivity, successful breeding began in third (BH) and fourth year, although unsuccessful attempts in second year (Gwinner 1965, BH). Most

Table 1. Clutch size of Common Ravens, from various locations in North America and compiled from several studies throughout Great Britain. Data shown as mean ± SD (range, *n*).

Location	Clutch size	Source
Oregon	6.0 ± 0.8 (3–7, 45)	Stiehl 1978
Idaho	5.6 ± 0.16* (*n* = 10)	Marzluff et al. 1995
Utah	5.4 ± 0.34 (3–7, 14)	Smith and Murphy 1973
California	5.4 ± 0.64 (4–6, 25)	Avery et al. 1993
Great Britain	4.8 (*n* = 1,027)	Ratcliffe 1997
Wyoming	4.6 ± 1.25 (1–7, 33)	Dunk et al. 1997
Ontario	4.6 ± 1.1 (*n* = 73)	Ewins 1991

*SE.

individuals breed annually; but some, perhaps older, ravens occasionally skip a year (BH).

Clutch. Three to 7 eggs. One nest in Washington had 8 eggs (McBee 1937). Based on 200 nests in studies in 6 areas, average clutch size in North America is 5.3 ± 0.56 SD (*n* = 6 studies; Table 1). No geographic variation identifiable.

Zero to one clutch laid / yr.

Annual and lifetime reproductive success. Hatching success (no. of eggs hatched / no. of eggs): 69% and 71% in Oregon and Utah, respectively (Smith and Murphy 1973, Stiehl 1985). In Oregon, 71% of nestling predation occurred 1–14 d after hatch. Nest failures were from predation (20 of 85 total nest attempts), starvation (Avery et al. 1993, BH), human disturbance (Stiehl 1978), and falling from nest (Stiehl 1985).

Brood size (no. of nestlings / female) ranged from an average of 3.3 in California (Knittle 1992; *n* = 11) to 4.2 in Oregon (Stiehl 1985; *n* = 45; Table 2). The mean from among 4 studies in w. U.S.: 3.7 ± 0.38 SD (range = 3.3–4.2) nestlings / female.

Nest success (no. of nests with ≥1 fledgling / total no. of nests; Appendix 2) ranged from 58% in Wyoming (Dorn 1972) to 100% in Utah (Smith and Murphy 1973), with the mean from 6 studies in e. and w. U.S. 72.7% ± 16.78 SD (range = 58–100%).

Percentage of nestlings fledged = 80% in California (Knittle 1992), 74% in Oregon (Stiehl 1985), but can be highly variable among years within a given area (0–100% in Maine; BH).

Fledgling success (no. fledged / no. of eggs) was 47% ± 3.3 SD (range = 40.9–57.1, *n* = 4 yr) in Utah (Smith and Murphy 1973) and 31% in Wyoming (Dorn 1972).

Annual reproductive success (total no. fledged / total no. of nests; Appendix 2) ranged from 1.7 fledglings / nest attempt in Wyoming (Dorn 1972) to 3.1 in Idaho (Steenhof et al. 1993). Mean annual

Table 2. Brood size (number of nestlings per female laying) of Common Ravens from four locations in the w. U.S. Data shown as mean ± SD (range, *n*). (*n* = number of nests; SD and range = among years, except for California where SD and range were among nests in one year).

Location	Brood size	Source
Oregon	4.2 ± 1.7 (4.0–4.4, 45)	Stiehl 1985
Idaho	3.6 ± 0.44 (2.7–4.0, 104)	Steenhof et al. 1993
Utah	3.8 ± 1.03 (2.5–5, 14)	Smith and Murphy 1973
California	3.3 ± 1.27 (1.0–5.0, 11)	Knittle 1992

reproductive success from among 6 studies in e. and w. North America was 2.5 ± 0.48 SD (range = 1.7–3.1). In Virginia, ravens nesting above 580 m tended to have lower reproductive success (2.4) than those below (3.1). No estimates of lifetime reproductive success available.

In Wyoming, birds that nested earliest had the greatest reproductive success (Dunk et al. 1997). No geographic trends are evident in the data.

Number of broods normally reared per season. Zero to one.

Proportion of females rearing one brood. See Annual and lifetime reproductive success, above.

LIFE SPAN AND SURVIVORSHIP

The record life span for a banded, wild raven is 13 yr, 4 mo (Clapp et al. 1983). One captive may have lived for 80 yr (Ratcliffe 1997), and captive birds at the Tower of London reportedly lived for >44 yr (Heinrich 1989).

DISEASE AND BODY PARASITES

Nineteen species of insects representing 11 genera from 6 families (Calliphoridae, Cerato-phyllidae, Hippoboscidae, Histeridae, Oecophor-idae, Staphylinidae) in 4 orders (Coleoptera, Diptera, Lepidoptera, Siphonoptera) have been found in raven nests, but probably only the Siphonop-terans are parasitic (Hicks 1959, 1962). No other reports on parasites.

CAUSES OF MORTALITY

Exposure. In Saskatchewan, 2 (out of 5) nestlings in one nest died of exposure from a late severe snow storm (Kozij and Dietrich 1986).

Predation. See Behavior: predation, above.

Competition with other species. In Idaho, a clutch was lost when Red-tailed Hawks usurped a raven's nest (Steenhof et al. 1987). Vultures, eagles, crows, and magpies frequent carrion eaten by ravens and are thus probable competitors.

Human interactions. See Conservation and management: effects of human activity, below.

Other causes. Largest two hatchlings smashed an egg and stepped on and killed a newly hatched sibling (Dorn 1972). Wind blew some nests off of power-line towers (Steenhof et al. 1993). Six birds were struck by lightning while roosting on a wood power-line pole during an intense electrical storm in central California (G. Rathbun pers. comm.).

RANGE

Initial dispersal from natal site. In North America, very little information on natal dispersal. In Wyoming, young dispersed up to 15 km from nest to dump in Aug; one young was found 35 km from nest in Oct, then roamed widely throughout fall (Dorn 1972). In a study of 163 patagial-tagged ravens in Idaho, 4 birds banded in nest returned to "natal area to breed" (Kochert et al. 1983). In Wales, median dispersal distance for 47 birds marked as juveniles was 23 km and the maximum was 317 km (Dare 1986).

Fidelity to breeding site and winter home range. Few data from marked birds. Of 10 nests reused second year in California, 2 were by same marked pair as previous year, 4 by one marked member of pairs from previous year, remainder were unmarked birds (Knittle 1992). (See Breeding: nest, above.)

Dispersal from breeding site or colony. Little information available. In Idaho, retention in study area was twice as high for adults tagged in winter as for nestlings (Marzluff et al. 1995). Birds of un-specified ages banded in winter in Oregon were found (presumably within the same season, but the dates are not specified) as far as 480 km away in almost all directions but west. Subadult birds banded in winter in Maine were also found in all directions, including in w. New York State and Nova Scotia and New Brunswick, Canada (BH). Adults marked in winter in Oregon nested up to 150 km away (Stiehl 1978). Data from Bird Banding Laboratory show average (no range or variance provided) distance moved between banding site and recovery site was 59 km (*n* = 95) but varied with age (adults = 94 km, *n* = 79; imm = 10 km, *n* = 2; "nestlings and locals" = 67 km, *n* = 14; Mahringer 1970). One bird was found 320 km from where caught. In central Wales, 0 of 231 ravens marked when young were found breeding within a 470 km² study area (Davis and Davis 1984).

Home range. Home-range size estimates vary by an order of magnitude, perhaps reflecting regional differences or differences in resource distribution or population densities. In Minnesota (Bruggers 1988), home range size = 40.5 km² (range = 27.3–195, *n* = 9); however, an additional 13 birds were too nomadic to estimate home ranges, covering mini-mum areas averaging 1,252 km². Eleven of these nomads were nonadults (5 hatch-year, 6 second-

year); 2 of 9 sedentary birds were hatch-year birds. Sedentary juveniles apparently spent the entire time from Jul to Jan in the vicinity of a landfill. In coastal California (Linz et al. 1992), median home range of 12 nesters was 1.2 km^2 (0.3–4.4), with no difference between males and females; median home range for nonnesting ravens = 8.2 km^2 (range = 2.2–45.8, n = 5). Median home-range size for non-breeders in spring = 19.5 km^2 ± 7.8 SD (mean = 14.2, n = 5); for breeding males = 1.8 km^2 ± 3.9 SD (mean = 7.6, n = 6), females = 0.8 km^2 ± 1.1 SD (mean = 1.2, n = 8). In the Mojave Desert of California, 12 breeding ravens hunted live food an average of 570 m ± 707.3 SD (n = 99 bouts) from their nest.

Individuals often spend all day at one small site, leaving only to sleep at a distant communal roost. In such cases, home-range size depends on distance between foraging site and roost. In Idaho, for instance, average distance from roost to feeding site was 6.9 km (max = 65.2 km, no variance estimate was provided, n = 31 ravens, juveniles, subadults, and adults). Not all birds demonstrate clear home ranges. For instance, 96/142 sightings of tagged birds in Michigan were at trap site in landfill (distance = 0 km), 6 were within 0.8–8.8 km, and 38 other sightings were 3–147 km away; average distance moved was 27 km. Population on study area was in a constant state of change with considerable ingress and egress (Mahringer 1970). The situation is very similar in a human-dominated landscape in the desert of California (WIB). In Maine, nonbreeders wandered widely over >1,800 km^2 (Heinrich 1988b). Considerable wandering and variability among 10 radio-tagged ravens; in general, individuals moved farther from the trap site over a 6-wk period, after first staying at a site for a few days. Many birds left the area even when abundant food was available, maybe searching for mates and suitable territories (Heinrich et al. 1994). In Nova Scotia, marked birds, particularly nonadults, were infrequently observed at the same site on 2 or more consecutive days (Boersma 1978).

POPULATION STATUS

Numbers. Estimating densities of this species is made difficult by 3 features of its behavior: (1) during certain times of day or year many, but not all, ravens are attracted to irregularly dispersed resources (e.g., landfills, highways, towns), resulting in a distribution that varies from clumped to dispersed; (2) many individuals occur in communal roosts or large, sometimes wandering, groups, while others remain in pairs or alone during all or part of the day or year; (3) even solitary birds may wander quickly over large areas (see Home range, above) making it likely that birds will be counted multiple times or missed, particularly in rugged terrain.

Estimates of density of breeding pairs, which are usually based on active nests, reported as 1 pair/ 1.4 km^2 in Wyoming (Dunk et al. 1994), 1 pair/ 4.7 km^2 in coastal California (Linz et al. 1992), 1 pair/22–25.2 km^2 in Oregon (Stiehl 1985), and 1 pair/30.6 km^2 in Virginia (Hooper et al. 1975). All of these estimates, however, fail to include non-breeders, which may be numerous in some areas and at some times. Multiple-year surveys based solely on nest occupancy do not show great variation in density of breeding pairs between contiguous years (Smith and Murphy 1973, Stiehl 1985), but surveys that account for nonbreeders demonstrate larger year-to-year fluctuations (Pearse 1938, Mahringer 1970). Measurements of internest distances, another view of nesting density, also vary considerably, from <300 m (Dorn 1972, Steenhof et al. 1993), in rare instances to 9.6 km (Harlow 1922).

Another way to measure raven density is road surveys. Roadside estimates vary from 0.06 to 33.3 individuals/100 km of road (Conner and Adkisson 1976, Knowles et al. 1989); however, numbers vary greatly even within the same region; e.g., in the desert of California, one study found 0.06–32.2 ravens/100 km of roads (Knowles et al. 1989). It is difficult to extrapolate data collected along roads to areas away from major roads because road surveys are biased by the species' attraction to roadkills and garbage (Knight and Kawashima 1993). The distance ravens will fly each day to scavenge from the road edge is unknown. Furthermore, raven numbers along roadsides vary with traffic volume or road type (Austin 1971) and with number of associated linear rights-of-way (Knight et al. 1995). Raven numbers also vary between landscape types (Knight et al. 1993) and between highway edges, power-line corridors, and open desert (Knight and Kawashima 1993).

Trends. By early twentieth century, raven populations were apparently well below previous levels in many parts of North America; the species had disappeared from New England, mid-Atlantic states, much of the Appalachians, and from portions of the Midwest and prairie states (Harlow 1922, Jones 1933, Schorger 1941, Jollie 1976, Houston 1977, Eustis 1978, Sutton 1984–1985). Causes attributed included widespread use of poisons and baited traps, disappearance of American bison, deforestation, conversion of land to agriculture, and increases in American Crow populations (Jollie 1976, Houston 1977). There is no evidence, however, that raven populations had declined greatly or distributions retreated in the North or West.

The second half of the twentieth century saw numbers increase and the species reclaim parts of its previous range. In the 1950s, it began inhabiting

cities in Saskatchewan, losing fear of man, searching for scraps of garbage (Houston 1977). Likewise an increase in sightings in Massachusetts in the 1940s; by 1976, ravens had returned to the Northeast as farms returned to forest; in 1978, first nesting in a long time for Lower Peninsula of Michigan; and in 1984, the first raven was seen at Cape May, NJ, in 50 yr (Snyder 1950, Jollie 1976, Eustis 1978, Sutton 1984–1985). Since the late 1960s, populations increased throughout much of its range in North America; e.g., in the Central Valley of California, raven sightings along roads increased by >7,600% between 1968 and 1992 (Boarman and Berry 1995).

POPULATION REGULATION

Factors affecting population levels probably vary from site to site. In regions with harsh winters, access to carcasses or other clumped, unpredictable food sources may be a major limiting factor (Dorn 1972, Marzluff and Heinrich 1991, Dunk et al. 1994). In the spring in Idaho, nesting density was correlated with ground squirrel density (Steenhof et al. 1985). In some nonforested regions, nesting substrate may be important (White and Cade 1971, White and Tanner-White 1988); in such areas power-line towers or Distant Early Warning radar towers provide nesting opportunities not otherwise available to ravens. In Idaho, a high-tension power line was installed in 1980; 1 raven nested in 1981, 9 in 1982, and 39 in 1983, and twice as many by 1987. Numbers of nesting ravens did not decline in the surrounding area as a result of the towers (Steenhof et al. 1993).

CONSERVATION AND MANAGEMENT

EFFECTS OF HUMAN ACTIVITY

Shooting and trapping. Generally wary of people, probably for good reason; may have been driven out of S. Carolina—shot at in retaliation for allegedly killing newborn lambs; often shot at in other areas as well (Knight 1984, McNair 1988, WIB). In Greenland, often shot, boiled, and eaten by Inuks (Bruemmer 1984). In the past, and likely now, Pueblo Indians trapped ravens, probably to use feathers for costumes and ceremonies and bones for making tools and musical instruments (Emslie 1981). Birds have been shot in California, Maine, Michigan, and Wyoming (Mahringer 1970, Dorn 1972, WIB, BH). Two died in coyote traps in Michigan (Mahringer 1970).

Pesticides. No data available on pesticide impacts in North America. No significant decrease in egg weight recorded in U.K. 1950–1969; no significant eggshell thinning; levels of several organochlorine residues relatively low there (Ratcliffe 1970). After 8 yr of widespread poisoning of meat baits (for an unspecified purpose) in one part of Scotland, number of breeding pairs of ravens dropped by 70% and number of successful breeding attempts dropped by 85% (Weir 1978).

Ingestion of plastics, lead, etc. Plastic bag material often found in pellets in Maine and California (BH, WIB).

Collisions with objects. Several chicks died when they became entangled in latticework of powerline towers (Kochert et al. 1984), one broke a leg in a picnic grill in Maine and another died entangled in fishing line in nest (BH). In Idaho, one nestling became entwined in wire used as nesting material, two were electrocuted by power lines, and one by the transformer bank of an irrigation pump (Young and Engel 1988). Fledglings and adults were killed by cars in Wyoming (Dorn 1972).

Degradation of habitat. Logging may have helped cause a decline in raven numbers over a 2-yr period in Michigan (Mahringer 1970) and logging is blamed for the disappearance of ravens from parts of Virginia and Pennsylvania in the beginning of the twentieth century (Harlow 1922, Jones 1935). In w. U.S., degradation of native habitat is likely responsible for a marked increase in raven populations by providing an overabundance of anthropogenic food (e.g., garbage), water (e.g., irrigation), and shelter (e.g., billboards and bridges; Boarman 1993).

Disturbance at nest and roost sites. Some individuals are evasive and quiet when humans are at nest, others defensive and vocal. One very evasive pair nesting near a popular fishing site was unsuccessful at rearing broods in 3 yr of study and maybe in 3 prior ones (Hooper 1977). Breeders are more timid and avoid people more strongly in areas of moderate human density and high persecution (e.g., farmland) than in areas with low human density and low persecution (e.g., rangeland; Knight 1984). Height of nests did not differ significantly between areas <0.8 km and those >0.8 km from a dwelling, nor was fledging success at nests within 0.4 km of roads significantly different from success at more distant nests (Hooper 1977). Removal of eggs from one nest resulted in nest abandonment by parents in Oregon (Littlefield 1986), and concern has been expressed that they are so disturbed by activities around the nest that their existence in some areas is threatened by human encroachment (Conner et al. 1976). This concern is not supported by their abundance or their close reliance on human-provided resources in the West and elsewhere (Boarman 1993).

Human/research impacts. Many other aspects of human activities do not negatively affect ravens. Electromagnetic radiation is probably not a problem

for ravens (or other raptors), because nesting success was not lower on towers (Steenhof et al. 1993). Raven abundance along corridors correlate to numbers of contiguous linear rights-of-ways (LROW), perhaps because more biological needs are met along the more complex LROW (Knight et al. 1995). Presence of anglers did not affect the presence of ravens along a river, but there were more ravens present and on the ground when anglers were absent; when anglers were present, ravens shifted foraging time along river from early morning to late afternoon (Knight et al. 1991). Significantly more ravens occur (mean ± SE) along power lines (73.5 ± 228.9) and highways (36.5 ± 92.4) than in natural desert controls (6.6 ± 18.1) during the spring in the Mojave and Colorado Deserts of California (Knight and Kawashima 1993). Significantly more ravens were observed in late spring in urban-suburban (30.5/100 km, 1.87) and agricultural (18.4/100 km, 2.75) areas than in rangeland (5.5/100 km, 1.6) or control (4.2/100 km, 2.16) areas. Numbers were higher in those areas because landfills, roadkills, water, and nesting sites are more abundant (Knight et al. 1993).

No adverse effects of research activities other than the occasional injury or death related to use of radio transmitters (Kochert et al. 1983, Knittle 1992, WIB). Egg-collecting, however, may have been the most common cause of nest failure in Great Britain (Ratcliffe 1997).

MANAGEMENT

Conservation and pest status. Status variable throughout range. Listed as extinct in New Jersey and Alabama, Endangered in Kentucky and Threatened in Tennessee, and a species of special concern in New York and Connecticut. Species protected in U.S. by the Migratory Bird Treaty Act of 1918 and in Canada by the Convention between the United States of America and the United Mexican States for the Protection of Migratory Birds and Game Mammals, 50 Stat. 1311; TS 912. In some places, such as the Netherlands (Renssen 1988) and Tennessee (D. P. Anderson pers. comm.), numbers have declined severely (Hooper 1973, Conner et al. 1976), requiring captive breeding or translocation programs for recovery. In other portions of range, and more recently, populations have grown so precipitously that ravens are considered a pest species (see Demography and populations: population status, above). In many of these and other areas, rather than symbols of wilderness, they are indicators of high human disturbance, being closely associated with garbage dumps, sewage ponds, highways, agricultural fields, urbanization, and other typical signs of human-altered landscapes (Boarman 1993).

Adaptability, predacious habits, and ability to benefit from resources provided by human activities sometimes place this species in conflict with human interests. Can be an agricultural pest eating or causing damage to grains, almonds, pistachios, conifer seedlings, and other economically valuable crops (Putman and Zasada 1985, Salmon et al. 1986, Schmidt-Koenig and Prinzinger 1992); may cause damage to livestock by pecking the eyes out of calves and lambs (Larsen and Dietrich 1970, K. Stueber pers. comm.; *cf.* Hooper 1977) and eating turkey eggs (Lounsbury 1972). Conflicts with hunting interests by taking waterfowl eggs in wildlife refuges (Stiehl 1978, *cf.* Dorn 1972)

Predation may be harming several populations of Threatened or Endangered animals, such as the desert tortoise (Boarman 1993, Boarman and Berry 1995), California Condor (Snyder et al. 1986), Least Tern (Knittle 1992), San Clemente Island Loggerhead Shrike (*Lanius ludovicianus*; B. Everett pers. comm.), Snowy Plover (*Charadrius alexandrinus*; Page et al. 1995), and Sandhill Crane (Littlefield 1986).

May also cause economic damage to human structures and objects. In Idaho, where thousands of Common Ravens roost in power-line towers, contamination of insulators on 500-kV power transmission lines may cause power outages (Dorn 1972). In Shenandoah National Park and elsewhere, ravens turn over garbage cans and strew garbage about (Tyrrell 1945, BH, WIB). In California, ravens foul satellite dishes at the Goldstone Deep Space Site (F. Battle pers. comm.) and peel specialized radar absorbent material off buildings at China Lake Naval Weapons Center (C. Weiss, T. Campbell pers. comm.). They peck holes in airplane wings in Alaska (BH) and steal golf balls in Virginia (Hooper 1977).

Measures proposed and taken. To protect breeders in Virginia, Hooper (1977) recommended the following prohibitions: (1) no people within 200 m of visible nests and 100 m of hidden nests; (2) no vehicles within 100 m of nests; (3) no parking within 200 m of nests; (4) no road construction within 200 m of nests; (5) no overlooks above cliff nests; and (6) no rock climbing during the breeding season.

To reduce economic damage and harm to wildlife populations caused by ravens, measures proposed fall into 3 major categories: lethal removal, behavioral modification, habitat modification.

Lethal removal of Common Ravens has been proposed to eliminate known offending birds as well as to reduce the overall number of birds that may be causing problems. In 1989, a nontargeted program used poisoning and shooting to reduce raven predation on desert tortoises in California. Ravens were to be removed by injecting hard-boiled chicken eggs with DRC-1339 (a highly specific avicide with an LD50 for adult ravens of 5.6 mg/kg;

Larsen and Dietrich 1970) and placing them on raised platforms; 1,500 ravens were to be shot at a landfill and in several natural-habitat areas (Rado 1993a; see below for results). DRC-1339 has also been used to remove egg-eating ravens in Oregon (Larsen and Dietrich 1970, Littlefield 1986). The long distance movements of ravens recorded in Oregon led to concerns that poisoning ravens at one site could affect raven populations several hundred kilometers away. Also, presence of compensatory predation indicated that an integrated pest management program, involving management of several predator species, should be implemented (Stiehl 1978).

In Oregon and California, egg baits were treated with taste-aversion chemicals to keep potential egg-eating ravens out of nesting areas of Sandhill Cranes and Least Terns (Nicolaus 1987, Knittle 1992).

Probably the most effective way to reduce the negative effects of ravens is habitat modification, either to prevent their use of the imperiled resource or to reduce overall population sizes by reducing the carrying capacity of the habitat (Engel and Young 1992a). Antiperch devices have been recommended for use on power-line towers to prevent fouling of insulators (Young and Engel 1988, Steenhof et al. 1993) and on fence posts to prevent use of fences for hunting perches (Bureau of Land Management 1990), although most hunting is probably done in flight. Changing garbage disposal methods (burning garbage, covering garbage daily or more frequently, using self-closing dumpsters) and minimizing the amount of carrion in specific areas (Dorn 1972, Stiehl 1978, Boarman 1993) will reduce resources available to ravens.

Effectiveness of measures. In the California program to protect desert tortoises, mentioned above, 106–120 ravens were killed. Although the program was halted by a Temporary Restraining Order filed by the Humane Society of the United States after 7 d, numbers of ravens were considerably reduced at a landfill, but numbers returned to precontrol levels within 2.5 mo (Rado 1993b). An additional 49 ravens, most of whom were implicated as tortoise-eaters by tortoise shells found beneath their nests, were shot in 1993 and 1994 (WIB).

In Oregon, 124 ravens were killed with DRC-1339-laced chicken eggs and 13 more were shot. Sandhill Crane productivity and recruitment increased compared with precontrol years. Estimated egg loss to ravens was 7%, down from a 17% average, but overall predation rates were lowered even more from 48.8% to 27.5% when coyotes were also removed (Littlefield 1986, Paullin 1987). Active lethal removal of ravens over a 5-yr period failed to reduce the proportion of Least Tern eggs lost to

raven predation in California (Avery et al. 1993), and raven reductions in Oregon from 1937 to 1972, including destruction of all nests, did not increase productivity of waterfowl (Stiehl 1978). When coyotes and ravens were both removed, however, nesting success of ducks, geese, and cranes increased (Paullin 1986). Farmers report they have moderate to excellent success reducing raven consumption of their pistachios by shooting at offending ravens (Salmon et al. 1986). Removal of two depredating pairs of ravens early in the breeding season stopped predation on Least Tern eggs for the remainder of the tern nesting season (Knittle 1992). Chemical removal of ravens in Oregon greatly reduced raven abundance, blinding of ewes, and deaths of lambs (Larsen and Dietrich 1970).

Ravens rapidly learned to avoid eating surrogate Sandhill Crane eggs that had been injected with the illness-producing substance U.C. 27867. Predation ceased much more rapidly within occupied territories, thereby affording protection for the eggs from nonterritorial, nonconditioned birds (Nicolaus 1987). The same result was observed with methiocarb injected into surrogate Least Tern eggs (Avery et al. 1991, 1993).

Results of tests with captive ravens using various antiperch devices were ambiguous. Individuals perched on Nixalite needle tape, completely avoided perches modified with Roost-No-More paste, frayed steel cable, loosely strung rope, and wooden pegs, although there were significant design flaws that rendered suspect conclusions concerning the cable, rope, and pegs (Dorn 1972). When wooden pegs were applied to roost towers, birds moved to a different tower. Pegging and putting shields over insulators reduced contamination of insulators on towers tested (Dorn 1972). Compaction of garbage followed by effective cover with 15 cm of dirt fill reduced the numbers of ravens using a landfill (WIB).

APPEARANCE

MOLTS AND PLUMAGE

Hatchlings. Altricial and unfeathered; contrary to Forbush (1927) and Baicich and Harrison (1997).

Juvenal plumage. For information on Prejuvenal molt see Breeding: young birds, above.

In American populations Juvenal plumage described as brownish black with greenish and purplish gloss on wing and tail feathers (Dwight 1900, Heinrich 1994a); smaller feathers somewhat loose in texture and throat feathers not elongated (Forbush 1927). Description of Eurasian juveniles similar. Head sooty black with little or no purplish gloss. Neck through rump, vent, and shorter upper- and undertail-coverts dull, dark gray, feathers with

darker tips, paler bases, and without gloss except on tips of lower mantle feathers. Longer tail-coverts, wings and tail black with slight purple gloss on tail-coverts, and purple blue gloss on wing feathers. Feather wear causes wings and tail to become duller and pale feather bases to become more visible within several weeks or months of fledging (Cramp and Perrins 1994, Heinrich 1994a).

Basic I plumage. Prebasic I molt partial; in American populations molt occurs Jun–Oct and includes body plumage and 0 (approx. 54 %) to 2 inner greater upperwing-coverts, but no remiges or rectrices (Dwight 1900, Pyle 1997). In Eurasian populations this molt described as including head and body feathers (with scattered Juvenal feathers sometimes remaining on vent, scapulars, or tail-coverts, especially in northernmost populations), variable numbers of lesser and median upperwing-coverts (with fewer replaced in northernmost populations), and occasionally R1 or other feathers. New incoming black feathers may appear in juveniles before Juvenal wing is completely grown (Cramp and Perrins 1994).

Basic I plumage similar to Definitive Basic plumage, but in American populations, as plumage becomes worn, retained Juvenal remiges and rectrices become brownish and frayed (Kerttu 1973, Heinrich 1994a). Description of Basic I plumage in Eurasian populations similar. Adult-like except remiges, tertials, many wing-coverts, rectrices, and sometimes scattered body feathers retained from Juvenal plumage duller and becoming more brownish with wear than neighboring Basic I feathers. Tertials, primaries, and rectrices, with narrower (less rounded or truncate) tips than adult feathers. Head with slightly less gloss and more bluish gloss than adult, and underparts less black than adult, feathers often fringed paler creating pale pattern of scaling (Cramp and Perrins 1994).

Definitive Basic plumage. Definitive Prebasic molt complete; occurs during summer of second calendar year (Rea and Kanteena 1968), May–Oct (Pyle 1997). In Michigan, molt lasted from late Apr or May to mid-Dec. Primaries replaced in order from P1 to P10 with 4–6 d between start of molt of each feather. Each primary took 4 wk to reach maximum length. Molt of secondaries began with molt of primary 4 and followed the following sequence: S1, S8, S9, S2, S10, S7, S3, S4, S5, S6. Molt of rectrices began with molt of primary 3 in early Jun, ended in mid-Oct, and progressed from the inner to outer pair (Kerttu 1973). For detailed description of molt in Eurasian populations see Cramp and Perrins 1994.

Plumage entirely black with purple, bluish, and greenish gloss. Tail characteristically wedge-shaped in flight. Throat feathers lanceolate and elongated creating shaggy appearance. remiges and rectrices do not become distinctly brownish with wear as in immatures (Kerttu 1973, Heinrich 1994a). Sexes similar. Description of Eurasian adults similar. Entire plumage deep black, glossed with purple to purplish blue. Greater and primary underwing-coverts, and under surface of remiges and rectrices glossy brown-black. Bases of head and body feathers gray, becoming palest on neck and mantle. As plumage becomes worn, gloss becomes more bluish or bronzy, and dull black feather centers of under-parts visible with glossy feather margins showing as distinct dark scaling. Sexes similar but female average slightly less purple with more dull black feather centers showing (Cramp and Perrins 1994).

BARE PARTS

Bill and gape. In hatchlings hard palate, soft palate, tongue, and mouth lining are deep pink to red, gape flanges yellow, and bill flesh pink. Bill becomes gray by 10 d. Base of bill yellowish on juvenile but entirely black thereafter. Inner lining of mouth and tongue is typically pink in juveniles and black in adults. Transition from pink to black is variable and probably depends on age and social status; dominant birds can have black mouths in first winter, and subordinates' mouths can remain pink or mottled for at least 2 yr (Kerttu 1973, Heinrich and Marzluff 1992, Cramp and Perrins 1994).

Iris. Iris changes from light blue in hatchlings to gray in most fledglings to dark brown in adult. Brown color begins around pupil in Jul of first year then progresses outward. Completely brown iris probably attained after 2 yr (Kerttu 1973), although there may be geographic variation in ontogeny of this character (BH).

Legs and feet. Flesh pink at hatching, becoming gray by 9–10 d, and black with gray soles thereafter (Cramp and Perrins 1994).

MEASUREMENTS

LINEAR

Linear measurements (mm ± SD) of 145 adult, second-year, and hatch-year Common Ravens from the w. Mojave Desert of California (Edwards Air Force Base, Kern Co.; WIB unpubl. data): tarsus 63.1 ± 3.74; wing cord 398.4 ± 21.07; culmen (from posterior end of upper mandible at center to tip) 65.3 ± 4.12. Female generally slightly smaller than male; born out by linear regression and discriminant functions analysis (Bruggers 1988, Knittle 1992). Marked differences occur geographically; northern and eastern subspecies (*C. c. principalis*) considerably larger than southwestern subspecies (*C. c. sinuatus*) (Oberholser 1918, Willett 1941).

MASS

See Appendix 1. Males generally heavier than females and northern and eastern subspecies heavier than western subspecies. Captive birds were 7% heavier in winter than in summer in Alaska (Schwan and Williams 1978).

OTHER

CULTURAL SIGNIFICANCE

Ravens are important symbols for many cultures. In 1666, Mascoutin Indians from Wisconsin were seen with raven skins and feathers on their girdles (Schorger 1941). Several famous poems show the historic superstition Western cultures hold about ravens (Sprunt 1956). Folklore and superstition surrounding ravens may be caused partly by their ability to appear suddenly in the woods, then suddenly disappear (Zirrer 1945), or by their attraction to carrion, including human, thus associating them with war and death. For more details see discussions in Heinrich 1989, 1999 and Ratcliffe 1997.

INTELLIGENCE

Anecdotes of the reputed intelligence of ravens are legion (Heinrich 1999), but there are few critical tests. Presumably any behavior is the result of a combination of innate tendencies, learning, and the ability to understand or "see through" a problem in order to execute a novel solution. We know of only one critical test of the raven's ability to solve a problem not normally encountered in the wild (hence not having an innate solution), and not previously encountered (hence not shaped by learning). In this test, hand-reared ravens were confronted with meat dangled from a 0.7 m string (Heinrich 1995b). Some birds were unable or unwilling to get the food, while others successfully got it on their first try by pulling the string up to their perch where it was attached, then successively reaching down, pulling the string up, stepping on the pulled-up loop of string, reaching down again until the meat was grasped. A series of different experiments indicated that those birds that pulled up the meat also understood the functional connection to the food, while those that did not pull up the meat showed no such apparent understanding. We also know of one experiment that demonstrated that ravens may be able to count to 7 (Koehler 1951). Some individuals were observed to cut grooves into frozen suet to help break off large pieces of fat (BH).

PRIORITIES FOR FUTURE RESEARCH

Very little detailed information is available on some basic life-history parameters of this species (e.g., age-specific fecundity and survivorship). Understanding of geographic variation in genetic divergence, morphology, life-history parameters, and vocalizations remains woefully inadequate. Parasites and diseases are unstudied. The annual cycle of nonbreeders, year-round territorial dynamics of breeders, and dispersal are poorly understood. Virtually no information is published on growth rates. Although ravens are "symbols of wilderness" and sensitive to human presence in some areas, in other areas they are abundant and bothersome, and managers need a better understanding of how ravens use human activities for resources. Where they are economic or conservation pests, methods to reduce their impacts need to be developed and tested.

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Appendix 1. Body mass (g) of Common Ravens from various locations in North America. Data shown as mean ± SD (range, n).

Location	Body mass	Source
Nova Scotia	1,230 (n = 15)	Elliot 1977
Alaska		
Winter	1,174 ± 197 (n = 11)	Schwan and Williams 1978
Summer	1,097 ± 127 (n = 11)	Schwan and Williams 1978
California (coast)		
Male	811 ± 63.3 (700–880, 6)	Linz et al. 1990
Female	754 ± 61.4 (680–800, 8)	Linz et al. 1990
California (desert)		
Sexes combined	785 ± 71.9 (585–985, 145)	WIB

Appendix 2. Nest success (number of nests with ≥1 fledgling/total number of nest with eggs) from six locations in w. and e. U.S.

Location	Nest success	Source
Utah	16%	Smith and Murphy 1973
California	13%	Knittle 1992
Idaho	477%*	Steenhof et al. 1993
Virginia	35%	Hopper et al. 1975
Oregon	85%	Stiehl 1985
Wyoming	24%	Dorn 1972

*Mean from across 7 yr.

Annual reproductive success (total number fledged/total number of nests with eggs) of Common Ravens in North America. Data given as mean ± SD (range, n). (n = number of nests; SD and range = among years; except for California, Virginia, and Wyoming where SD and range were among nests in one year).

Location	Annual reproductive success	Source
Idaho	3.1 ± 0.29 (2.5–3.4, 104)	Steenhof et al. 1993
Virginia	2.8 (1–4, 44)	Hooper 1977
Utah	2.6 ± 0.31 (2.5–3.0, 14)	Smith and Murphy 1973
California	2.5 ± 1.75 (0–5, 11)	Knittle 1992
Oregon	2.3 ± 2.0 (2.2–2.5, 53)	Stiehl 1978
Wyoming	1.7 ± 1.6 (0–4, 24)	Dorn 1972

The Birds of North America

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