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2. EXPOSURE FACTORS AND DESCRIPTIONS OF SELECTED SPECIES

Chapter 2 includes exposure profiles for the selected species in three subsections: birds (Section 2.1), mammals (Section 2.2), and reptiles and amphibians (Section 2.3). Each species profile follows the same format, beginning with an introduction to the taxonomic group to which the species belongs and a qualitative description of relevant aspects of the species' natural history. Next, a list of similar species is provided to help identify species that might share certain exposure characteristics, although they may have different geographic ranges, diets, and habitat preferences. Each species profile then presents a series of tables presenting values for normalizing and contact rate factors, dietary composition, population dynamics, and seasonal activity patterns that represent the range of values that we identified in our literature review. Table format is described in Section 1.5. Data on soil and sediment ingestion are limited; we present these data in a separate section (4.1.3) for easy comparison among species. Finally, each profile includes the references cited in the species profile and in the corresponding Appendix tables.

2.1. BIRDS

Table 2-1 lists the bird species described in this section. For range maps, refer to the general references identified in individual species profiles. The remainder of this section is organized by species in the order presented in Table 2-1. The availability of published information varies substantially among species, as is reflected in the profiles. Some species include two or more subspecies; these are indicated in the profiles when reported by the investigators. For many studies, the subspecies, although not identified, can be inferred from the study location and geographic range of the subspecies. Average lengths of birds are reported from museum study skins measured from bill tip to tail tip. Body weight is reported as fresh wet weight with plumage, unless otherwise noted.

Table 2-1. Birds Included in the Handbook

Order	Family	Common name	Scientific name	Section
Ciconiformes	Ardeidae	great blue heron	<i>Ardea herodias</i>	2.1.1
Anseriformes	Anatidae	Canada goose	<i>Branta canadensis</i>	2.1.2
		mallard	<i>Anas platyrhynchos</i>	2.1.3
		lesser scaup	<i>Aythya affinis</i>	2.1.4
Falconiformes	Accipitridae	osprey	<i>Pandion haliaetus</i>	2.1.5
		red-tailed hawk	<i>Buteo jamaicensis</i>	2.1.6
		bald eagle	<i>Haliaeetus leucocephalus</i>	2.1.7
	Falconidae	American kestrel	<i>Falco sparverius</i>	2.1.8
Galliformes	Phasianidae	northern bobwhite	<i>Colinus virginianus</i>	2.1.9
Charadriiformes	Scolopacidae	American woodcock	<i>Scolopax minor</i>	2.1.10
		spotted sandpiper	<i>Actitis macularia</i>	2.1.11
	Laridae	herring gull	<i>Larus argentatus</i>	2.1.12
Coraciiformes	Alcedinidae	belted kingfisher	<i>Ceryle alcyon</i>	2.1.13
Passeriformes	Troglodytidae	marsh wren	<i>Cistothorus palustris</i>	2.1.14
	Muscicapidae	American robin	<i>Turdus migratorius</i>	2.1.15

2.1.1. Great Blue Heron (herons)

Order *Ciconiiformes*, Family *Ardeidae*. Herons, egrets, and bitterns are medium to large wading birds with long necks and spear-like bills. Nearly all species feed primarily on aquatic animal life (e.g., fish, frogs, crayfish, insects) and are common along the margins of most freshwater and saltwater bodies and wetlands (Kushlan, 1978). Their long legs, necks, and bills are adapted for wading in shallow water and stabbing prey. Most species build their nests in trees near their foraging habitat, and many nest colonially. Members of this group range in size from the least bittern (28 to 36 cm bill tip to tail tip) to the great blue heron (106 to 132 cm tall). The sexes are similar in size and appearance.

Selected species

The great blue heron (*Ardea herodias*) is the largest member of the group in North America and feeds primarily on aquatic animals. It is widely distributed in both saltwater and freshwater environments. There are four subspecies in the United States and Canada: *A. h. wardi* (Kansas and Oklahoma across the Mississippi River to Florida), *A. h. herodias* (remainder of the North and Central American range), *A. h. fannini* (Pacific coast of North America from Alaska to Washington), and *A. h. occidentalis* (extreme south of Florida) (Bancroft, 1969, cited in Hancock and Kushlan, 1984). *A. h. occidentalis* (the great white heron) is an all white color morph that was formerly considered a separate species (National Geographic Society, 1987).

Body size. Males average slightly heavier in weight than females (Hartman, 1961; Palmer, 1962). Northern continental herons are somewhat smaller than those found in the south (Palmer, 1962). Quinney (1982) determined a relationship between age and body weight for nestling great blue herons ($r = 0.996$, $N = 16$ nestlings, and 274 measurements):

$$BW = 55.6 \times A - 47.4$$

where BW equals body weight in grams and A equals age in days.

Habitat. Great blue herons inhabit a variety of freshwater and marine areas, including freshwater lakes and rivers, brackish marshes, lagoons, mangroves, and coastal wetlands, particularly where small fish are plentiful in shallow areas (Spendelow and Patton, 1988; Short and Cooper, 1985). They are often seen on tidal flats and sandbars and occasionally forage in wet meadows, pastures, and other terrestrial habitats (Palmer, 1962). Great blue herons tend to nest in dense colonies, or heronries. The location of the heronry is generally close to foraging grounds, and tall trees are preferred over shorter trees or bushes for nest sites (Bent, 1926; Palmer, 1962; Gibbs et al., 1987). They also may nest on the ground, on rock ledges, or on sea cliffs (Palmer, 1962).

Food habits. Fish are the preferred prey, but great blues also eat amphibians, reptiles, crustaceans, insects, birds, and mammals (Alexander, 1977; Bent, 1926; Hoffman, 1978; Kirkpatrick, 1940; Peifer, 1979). When fishing, they mainly use two foraging techniques: standing still and waiting for fish to swim within striking distance or

slow wading to catch more sedentary prey (such as flounder and sculpin) (Bent, 1926; Willard, 1977). To fish, they require shallow waters (up to 0.5 m) with a firm substrate (Short and Cooper, 1985). Fish up to about 20 cm in length were dominant in the diet of herons foraging in southwestern Lake Erie (Hoffman, 1978), and 95 percent of fish consumed by great blues in a Wisconsin population were less than 25 cm in length (Kirkpatrick, 1940). Great blues sometimes forage in wet meadows and pastures in pursuit of lizards, small mammals, and large insects (Palmer, 1962; Peifer, 1979). In northern areas, small mammals such as meadow voles may be an important part of the diet early in the breeding season, possibly because some aquatic foraging areas may still be partially frozen when the herons arrive (Collazo, 1985). Consumption of larger prey (fish, frogs, rodents) is often followed by drinks of water (Hedeem, 1967); terrestrial prey such as voles are usually dunked in water before they are swallowed (Peifer, 1979). Adult herons tend to deliver the same type and size of food to their nestlings that they consume themselves, but they deliver it well digested for young nestlings and less well digested as the nestlings grow (Kushlan, 1978). Adults tend to feed solitarily, although they may feed in single or mixed species flocks where there are large concentrations of prey (Bayer, 1978; Krebs, 1974; Kushlan, 1978; Willard, 1977); fledglings are frequently seen foraging together (Dowd and Flake, 1985). Kushlan (1978) developed a regression equation relating the amount of food ingested per day to body weight for wading birds (N = seven species):

$$\log(\text{FI}) = 0.966 \log(\text{BW}) - 0.640$$

where FI equals food ingestion in grams per day and BW equals body weight in grams.

Molt. Adults undergo a complete molt in the late summer and fall and a partial molt of the contour feathers in the late winter and early spring (Bent, 1926). Young herons attain full adult plumage in the summer/fall molt at the end of their second year (Bent, 1926).

Migration. In the northern part of its range, most great blues are migratory, some moving to the southern Atlantic and Gulf States to overwinter with the resident populations of herons (Bent, 1926; Palmer, 1962), others continuing on to Cuba and Central and South America (Hancock and Kushlan, 1984). Most migrating herons leave their breeding grounds by October or November and return between February and April (Bent, 1926).

Breeding activities and social organization. The male great blue heron selects the site for the breeding territory, and nests generally consist of a stick platform over 1 m in diameter (Palmer, 1962). Great blues often use a nest for more than 1 year, expanding it with each use (Palmer, 1962). Mean clutch sizes range from three to five (see table); in general, clutch size tends to increase with latitude (Pratt, 1972). Only one brood is raised per year; however, if a clutch is destroyed, great blues may lay a replacement clutch, usually with fewer eggs than the initial clutch (Palmer, 1962; Pratt and Winkler, 1985). Both parents incubate and feed the young (Palmer, 1962; Hancock and Kushlan, 1984). During the breeding season, great blues are monogamous and colonial, with from a few to hundreds of pairs nesting in the same area or heronry (Gibbs et al., 1987). Colonies may

include other species, such as great egrets or double-crested cormorants (Pratt and Winkler, 1985; Mock et al., 1987).

Home range and resources. Breeding colonies are generally close to foraging grounds (Bent, 1926; Palmer, 1962; Gibbs et al., 1987). Mathisen and Richards (1978) found the distance between heronries and possible feeding areas in Minnesota lakes to range from 0 to 4.2 km, averaging 1.8 km. Another study found that most heronries along the North Carolina coast were located near inlets with large concentrations of fish, an average of 7 to 8 km away (Parnell and Soots, 1978, cited in Short and Cooper, 1985). Fifteen to 20 km is the farthest great blue herons regularly travel between foraging areas and colonies (Gibbs et al., 1987; Gibbs, 1991; Peifer, 1979). In the northern portion of their range, great blue herons often build nests in tall trees over dry land, whereas in the southern part of their range, they usually nest in swamp trees, including mangroves (Palmer, 1962). Each breeding pair defends a small territory around the nest, the size of which depends on local habitat and the birds' stage of reproduction (Hancock and Kushlan, 1984). Herons in some areas also defend feeding territories (Peifer, 1979). In other areas, great blues appear to be opportunistic foragers, lacking strict fidelity to particular feeding sites (Dowd and Flake, 1985). A study in North Dakota found that herons often returned to the same general areas, but different individuals often used the same areas at different times (Dowd and Flake, 1985).

Population density. Because great blues nest colonially, local population density (i.e., colony density, colony size, and number of colonies) varies with the availability of suitable nesting habitat as well as foraging habitat. On islands in coastal Maine, Gibbs and others (1987) found a significant correlation between colony size and the area of tidal and intertidal wetlands within 20 km of the colonies, which was the longest distance herons in the study colonies traveled on foraging trips. In western Oregon, the size of heronries was found to range from 32 to 161 active nests; the area enclosed by peripheral nest trees within the colonies ranged from 0.08 to 1.21 ha (Werschkul et al., 1977).

Population dynamics. Most nestling loss is a result of starvation, although some losses to predation do occur (Collazo, 1981; Hancock and Kushlan, 1984). In a study of 243 nests in a coastal California colony, 65 percent of the chicks fledged, 20 percent starved, 7 percent were taken by predators, and 7 percent were lost to other causes (Pratt and Winkler, 1985). Estimates of the number of young fledged each year by breeding pairs range from 0.85 to 3.1 (Pratt, 1970; Pratt, 1972; McAloney, 1973; Pratt and Winkler, 1985; Quinney, 1982). Based on banding studies, about two-thirds of the fledglings do not survive more than 1 year, although they may survive better in protected wildlife refuges (Bayer, 1981a). Values for later years indicate that about one-third to one-fifth of the 2-year-old and older birds are lost each year (Bayer, 1981a; Henny, 1972; Owen, 1959).

Similar species (from general references)

- The great egret (*Casmerodius albus*) is almost the same size (96 cm length) as the great blue heron and is found over a limited range in the breeding season, including areas in the central and eastern United States and the east and west coasts. It winters in coastal areas of the United States and in

to Mexico and farther south. The great egret's habitat preferences are similar those of the great blue heron.

- The snowy egret (*Egretta thula*), one of the medium-sized herons (51 to 69 cm), shuffles its feet to stir up benthic aquatic prey. It is found mostly in freshwater and saltwater marshes but also sometimes follows cattle and other livestock as does the cattle egret. It breeds in parts of the western, southeastern, and east coasts of the United States and winters along both coasts of the southern United States and farther south.
- The cattle egret (*Bubulcus ibis*) is seen in agricultural pastures and fields, where it follows livestock to pick up insects disturbed by grazing. An Old World species, it was introduced into South America and reached Florida in the 1950's. It reached California by the 1960's and has been continuing to expand its range.
- The green-backed heron (*Butorides striatus*), one of the smaller herons (41 to 56 cm), breeds over most of the United States except for the northwest and southern midwest. It has a winter range similar to that of the snowy egret and seems to prefer water bodies with woodland cover.
- The tricolored heron (*Egretta tricolor*) (formerly known as the Louisiana heron) is common in salt marshes and mangrove swamps of the east and gulf coasts, but it is rare inland.
- The little blue heron (*Egretta caerulea*) is common in freshwater ponds, lakes, and marshes and coastal saltwater wetlands of the Gulf Coast States. Juveniles are easily confused with juvenile snowy egrets. This species hunts by walking slowly in shallow waters, and its diet typically includes fish, amphibians, crayfish, and insects.
- The black-crowned night heron (*Nycticorax nycticorax*), characterized by a heavy body, short thick neck, and short legs (64 cm), is a common heron of freshwater swamps and tidal marshes, roosting by day in trees. It typically feeds by night, predominantly on aquatic species, fish, amphibians, and insects. This heron is extremely widespread, occurring in North and South America, Eurasia, and Africa. It breeds over much of the United States and parts of central Canada and winters along both coasts of the United States and farther south.
- The yellow-crowned night heron (*Nyctanassa violacea*) (61 cm) is similar to the black-crowned but is more restricted in its range to the southeastern United States. It roosts in trees in wet woods, swamps, and low coastal shrubs.
- The American bittern (*Botaurus lentiginosus*), another of the medium-sized herons (58 to 70 cm), is a relatively common but elusive inhabitant of freshwater and brackish marshes and reedy lakes. It is a solitary feeder,

consuming fish, crayfish, reptiles, amphibians, insects, and even small mammals. Its breeding range includes most of Canada and the United States, although much of the southern United States is inhabited only during the winter.

- The least bittern (*Ixobrychus exilis*), the smallest of the North American herons (33 cm), also is an elusive inhabitant of reedy areas. Its breeding range is restricted largely to the eastern half of the United States.

General references

Hancock and Kushlan (1984); Robbins et al. (1983); National Geographic Society (1987); Palmer (1962); Short and Cooper (1985).

Great Blue Heron (*Ardea herodias*)

<i>Factors</i>	<i>Age/Sex/ Cond./Seas.</i>	<i>Mean</i>	<i>Range or (95% CI of mean)</i>	<i>Location</i>	<i>Reference</i>	<i>Note No.</i>
Body Weight (g)	A B	2,229 ± 762 SD	1,940 - 2,970 1,370 - 2,750	eastern North America	Quinney, 1982	1
	A F	2,204 ± 337 SD		NS	Hartman, 1961	
	A M	2,576 ± 299 SD				
	yearlings	2,340 ± 490 SD		central Oregon	Bayer, 1981b	
	juveniles	1,990 ± 550 SD				
	nestlings:			Nova Scotia, Canada	McAloney, 1973	
	day 1	86				
	day 5	170				
	day 10	567				
	day 15	983				
day 20	1,115					
day 25	1,441					
day 30	1,593					
day 35	1,786					
day 40	2,055					
Metabolic Rate (kcal/kg-day)	A B basal	62	(78 - 353)		estimated	2
	A B free-living	165			estimated	3
Food Ingestion Rate (g/g-day)	A B	0.18		NS	Kushlan, 1978	4
Water Ingestion Rate (g/g-day)	A B	0.045			estimated	5
Inhalation Rate (m ³ /day)	A B	0.76			estimated	6
Surface Area (cm ²)	A B	1,711			estimated	7

2-8

Great Blue Heron

Great Blue Heron (*Ardea herodias*)

<i>Dietary Composition</i>	Spring	Summer	Fall	Winter	Location/Habitat (measure)	Reference	Note No.
trout non-trout fish crustaceans/amphibians		59 39 2			lower Michigan/lake (% wet weight; stomach contents)	Alexander, 1977	
trout non-trout fish crustaceans amphibians birds and mammals		89 5 1 4 1			lower Michigan/river (% wet weight; stomach contents)	Alexander, 1977	
Atlantic silverside mummichog American eel <i>Gaspereaux</i> pollack yellow perch		3.6 2.4 52.6 29.9 8.9 2.6			Nova Scotia/Boot Island (% wet weight; items regurgitated by nestlings)	Quinney, 1982	
staghorn sculpin small medium large starry flounder small medium large other small medium		27.8 7.6 2.2 15.0 8.1 5.2 30.6 3.5			Vancouver, BC/coastal island (% of fish observed caught; small = less than 1/3 beak length; medium = about 1/2 beak length; large = longer than beak; other includes shiner sea perch and penpoint gunnels)	Krebs, 1974	

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Great Blue Heron

Great Blue Heron (*Ardea herodias*)

<i>Population Dynamics</i>	<i>Age/Sex Cond./Seas.</i>	<i>Mean</i>	<i>Range</i>	<i>Location/Habitat</i>	<i>Reference</i>	<i>Note No.</i>
Size Feeding Territory	A B fall A B winter	0.6 ± 0.1 SD ha 8.4 ± 5.4 SD ha		Oregon/freshwater marsh Oregon/estuary	Bayer, 1978	
Foraging Distance from Colony	A B summer	3.1 km	up to 24.4 km	South Dakota/river & streams	Dowd & Flake, 1985	8
	A B summer	7 to 8 km		North Carolina/coastal	Parnell & Soots, 1978	
Population Density	summer along stream along river	2.3 birds/km 3.6 birds/km		North Dakota/rivers & streams	Dowd & Flake, 1985	
	summer	149 ± 53 SD nests/ha		Maine/coastal islands	Gibbs et al., 1987	
	summer	461 nests/ha	447 - 475	Oregon/coastal island	Werschkul et al., 1977	
Clutch Size		3.16 ± 0.04 SE	1 - 5	California/coastal canyon	Pratt & Winkler, 1985	9
		4.17 ± 0.85 SD	3 - 6	Nova Scotia/island	McAloney, 1973	
		4.37	3 - 6	Pennsylvania/NS	Miller, 1943	
Clutches/Year		1		Pennsylvania; Oregon/NS	Miller, 1943; English, 1978	10
Days Incubation		27.1	25 - 30	Nova Scotia/island	McAloney, 1973	
		28		United States/NS	Bent, 1926	
Age at Fledging (days)		45 60 49 to 56		Nova Scotia/island NS/NS Nova Scotia/island	McAloney, 1973 Hancock & Kushlan, 1984 Quinney, 1982	11
Number Fledge per Pair		1.7 1.96 2.8		central California/coastal northwest Oregon/river Nova Scotia/island	Pratt, 1972 English, 1978 Quinney, 1982	

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Great Blue Heron

<i>Population Dynamics</i>	<i>Age/Sex Cond./Seas.</i>	<i>Mean</i>	<i>Range</i>	<i>Location/Habitat</i>	<i>Reference</i>	<i>Note No.</i>
Number Fledge per Successful Nest		2.19 ± 0.25 SD 2.43 3.09	2 - 3	central California/coastal northwest Oregon/river Nova Scotia/island	Pratt & Winkler, 1985 English, 1978 McAloney, 1973	
Age at Sexual Maturity	B	2 years		NS	Bent, 1926	
Annual Mortality Rates (percent)	during 1st yr during 2nd yr during 3rd yr	64 36 22		United States and Canada/NS	Henny, 1972	
<i>Seasonal Activity</i>	<i>Begin</i>	<i>Peak</i>	<i>End</i>	<i>Location</i>	<i>Reference</i>	<i>Note No.</i>
Mating/Laying	Nov. to Dec. mid-February mid-March late March mid-April	mid-March	April June	Florida central California northwest Oregon Pennsylvania Nova Scotia	Howell, 1932 Pratt & Winkler, 1985 English, 1978 Miller, 1943 McAloney, 1973	9
		early May	early April late May			9
Hatching	mid-April mid-May	early May	mid-July	northwest Oregon Idaho Ohio	English, 1978 Collazo, 1981 Hoffman & Curnow, 1979	
Migration (fall)	mid-Sept.		late October	northern US	Palmer, 1962	
(spring arrival)	mid-February mid-March late March		mid-March	western Oregon Wisconsin; Minnesota Nova Scotia	Werschkul et al., 1977 Bent, 1926 Bent, 1926	

- 1 As cited in Dunning, 1984.
- 2 Estimated using equation 3-28 (Lasiewski and Dawson, 1967) and body weights from Quinney (1982).
- 3 Estimated using equation 3-37 (Nagy, 1987) and body weights from Quinney (1982).
- 4 Estimated from Kushlan's (1978) allometric equation for wading birds, assuming a body weight of 2,230 g.
- 5 Estimated using equation 3-15 (Calder and Braun, 1983) and body weights from Quinney (1982).
- 6 Estimated using equation 3-19 (Lasiewski and Calder, 1971) and body weights from Quinney (1982).

Great Blue Heron (*Ardea herodias*)

- 7 Estimated using equation 3-21 (Meeh, 1879 and Rubner, 1883, as cited in Walsberg and King, 1978) and body weights from Quinney (1982).
- 8 Cited in Short and Cooper (1985).
- 9 Cited in Palmer (1962).
- 10 May replace clutch if eggs are lost, but only rear one brood (Henny, 1972).
- 11 Young fed around colony for 10 days after leaving nest at 45 days of age.

2-12

Great Blue Heron

Great Blue Heron (*Ardea herodias*)

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2.1.2. Canada Goose (geese)

Order *Anseriformes*, Family *Anatidae*. Geese are large herbivorous waterfowl that feed on grains, grass sprouts, and some aquatic vegetation. Although adapted for life on the water, they forage primarily in open fields. They breed in open forested areas near lake shores and coastal marshes from the arctic tundra through temperate climates. These birds migrate in noisy flocks in the familiar V-formation, stopping in cultivated fields, wetlands, and grasslands to feed. Geese show a wide variation in size even within a species; the sexes look alike.

Selected species

The Canada goose (*Branta canadensis*) is the most widespread and abundant goose in North America. It is a popular game species and is commonly encountered on cultivated fields, golf courses, other parklands, and wetland refuge areas. Depending on subspecies, these geese can range in size from 64 to 114 cm (bill tip to tail tip), the larger geese breeding in more southerly locations than the smaller subspecies. The reverse is true in winter, with the larger subspecies wintering in the more northerly parts of the range (Palmer, 1962). The number of existing recognized subspecies varies, but most ornithologists agree that there are 11: *canadensis* (Atlantic Canada goose), *fulva* (Vancouver Canada goose), *hutchinsii* (Richardson's Canada goose), *interior* (interior Canada goose), *leucopareia* (Aleutian Canada goose), *maxima* (giant Canada goose), *minima* (cackling Canada goose), *moffitti* (Great Basin or western Canada goose), *occidentalis* (dusky Canada goose), *parvipes* (lesser Canada goose), and *taverneri* (Taverner's Canada goose) (Bellrose, 1976; Johnson et al., 1979; Palmer, 1962). Several subspecies usually mingle during migration and in wintering areas, but they breed in geographically distinct ranges. Six of the subspecies breed in Alaska (*fulva*, *leucopareia*, *minima*, *occidentalis*, *parvipes*, and *taverneri*) (Johnson et al., 1979). The *leucopareia* subspecies, found in Oregon, Washington, California, and Alaska, currently is a United States federally designated threatened species (50 CFR 17.11, 1992). It is only known to breed on one of the western Aleutian islands off Alaska (Byrd and Woolington, 1983). See Bellrose (1976) for ranges, migration corridors, and wintering areas of specific subspecies and populations.

Body size. Canada geese subspecies vary greatly in size, but males are on average larger than females (see table). Body weight reaches its maximum just prior to or during the spring migration and then declines during egg-laying and incubation, sometimes by as much as 20 percent (Mainguy and Thomas, 1985; McLandress and Raveling, 1981). Most of the weight lost during incubation reflects loss of fat, which can provide over 80 percent of the energy requirements for the incubating females (Mainguy and Thomas, 1985; Murphy and Boag, 1989). Young are similar to parents in size by 2 months of age (Palmer, 1962).

Habitat. Breeding habitat includes tundra, forest muskeg in the far north, tall- and shortgrass prairie, marshes, ponds, and lakes. Most nesting sites are close to open water with high visibility in all directions (Palmer, 1962; Steel et al., 1957). In many areas, Canada geese nest predominantly on islands in ponds or lakes (Geis, 1956). Former

muskrat houses often serve as nest sites in marshes (Steel et al., 1957). Brood-rearing habitats, on the other hand, require adequate cover, and riparian areas are used more frequently than open water (Eberhardt et al., 1989a). During the fall and winter in Maryland, Harvey et al. (1988) found Canada geese to spend 57 percent of their time in farmlands (mostly corn, soybeans, and winter wheat fields) and 24 percent in forested areas.

Food habits. Canada geese are almost exclusively vegetarian, and feeding activity is concentrated in areas where food is plentiful (e.g., standing crops, scattered whole grain) (Palmer, 1962). They are primarily grazers, but must consume grit at some point to assure proper digestion (Palmer, 1962). They prefer certain foods, but will change their diet depending on the availability of a food type (Coleman and Boag, 1987). For example, when water levels are low in the south Yukon (Canada) river delta, Canada geese forage on rhizomes of *Potamogeton richardsonii* even though other forage is available; at higher water levels when the *Potamogeton* is unreachable, the geese will feed on other plants (Coleman and Boag, 1987). During fall, geese often consume green crops (e.g., winter wheat). During winter, however, they consume more energy-rich foods such as corn (Harvey et al., 1988; McLandress and Raveling, 1981). In late winter and early spring, green crops that are high in nitrogen and other important nutrients again constitute an important part of the diet (McLandress and Raveling, 1981). Canada geese often feed preferentially on the blade tips of many plants, which are higher in nitrogen than other parts of the plant (Buchsbaum et al., 1981). In Minnesota, Canada geese begin consuming green grasses as soon as they are exposed by the melting snow (McLandress and Raveling, 1981). In Maryland, on the other hand, Harvey et al. (1988) found that Canada geese did not begin consuming green crops before migration to the breeding grounds, indicating that this population may rely on green forage available at staging areas to obtain the protein and lipids required for reproduction. In the spring in Falmouth Harbor, Massachusetts, Canada geese initially consume predominantly the marsh grasses *Spartina spp.* and rushes *Juncus gerardi*, which are high in protein (Buchsbaum and Valiela, 1987). As the summer progresses, however, they feed increasingly on submerged eelgrass, *Zostera marina*, which provides more carbohydrates (Buchsbaum and Valiela, 1987).

Molt. Nonbreeders and yearlings migrate to a separate molting ground soon after arrival at the breeding grounds, while breeding birds molt on the brood-rearing grounds (Bellrose, 1976). Molting occurs earlier in nonbreeders, at least a month earlier in the larger subspecies (Palmer, 1962). Molting parents do not regain flight feathers until just prior to the time when their young first attain flight (Palmer, 1962). The flightless period of *B. c. interior* is estimated to be 32 days. For *B. c. maxima* and *B. c. moffitti*, the flightless period lasts from 39 to 40 days (Balham, 1954; Hanson, 1965, as cited in Palmer, 1962).

Migration. Migratory Canada geese leave their breeding grounds during late summer and early autumn; they return in the spring around the time the first water is opening (i.e., ice melting) but well before snow cover has disappeared (Bellrose, 1976). Spring migration begins later for northerly populations, with geese that winter in mild climates departing as early as mid-January, while those wintering in the coldest areas do not move northward until the beginning of March (Bellrose, 1976). The bulk of the migrants typically arrive on the summer breeding grounds 3 weeks after the first birds

(Bellrose, 1976). Some populations have become resident year-round, for example, *B. c. maxima* in Missouri (Brakhage, 1965) and in southeast Georgia and southwest Alabama (Combs et al., 1984). During both the spring and fall migrations, geese tend to gather in large flocks and feed for several weeks in "staging" areas along major waterfowl flyways (Bellrose, 1976).

Breeding activities and social organization. Canada geese arrive on the breeding grounds in flocks, and soon after, the male becomes territorial and aggressive toward other birds (Palmer, 1962). Lifelong monogamy following their first breeding is the general rule with these geese (Palmer, 1962). Nests are built on the ground in a position with good visibility (Palmer, 1962). During incubation the male stands guard, while the female incubates the eggs, which she normally leaves two or three times daily to feed, bath, drink, and preen (Murphy and Boag, 1989). Both parents accompany the young through the brood period (Bellrose, 1976; Brakhage, 1965). Canada geese return to the breeding grounds as family units, but the yearlings leave their parents soon after arrival (Bellrose, 1976).

Home range and resources. The foraging home range of Canada geese varies with season, latitude, and breeding condition. Soon after hatching, goose families move away from the nesting sites to other areas with adequate cover and forage to rear their broods (Byrd and Woolington, 1983). Newly hatched families may have to travel 10 to 20 km from the nest site to reach areas with adequate aquatic vegetation or pasture grasses (Geis, 1956). Although the families stay predominantly on land, often in riparian areas, they usually are close to water. Eberhardt et al. (1989a) found goslings within 5 m of water most of the time; only 7 percent of sightings were farther than 50 m away. During the spring and fall migrations and in winter, Canada geese can be found on open water or refuges near grain fields or coastal estuaries (Leopold et al., 1981).

Population density. Breeding population densities of Canada geese vary widely. Low nesting densities (i.e., less than 0.005 per hectare) are common in the Northwest Territories of Canada (Smith and Sutton, 1953, 1954) and intermediate densities (i.e., 0.02 to 0.7 per hectare) have been reported for Alaska (Cornley et al., 1985). In some more southerly locations (e.g., California), colonial nesting situations have been reported, with as many as 32 nests located on half an acre (Naylor, 1953, as cited in Palmer, 1962).

Population dynamics. The earliest Canada geese begin breeding is around 2 to 3 years of age (MacInnes and Dunn, 1988; Brakhage, 1965). In the larger subspecies, only a small proportion of the birds under 4 years may attempt to breed. For example, in Manitoba, Moser and Rusch (1989) found that only 7 percent of 2-year-old and 15 percent of 3-year-old *B. c. interior* laid eggs. Canada geese only attempt to rear one brood per year. In the more southerly latitudes, Canada geese will reneest if a clutch is lost prior to incubation (Brakhage, 1965; Geis, 1956). In general, both clutch size and success at rearing goslings increase with the age of the breeder (Brakhage, 1965). Raveling (1981) found that older *B. c. maxima* (4 plus years) raised more than twice as many goslings to fledging as did younger (2 to 3 years) birds. Population age structure and annual mortality vary with hunting pressure as well as natural factors.

Similar species (from general references)

- The Brant goose (*Branta bernicla*) is approximately the size of the smaller Canada geese subspecies (length 25 cm). It is primarily a sea goose and is rare inland. It winters along both the east and west coasts of the United States, where it feeds on aquatic plants in shallow bays and estuaries. It breeds in the high arctic.
- The greater white-fronted goose (*Anser albifrons*) is limited to certain areas west of the Mississippi River and averages 71 cm in length. Its habits are similar to those of other geese.
- The snow goose (*Chen caerulescens*) breeds in the Arctic and winters in selected coastal areas across the United States. However, this average-sized goose (71 cm) is a migratory visitor to much of the central United States.
- The Ross' goose (*Chen rosii*) breeds in the high arctic tundra and winters in some areas of the southwest United States. This relatively small (58 cm) goose is a rare visitor to the mid-Atlantic States and is always seen with snow geese.

General references

Bellrose (1976); Kortright (1955); National Geographic Society (1987); Palmer (1962).

Canada Goose (*Branta canadensis*)

<i>Factors</i>	<i>Age/Sex/ Cond./Seas.</i>	<i>Mean</i>	<i>Range or (95% CI of mean)</i>	<i>Location (subspecies)</i>	<i>Reference</i>	<i>Note No.</i>	
Body Weight (g)	A M late sum. A F late sum.	1,443 ± 32 SE 1,362 ± 54 SE	1,260 - 1,605 1,195 - 1,590	Alaska (<i>minima</i>)	Raveling, 1979		
	A M winter A F winter	2,769 ± 30 SE 2,472 ± 23 SE		Colorado (<i>parvipes</i>)	Grieb, 1970		
	A M not spec. A F not spec.	3,992 3,447		NS (<i>canadensis</i>)	Webster (unpublished) in Bellrose, 1976		
	A M fall A F fall	4,212 ± 35 SE 3,550 ± 31 SE	3,799 - 4,727 3,147 - 3,856	Illinois (<i>interior</i>)	Raveling, 1968		
	A M late sum. A F late sum.	4,960 4,160		Missouri (<i>maxima</i>)	Brakhage, 1965		
	M at hatching F at hatching	108.7 109.5		Alberta (<i>moffitti</i>)	LeBlanc, 1987b		
	B day 10 B day 20 B day 30 B day 40 B day 47		150 450 755 950 1,050	Alaska (<i>minima</i>)	Sedinger, 1986		1
	B day 0 B day 9 B day 16 B day 30 B day 44 B day 51		110 240 440 1,400 2,400 2,600	NS (<i>moffitti</i>)	Williams (unpublished) in Palmer, 1976		
	M at fledging F at fledging	87% adult wt 89% adult wt		Alaska (<i>minima</i>)	Sedinger, 1986		

Canada Goose (*Branta canadensis*)

<i>Factors</i>	<i>Age/Sex/ Cond./Seas.</i>	<i>Mean</i>	<i>Range or (95% CI of mean)</i>	<i>Location (subspecies)</i>	<i>Reference</i>	<i>Note No.</i>
Body Fat (g lipid)	F fall migr. F winter F spring migr. F prelaying F end incub. F early molt	182 ± 24 SE 57 ± 6 SE 172 ± 25 SE 171 (no SE; N=2) 33 ± 5 SE 108 ± 13 SE	117 - 264 34 - 71 68 - 362 136 - 205 14 - 51 62 - 179	Alaska in winter (<i>minima</i>) California in summer	Raveling, 1979	
	F prelaying F incubating F late incub. F molting	751 ± 45 SE 611 ± 40 SE 166 ± 18 SE 485 ± 37 SE		Ontario, Canada (<i>maxima</i>)	Thomas et al., 1983	
Egg Weight (g)		96 127 163		NS (<i>minima</i>) NS (<i>leucopa</i>) Alberta, Canada (<i>moffitti</i>)	Owen, 1980 Owen, 1980 LeBlanc, 1987a	2 2
	Metabolic Rate (kcal/kg-day)	free-living: A M winter A M spring A M summer A M fall	105 - 209 105 - 203 115 - 253 100 - 209	Illinois in winter (<i>interior</i>) Ontario, Canada in summer	Williams & Kendeigh, 1982	3
		A F spring A F summer	130 - 220 143 - 274	(<i>interior</i>)	Williams & Kendeigh, 1982	3
	free-living: A M A F	185 187	(87 - 391) (88 - 397)	(<i>minima</i>)	estimated	4a
	A M A F	141 147	(65 - 304) (69 - 316)	(<i>interior</i>)	estimated	4b
	A M A F	135 142	(63 - 292) (66 - 305)	(<i>maxima</i>)	estimated	4c

Canada Goose (*Branta canadensis*)

<i>Factors</i>	<i>Age/Sex/ Cond./Seas.</i>	<i>Mean</i>	<i>Range or (95% CI of mean)</i>		<i>Location (subspecies)</i>	<i>Reference</i>	<i>Note No.</i>
Food Ingestion Rate (g/g-day)	A M winter A F winter	0.030 0.033			(<i>interior</i>) captive	Joyner et al., 1984	5
	A M spring A F spring	0.030 0.031			(<i>interior</i>) captive	Joyner et al., 1984	5
Water Ingestion Rate (g/g-day)	A M A F	0.052 0.053			(<i>minima</i>)	estimated	6a
	A M A F	0.035 0.037			(<i>maxima</i>)	estimated	6b
Inhalation Rate (m ³ /day)	A M A F	0.54 0.52			(<i>minima</i>)	estimated	7a
	A M A F	1.40 1.22			(<i>maxima</i>)	estimated	7b
Surface Area (cm ²)	A M A F	1,280 1,230			(<i>minima</i>)	estimated	8a
	A M A F	2,920 2,590			(<i>maxima</i>)	estimated	8b
<i>Dietary Composition</i>	<i>Spring</i>	<i>Summer</i>	<i>Fall</i>	<i>Winter</i>	<i>Location/Habitat (measure)</i>	<i>Reference</i>	<i>Note No.</i>
sedges native grasses corn kernels animal other				63 11 22 0.01 4	North Carolina/lake (% volume; crop and gizzard contents)	Yelverton & Quay, 1959	

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Canada Goose

Canada Goose (*Branta canadensis*)

<i>Dietary Composition</i>	Spring	Summer	Fall	Winter	Location/Habitat (measure)	Reference	Note No.
<i>Equisetum sp.</i> (shoot)	9.2				Ontario, Canada/bay (% dry weight; esophagus and proventriculus contents)	Prevett et al., 1985	
<i>Triglochin palustris</i> (root)	3.4						
grasses (root)	23.4						
(shoot)	2.1						
sedges (shoot)	25.3						
(root)	5.3						
(reed)	17.9						
<i>Plantago maritima</i> (root)	6.5						
unidentified plants	6.1						
invertebrates	0.7						
corn			23		Wisconsin/marsh (% dry volume; gizzard and proventriculus contents)	Craven & Hunt, 1984	
unidentified plants			8.6				
alfalfa			10.4				
<i>Gramineae</i>			12.6				
oats			25.1				
<i>Setaria lutescens</i>			8.4				
<i>Trifolium repens</i>			10.9				
<i>Population Dynamics</i>	Age/Sex/ Cond./Seas.	Mean	Range		Location (subspecies)/ habitat ^a	Reference	Note No.
Home Range Size	A F & brood	983 ± 822 SD ha	290 - 2,830		Washington (<i>moffitti</i>)/river	Eberhardt et al., 1989a	
	A F & brood	8.8 ± 4.4 SD km	2.8 - 18.1		Washington (<i>moffitti</i>)/river	Eberhardt et al., 1989a	

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Canada Goose

Canada Goose (*Branta canadensis*)

<i>Population Dynamics</i>	<i>Age/Sex/Cond./Seas.</i>	<i>Mean</i>	<i>Range</i>	<i>Location (subspecies)/habitat^a</i>	<i>Reference</i>	<i>Note No.</i>
Population Density	summer	16.6 nests/ha	0.02-12.4 nests/ha	various locations	Cooper, 1978	9
		1.3 nests/ha		Montana (<i>moffitti</i>)/ on 0.2-0.8 ha island	Geis, 1956	
		0.35 nests/ha		Montana (<i>moffitti</i>)/ on 8-121 ha island	Byrd & Woolington, 1983	
	fall	22 birds/ha		Alaska (<i>leucopus</i>)/ island preferred habitat	Humburg et al., 1985	
	winter	4 birds/ha		Missouri/wildlife refuge	Humburg et al., 1985	
Clutch Size		4.7	2 - 8	Alaska (<i>minima</i>)	Spencer et al., 1951	10
		5.6 ± 0.1 SE		Alaska (<i>leucopa</i>)	Byrd & Woolington, 1983	
		4.6		Ontario, Canada (<i>interior</i>)	Raveling & Lumsden, 1977	2
		5.6		Alabama, Georgia (<i>maxima</i>)	Combs et al., 1984	
Clutches/Year		1		Missouri	Brakhage, 1985	
Days Incubation		25		NS (<i>minima</i>)	Laidley, 1939	10
		28		Missouri (<i>maxima</i>)	Brakhage, 1965	
Age at Fledging (days)		40-46		Alaska (<i>minima</i>)	Mickelson, 1973	11
		55		NS (<i>leucopa</i>)	Lee (pers. comm.) in Byrd & Woolington, 1983	
		63		Ontario, Canada (<i>interior</i>)	Hanson, 1965	11
		71-73		Michigan (<i>maxima</i>)	Sherwood, 1965	11
Percent Nests Successful		91	89 - 93 27 - 64	Alaska/island (<i>leucopa</i>)	Byrd & Woolington, 1983	
		44		Alabama, Georgia (<i>maxima</i>)	Combs et al., 1984	
Number Fledge per Active Nest		2.19 ± 2.42 SD	0 - 7	Washington (<i>moffitti</i>)	Eberhardt et al., 1989b	

Canada Goose (*Branta canadensis*)

<i>Population Dynamics</i>	<i>Age/Sex/Cond./Seas.</i>	<i>Mean</i>	<i>Range</i>	<i>Location (subspecies)/habitat^a</i>	<i>Reference</i>	<i>Note No.</i>
Number Fledge per Successful Nest		4.0 ± 0.008 SE 2.2 3.9 ± 1.9 SD	1 - 7 1 - 7	Alaska (<i>leucopa</i>) IL, WI (<i>interior</i>) Washington (<i>moffitti</i>)	Byrd & Woolington, 1983 Hardy & Tacha, 1989 Eberhardt et al., 1989b	12
Age at Sexual Maturity	B F M F	2 - 3 4 - 5 2 - 3 2 - 3	 > 2 > 1 > 2	Northwest Territories (smaller subspecies) Manitoba, Canada (<i>interior</i>) Missouri (<i>maxima</i>)	MacInnes & Dunn, 1988 Moser & Rusch, 1989 Brakhage, 1965	
Annual Mortality Rates (percent)	A B J B A B J B A B J B	35.9 46.0 28 ± 0.8 SD 49 ± 3.7 SD 22.9 37.0		Alaska (<i>minima</i>) California, Nevada (<i>moffitti</i>) Ohio (<i>maxima</i>)	Nelson & Hansen, 1959 Rienecker, 1987 Cummings, 1973	11 11
<i>Seasonal Activity</i>	<i>Begin</i>	<i>Peak</i>	<i>End</i>	<i>Location (subspecies)</i>	<i>Reference</i>	<i>Note No.</i>
Mating/Laying	late February early March mid-March early April early April late May	March - April late March late March - April mid-April late May	mid-May May early May mid-April early June	Georgia, Alabama (<i>maxima</i>) OR, WA, CA (<i>moffitti</i>) Montana (<i>moffitti</i>) Idaho (<i>moffitti</i>) Ontario, Canada (<i>maxima</i>) Alaska (<i>leucopa</i>)	Combs et al., 1984 McCabe, 1979; Bellrose, 1976 Geis, 1956 Steel et al., 1957 Mainguy & Thomas, 1985 Byrd & Woolington, 1983	
Hatching	March mid-April early May	April - May late April - May mid-May early July	early June late May late June	Georgia, Alabama (<i>maxima</i>) Montana (<i>moffitti</i>) Idaho (<i>moffitti</i>) Alaska (<i>leucopa</i>)	Combs et al., 1984 Geis, 1956 Steel et al., 1957 Byrd & Woolington, 1983	

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Canada Goose

Canada Goose (*Branta canadensis*)

Seasonal Activity	Begin	Peak	End	Location (subspecies)	Reference	Note No.
Molt (fall)	mid-June mid-July late June	mid-August	late August late October	Idaho (<i>moffitti</i>) Alaska (<i>leucopa</i>) Illinois (<i>interior</i>)	Steel et al., 1957 Byrd & Woolington, 1983 Williams & Kendeigh, 1982	
Migration fall	mid-Sept. October	November early November	mid-December	arrive south Illinois (<i>interior</i>) arrive CO, TX (<i>parvipes</i>)	Bell & Klimstra, 1970 Grieb, 1970	
spring	February late March	early March early April		leave Illinois (<i>interior</i>) leave Minnesota (<i>maxima</i>)	Bell & Klimstra, 1970 Raveling, 1978b	

- 1 Weights estimated from graph.
- 2 Cited in Dunn and MacInnes (1987).
- 3 Estimated range of existence to maximum free-living metabolism at typical breeding ground (Ontario, Canada in spring and summer) and at typical wintering ground (south Illinois in fall and winter). Estimated using regression equations developed by the authors, measures of metabolic rates at temperatures from -40 to 41 °C, and temperatures typical for the season and location.
- 4 Estimated using equation 3-37 (Nagy, 1987) and body weights from (a) Raveling (1979); (b) Raveling (1968); and (c) Brakhage (1965).
- 5 Reported as grams dry weight of feed; corrected to grams wet weight of feed using the measured moisture content of 11 percent (on average) of the feed items (i.e., corn, sunflower seeds, wheat, and milo).
- 6 Estimated using equation 3-15 (Calder and Braun, 1983) and body weights from (a) Raveling (1979) and (b) Brakhage (1965).
- 7 Estimated using equation 3-19 (Lasiewski and Calder, 1971) and body weights from (a) Raveling (1979) and (b) Brakhage (1965).
- 8 Estimated using equation 3-21 (Meeh, 1879 and Rubner, 1883, as cited in Walsberg and King, 1978) and body weights from (a) Raveling (1979) and (b) Brakhage (1965).
- 9 Summarizing several studies, cited in Byrd & Woolington (1983).
- 10 Cited in Palmer (1976).
- 11 Cited in Bellrose (1976).
- 12 For parents older than 5 years of age.

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Canada Goose

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2.1.3. Mallard (surface-feeding ducks)

Order *Anseriformes*, Family *Anatidae*. Surface-feeding ducks are the most familiar ducks of freshwater and saltwater wetlands. They feed by dabbling and tipping up in shallow water, often filtering through soft mud for food. They feed primarily on seeds of aquatic plants and cultivated grains, although they also consume aquatic invertebrates, particularly during the breeding season (Jorde et al., 1983; Swanson et al., 1985). All species have a bright colored patch of feathers on the trailing edge of each wing, and the overall plumage of the males is more colorful than that of the females. Dabbling ducks range in size from the green-winged teal (average 37 cm bill tip to tail tip) to the northern pintail (average 66 cm).

Selected species

The mallard (*Anas platyrhynchos*) feeds mostly on aquatic plants, seeds, and aquatic invertebrates, depending on the season, and forages in ponds and wetlands by dabbling and filtering through sediments. It is widespread throughout most of the United States and is the most abundant of the United States ducks (USFWS, 1991). In the past decade, however, its numbers have declined markedly across its principal range in the mid-continental region because of habitat degradation and drought (USFWS, 1991). Mallards interbreed with domestic ducks and black ducks (*Anas rubripes*).

Body size. Mallards average 58 cm from bill tip to tail tip. Male mallards are generally heavier than females (Delnicki and Reinecke, 1986; Whyte and Bolen, 1984; see table). Female mallards lose weight during the laying and incubation periods; males lose weight from their spring arrival through the peak of the breeding season and then gain weight while the females are incubating (Lokemoen et al., 1990a).

Habitat. Wintering mallards prefer natural bottomland wetlands and rivers to reservoirs and farm ponds (Heitmeyer and Vohs, 1984); water depths of 20 to 40 cm are optimum for foraging (Heitmeyer, 1985, cited in Allen, 1987). The primary habitat requirement for nesting appears to be dense grassy vegetation at least a half meter high (Bellrose, 1976). Mallards prefer areas that provide concealment from predators such as seeded cover (fields established on former croplands) (Klett et al., 1988; Lokemoen et al., 1990b), cool-season introduced legumes and grasses (Duebbert and Lokemoen, 1976), and idle grassland with tall, dense, rank cover in the area (Duebbert and Kantrud, 1974). Nests usually are located within a few kilometers of water, but if choice nesting habitat is not available nearby, females may nest further away (Bellrose, 1976; Duebbert and Lokemoen, 1976).

Food habits. In winter, mallards feed primarily on seeds but also on invertebrates associated with leaf litter and wetlands, mast, agricultural grains, and to a limited extent, leaves, buds, stems, rootlets, and tubers (Goodman and Fisher, 1962; Heitmeyer, 1985, cited in Allen, 1987). In spring, females shift from a largely herbivorous diet to a diet of mainly invertebrates to obtain protein for their prebasic molt and then for egg production (Swanson and Meyer, 1973; Swanson et al., 1979; Swanson et al., 1985; Heitmeyer, 1988b). Laying females consume a higher proportion of animal foods on the breeding

grounds than do males or nonlaying females (Swanson et al., 1985). The animal diet continues throughout the summer, as many females lay clutches to replace destroyed nests (Swanson et al., 1979; Swanson et al., 1985). Ducklings also consume aquatic invertebrates almost exclusively, particularly during the period of rapid growth (Chura, 1961). Mallards concentrate in wetlands at night, apparently feeding on emerging insects (Swanson and Meyer, 1973). Flocks may feed in unharvested grain fields and stubble fields during fall and winter (Dillon, 1959). During periods of food shortage, fat reserves are used as an energy source. During breeding, females continue to feed but also use fat to meet the demands of egg production; females may lose 25 percent of their body mass (in fat) during laying and early incubation (Krapu, 1981).

Molt. Female mallards molt into basic plumage in late winter or early spring, except for the wing molt, which is delayed until about the time broods are fledged. In males, head-body-tail molt commences in early summer and overlaps or is followed by the wing molt. Mallards generally are flightless for about 25 days during the wing molt (Palmer, 1976).

Migration. Although the mallard winters in all four waterfowl flyways of North America (i.e., Pacific, Central, Mississippi, and Atlantic), the Mississippi flyway (alluvial valley from Missouri to the Gulf of Mexico) contains the highest numbers (Bellrose, 1976). Human creation and alteration of water bodies and plant communities have changed the migration and wintering patterns of mallards; in North America the ducks winter farther north than in the past (Jorde et al., 1983). Mallards tend to arrive at their wintering grounds in the Mississippi Valley in mid-September through early November and depart for their northerly breeding grounds again in March (Fredrickson and Heitmeyer, 1988). Adult females that reproduce successfully are likely to return to the same nesting ground the following year (Lokemoen et al., 1990a, 1990b).

Breeding activities and social organization. Older females arrive at breeding grounds earlier than yearling birds, which probably increases their chances of reproductive success because they can select the best nest sites (Lokemoen et al., 1990b). First clutches are generally finished by mid-April in the southern part of the breeding range and late April to May in the northern United States (Palmer, 1976). High rates of nest failure require females to reneest persistently to reproduce successfully (Swanson et al., 1985). Average clutch size decreases as the season progresses because the clutch size of reneesting females is smaller than initial clutches (Eldridge and Krapu, 1988; Lokemoen et al., 1990b). Older females produce larger clutches than do yearlings (Lokemoen et al., 1990a). Mallards mate for one breeding season, and males typically leave the females at the onset of incubation (Palmer, 1976). Females remain with the brood until fledging. Mallards are serially monogamous and thus remate annually (Palmer, 1976).

Home range and resources. Each pair of mallards uses a home range, and the drake commonly establishes a territory that he defends against other mallards (Bellrose, 1976). Home-range size depends on habitat, in particular the type and distribution of water habitats (e.g., prairie potholes, rivers), and population density (Bellrose, 1976; Dwyer et al., 1979; Kirby et al., 1985).

Population density. Mallard densities during the breeding season are positively correlated with availability of terrestrial cover for nesting and with availability of wetlands and ponds that provide the aquatic diet of mallards (Pospahala et al., 1974). Availability of suitable wetland habitat for breeding and wintering depends on environmental conditions (e.g., rainfall) (Heitmeyer and Vohs, 1984; Lokemoen et al., 1990a). Average densities of breeding mallards in the prairie pothole region range from 0.006 to 0.67 pairs per hectare (Duebber and Kantrud, 1974; Duebber and Lokemoen, 1976; Kantrud and Stewart, 1977; Lokemoen et al., 1990b). Mallards attain their highest densities in prairie and parkland of the southern prairie provinces and in the Cooper River and Athabasca River deltas of Canada (Johnson and Grier, 1988).

Population dynamics. Nest success or failure is an important factor affecting mallard populations. Mammalian predation is the main cause of nest failure, followed by human disturbance (e.g., farming operations) and adverse weather conditions (Klett et al., 1988; Lokemoen et al., 1988). Mammalian predators include fox, badger, and skunk; crows also prey on mallard nests (Johnson et al., 1988). Mallards usually renest if the first nest fails (Palmer, 1976). Juvenile survival depends on food and preferred habitat availability, factors that in turn are affected by environmental conditions. For example, high rainfall is related to increased wetland area, which is positively correlated with duckling growth (Lokemoen et al., 1990a). Annual adult mortality rates vary with year, location, hunting pressure, age, and sex. Females suffer greater natural mortality rates (e.g., typical values of 40 to 50 percent) than do males (e.g., typical values of 30 to 40 percent) (Chu and Hestbeck, 1989). By fall, there is a higher proportion of males than females in most populations (Bellrose, 1976). Immature mortality rates of 70 percent have been recorded in many areas, although lower immature mortality rates are more common (Bellrose, 1976; Chu and Hestbeck, 1989). Annual mortality rates also are greater in areas with higher hunting pressure (Bellrose, 1976).

Similar species (from general references)

- The American black duck (*Anas rubripes*) is only present in the wooded parts of northeastern and north central United States. It nests near woodland lakes and streams or in freshwater and tidal marshes. It is similar in size (58 cm) to mallards using the same habitats.
- The northern pintail (*Anas acuta*) is widespread, occurring in most parts of North America and breeding throughout Canada and the north central United States. Although formerly fairly abundant, North American pintail populations have declined dramatically during the past decade (USFWS, 1991). It prefers marshes and open areas with ponds and lakes. Pintails average slightly longer (66 cm) than mallards.
- The gadwall (*Anas strepera*) (51 cm) occurs throughout most of the United States. In Canada, its breeding range is limited to the south central potholes region. It is more common in the west than in the east.
- The American wigeon (*Anas americana*) (48 cm) breeds throughout most of Canada and in the prairie pothole regions of the United States. It winters

along both the east and west coasts of the United States as well as farther south into Mexico.

- Northern shovelers (*Anas clypeata*) (48 cm), inhabitants of marshes, ponds, and bays, breed throughout mid to western Canada and the prairie pothole regions of the United States. They winter along the gulf coast, southern Atlantic coast, in Texas, and a few other southwestern states as well as throughout Mexico.
- Blue-winged teal (*Anas discors*) (39 cm) are fairly common in open country in marshes and on ponds and lakes. Breeding populations occur throughout the central United States and Canada, but wintering populations are restricted to Atlantic and Pacific coastal areas.
- The green-winged teal (*Anas crecca*) (37 cm) is the smallest of the dabbling ducks. *A. c. carolinensis* is the most common subspecies in the United States. It breeds throughout most of Canada and the prairie pothole region of the United States. It overwinters in the southern half of the United States and in Mexico.
- Cinnamon teal (*Anas cyanoptera*) (41 cm) breeding populations are restricted to the western United States and Mexico, with few reaching southern Canada. Some populations in California and Mexico are year-round residents.

General references

Allen (1987); National Geographic Society (1987); Pospahala et al. (1974); Palmer (1976); Bellrose (1976).

Mallard Duck (*Anas platyrhynchos*)

<i>Factors</i>	<i>Age/Sex/ Cond./Seas.</i>	<i>Mean</i>	<i>Range or (95% CI of mean)</i>	<i>Location</i>	<i>Reference</i>	<i>Note No.</i>		
Body Weight (g)	A M A F	1,225 1,043	up to 1,814 up to 1,633	throughout North America	Nelson & Martin, 1953			
	A M winter A F winter	1,246 ± 108 SD 1,095 ± 106 SD		western Mississippi (alluvial valley)	Delnicki & Reinecke, 1986			
	A M winter A F winter	1,237 ± 118 SD 1,088 ± 105 SD		Texas	Whyte & Bolen, 1984			
	A F spring	1,197 ± 105 SD		North Dakota	Krapu & Doty, 1979			
	egg	52.2		32.2 - 66.7	North Dakota	Eldridge & Krapu, 1988		
	at hatching	32.4 ± 2.4 SD			central North Dakota	Lokemoen et al., 1990a		
	B at 3.5 days	32.4 ± 2.4 SD			central North Dakota	Lokemoen et al., 1990b		
	F at 9.5 days F at 15.5 days F at 30.5 days F fledging at 56.0 days	115 ± 37 SD 265 ± 92 SD 401 ± 92 SD 740 ± 115 SD			central North Dakota	Lokemoen et al., 1990b		
	M at 9.5 days M at 15.5 days M at 30.5 days M fledging at 56.0 days	92 ± 12 SD 215 ± 5 SD 460 ± 93 SD 817 ± 91 SD			central North Dakota	Lokemoen et al., 1990b		
	Body Fat (g lipid)	A M winter A F winter		174 ± 66 SD 171 ± 56 SD		Texas	Whyte & Bolen, 1984	
		A F April Y F April A F June Y F June		106 ± 34 SD 82 ± 37 SD 22 ± 22 SD 9.6 ± 8.3 SD		North Dakota	Krapu & Doty, 1979	

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Mallard

Mallard Duck (*Anas platyrhynchos*)

<i>Factors</i>	<i>Age/Sex/ Cond./Seas.</i>	<i>Mean</i>	<i>Range or (95% CI of mean)</i>	<i>Location</i>	<i>Reference</i>	<i>Note No.</i>
Metabolic Rate (kcal/kg-day)	A F basal	77		Texas	estimated	1
	A M basal	73			Whyte & Bolen, 1984	2
	A F winter	280	(94 - 424)		estimated	3
A M winter	220	(91 - 408)				
Food Ingestion Rate (g/g-day)						4
Water Ingestion Rate (g/g-day)	A F	0.058			estimated	5
	A M	0.055				
Inhalation Rate (m ³ /day)	A F	0.42			estimated	6
	A M	0.48				
Surface Area (cm ²)	A F	1,030			estimated	7
	A M	1,148				
<i>Dietary Composition</i>				<i>Location/Habitat (measure)</i>	<i>Reference</i>	<i>Note No.</i>
adults:			Winter	Louisiana/coastal marsh and prairie (% volume; gullet contents)	Dillon, 1959	
rice			24			
jungle rice			21			
brownseed paspalum			19			
barnyard grass			8.0			
red rice			8.0			
knot grass			6.5			
signal grass			2.5			
coast cockspur			1.9			
Mamaica sawgrass			1.3			
snails			1.0			
other			6.8			

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Mallard

Mallard Duck (*Anas platyrhynchos*)

<i>Dietary Composition</i>				Location/Habitat (measure)	Reference	Note No.
breeding female: (total animal)	April (67.8)	May (66.8)	June (89.4)	south central North Dakota/prairie potholes (% wet volume; esophagus contents)	Swanson et al., 1985	
gastropods	trace	24.9	16.5			
insects	13.1	25.6	48.1			
crustacea	7.9	15.1	13.9			
annelids	38.3	0.2	10.9			
misc. animal	8.5	1.0	-			
(total plant)	(32.2)	(33.2)	(10.6)			
seeds	28.7	28.7	10.6			
tubers	2.4	4.3	-			
stems	1.1	0.2	-			
<i>Population Dynamics</i>	Age/Sex Cond./Seas.	Mean	Range	Location/Habitat	Reference	Note No.
Home Range Size (ha)	spring: A F total	468 ± 159 SD	307 - 719	North Dakota/prairie potholes	Dwyer et al., 1979	
	A F laying	111 ± 76 SD	38 - 240			
	spring: A F	540	40 - 1,440	Minnesota/wetlands, river	Kirby et al., 1985	
	A M	620	70 - 1,140			
Population Density (pairs/ha)	A B spring (area 1)	0.036	0.006 - 0.076	central North Dakota/range of 6 years of data from two different pothole areas	Lokemoen et al., 1990a	
	A B spring (area 2)	0.047	0.031 - 0.087			
Clutch Size	yearling A	9.3 ± 1.7 SE 10.3 ± 1.1 SE 9	1 - 18	North Dakota/prairie potholes NS/NS	Krapu & Doty, 1979 Bellrose, 1976	
Clutches /Year	if lost		up to 4.5	North Dakota/experimental ponds (nests purposely destroyed)	Swanson, unpublished in Swanson et al., 1985	
	if successful	1		North America/NS	Bellrose, 1976	
Days Incubation		26 25	23 - 29	NS/NS North Dakota/wetlands	Bent, 1923 Klett & Johnson, 1982	8

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Mallard

Mallard Duck (*Anas platyrhynchos*)

<i>Population Dynamics</i>	<i>Age/Sex Cond./Seas.</i>	<i>Mean</i>	<i>Range</i>	<i>Location/Habitat</i>	<i>Reference</i>	<i>Note No.</i>
Age at Fledging (days)		52 - 60		NS/NS	Bellrose, 1976	
		56		central North Dakota/ potholes	Lokemoen et al., 1990a	
Percent Nests Successful		51 - 61		South Dakota/prairie potholes and fields	Duebber & Lokemoen, 1976	
		9 - 10		eastern South Dakota/ potholes	Klett et al., 1988	
Number Fledge per Successful Nest		4.9		NS/NS	Cowardin & Johnson, 1979	9
		8.4		United States/NS	Bellrose, 1976	
Age at Sexual Maturity		1 yr		United States/NS	Krapu & Doty, 1979	
Annual Mortality Rates (percent)	A M	27.2		eastern-central flyway/NS	Bellrose, 1976	
	A F	38.2				
	A M fall	40.1 ± 3.1 SE	22 - 51	western mid-Atlantic/NS 1971 to 1985	Chu & Hestbeck, 1989	
	J M fall	41.1 ± 7.2 SE	31 - 59			
	A F fall	49.9 ± 3.3 SE	20 - 72			
	J F fall	48.8 ± 6.0 SE	15 - 68			
	A M fall	39.0 ± 2.3 SE	9 - 60	northeastern United States/NS 1971 to 1985	Chu & Hestbeck, 1989	
J M fall	48.1 ± 5.3 SE	7 - 69				
A F fall	51.5 ± 1.9 SE	33 - 64				
J F fall	56.8 ± 3.2 SE	38 - 68				
<i>Seasonal Activity</i>	<i>Begin</i>	<i>Peak</i>	<i>End</i>	<i>Location</i>	<i>Reference</i>	<i>Note No.</i>
Mating	early April	May early May	mid-July	CA, UT, MT, SD, NY, VT south central N Dakota	Bellrose, 1976 Krapu & Doty, 1979	
Hatching		June		NW Territory, Canada	Toft et al., 1984	

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Mallard

Mallard Duck (*Anas platyrhynchos*)

<i>Seasonal Activity</i>	Begin	Peak	End	Location	Reference	Note No.
Molt spring fall	December mid-Sept.		March November	Mississippi Valley	Fredrickson & Heitmeyer, 1988	
Migration spring fall	mid-March mid-October	November	mid-May	arrive north central US leave northern US	Johnson et al., 1987 Palmer, 1976	

- 1 Estimated using equation 3-28 (Lasiewski and Dawson, 1967) and body weights from Nelson and Martin (1953).
- 2 Estimated daily existence energy at 0°C.
- 3 Estimated using equation 3-37 (Nagy, 1987) and body weights from Nelson and Martin (1953).
- 4 See Chapters 3 and 4 for methods of estimating food ingestion rates from free-living metabolic rate and dietary composition.
- 5 Estimated using equation 3-15 (Calder and Braun, 1983) and body weights from Nelson and Martin (1953).
- 6 Estimated using equation 3-19 (Lasiewski and Calder, 1971) and body weights from Nelson and Martin (1953).
- 7 Estimated using equation 3-21 (Meeh, 1879 and Rubner, 1883, as cited in Walsberg and King, 1978) and body weights from Nelson and Martin (1953).
- 8 Cited in Palmer (1976).
- 9 Cited in Johnson et al. (1987).

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2.1.4. Lesser Scaup (bay ducks)

Order *Anseriformes*, Family *Anatidae*. Bay ducks are adapted for diving and characteristically need a running start to become airborne because their legs are located further back on their body than on other ducks. They breed at mid to high latitudes and winter in flocks on large water bodies and in protected coastal bays and river mouths. Bay ducks dive for their food, and their diet is omnivorous (i.e., both plant and animal matter) and depends on the seasonal and regional abundance of food resources. Because of their food habits, bay ducks prefer deeper, more permanent ponds than dabbling ducks (Bellrose, 1976). The sexes vary in coloration, and different bay duck species range in length from 42 to 53 cm (bill tip to tail tip).

Selected species

The lesser scaup (*Aythya affinis*) is one of the most abundant North American ducks (Allen, 1986). They breed principally throughout western Canada and Alaska, although their breeding range extends into the western United States as far south as Colorado and Ohio. Lesser scaup winter in the United States in the Mississippi flyway and the Atlantic flyway (Bellrose, 1976). They also winter along all coastal areas in the southern states and into Mexico (National Geographic Society, 1987).

Body size. The lesser scaup averages 42 cm from bill tip to tail tip. Males are larger and more colorful than the brown females (Bellrose, 1976; see table). Following their postbreeding molt, scaups increase their fat reserves in preparation for migration (Austin and Fredrickson, 1987; see table).

Habitat. Lesser scaup are found on large lakes and bays during the fall and winter and are common on smaller bodies of water (e.g., ponds) during the spring. They breed in the prairie potholes region, most often on permanent or semipermanent wetlands of 0.85 to 2.0 ha with trees and shrubs bordering at least half of the shorelines (Bellrose, 1976; Smith, 1971, cited in Allen, 1986). Primary brood habitat is characterized by permanent wetlands dominated by emergent vegetation (Smith, 1971, cited in Allen, 1986). In a study of ducks wintering in South Carolina, Bergan and Smith (1989) found lesser scaup would forage primarily in areas with submergent vegetation but also in areas of emergent vegetation, shallow open water, and floating-leaved vegetation. They found some differences in foraging habitat use by season and between males and females. In particular, females tended to use more shallow habitats than males, and males preferred open water in late fall (Bergan and Smith, 1989).

Food habits. Most populations of lesser scaup consume primarily aquatic invertebrates, both from the water column and from the surfaces of aquatic vegetation and other substrates (Tome and Wrubleski, 1988; Bartonek and Hickey, 1969). Common prey include snails, clams, scuds (amphipods), midges, chironomids, and leeches (see table). Scaup are omnivorous, however, and the percentage of plant materials (almost exclusively seeds) in the diet varies seasonally as the availability of different foods changes (Afton et al., 1991; Dirschl, 1969; Rogers and Korschgen, 1966). When seeds are locally abundant, they may be consumed in large quantities (Dirschl, 1969). Breeding females and ducklings

eat mostly aquatic invertebrates (Sugden, 1973). Young ducklings feed primarily on water-column invertebrates (e.g., phantom midges, clam shrimps, water mites), whereas older ducklings forage mainly on bottom-dwelling invertebrates (e.g., scuds or amphipods, dragonflies, caddisflies) (Bartonek and Murdy, 1970). During the winter, there are no significant differences in diet between juveniles and adults or between males and females (Afton et al., 1991).

Molt. Nonbreeding and postbreeding males and nonbreeding females generally leave the breeding grounds in June to molt on lakes. However, some males complete their molt on the breeding grounds (Trauger, 1971, cited in Bellrose, 1976). Large flocks of molting birds become flightless during the wing molt phase, which begins in July and is usually complete by late August (McKnight and Buss, 1962).

Migration. The axis of the main migration corridor extends from the breeding grounds on the Yukon Flats, Alaska, to wintering areas in Florida (Bellrose, 1976). Most scaup winter in the United States, with the greatest numbers in the Mississippi flyway and the Atlantic flyway. They start to arrive at their wintering areas in mid-October (Bellrose, 1976). The timing of northward migration in the spring varies from February to May (Bellrose, 1976). Before migration, scaup gain weight by increasing their body fat content (Austin and Fredrickson, 1987).

Breeding activities and social organization. Scaup build nests on the ground among tall grasses, shrubs, or forbs where plant heights range from 20 to 60 cm (Hines, 1977). Nests can be located along the edge of shorelines to upland areas (Bellrose, 1976). Courtship and pair bonds start to form on the wintering grounds, and pairs typically remain together for only one season. Males do not remain long after incubation commences (Trauger, 1971, cited in Bellrose, 1976). The female and her brood leave the vicinity of the nest shortly after the ducklings have hatched. Most broods are on their own by 4 to 5 weeks of age (Gehrman, 1951, cited in Bellrose, 1976) and fledge between 7 and 9 weeks of age (Bellrose, 1976; Lightbody and Ankney, 1984). Females of this species often lay eggs in other lesser scaup nests (nest parasitism), which can result in large compound clutches of lesser scaup eggs in a single nest (Hines, 1977). Hines (1977) also found that mixing of broods was common in Saskatchewan; by August, groups of 15 to 40 ducklings led by two to three hens would be common. Female lesser scaup also occasionally lay eggs in the nests of other ducks (e.g., gadwall; Hines, 1977).

Home range and resources. Relatively small nesting territories and large highly overlapping foraging ranges are characteristic of lesser scaup (Hammel, 1973, cited in Allen, 1986). Several pairs can nest in close proximity without aggression, each defending only a small area immediately surrounding the nest (Bellrose, 1976; Vermeer, 1970). In Manitoba, Hammel (1973) estimated the mean minimum foraging home range to be 89 ± 6.5 ha. Initial areas occupied by pairs usually contain stumps, logs, boulders, or beaches as loafing sites, but later lesser scaup rely solely on open water (Gehrman, 1951, cited in Bellrose, 1976).

Population density. In winter, local densities of scaup can be very high, as large flocks float on favored feeding areas (Bellrose, 1976). In summer, the density of breeding

pairs increases with the permanence and size of the ponds (Kantrud and Stewart, 1977; see table).

Population dynamics. In some populations, many yearling and some 2-year-olds do not breed; the proportion breeding tends to increase with improving water and habitat conditions (Afton, 1984; McKnight and Buss, 1962). In a 4-year study in Manitoba, Afton (1984) found that, on average, 30 percent of 1-year-olds and 10 percent of 2-year-olds, did not breed. Clutch size and reproductive performance of adult females generally increase with age (Afton, 1984). Most nest failures are due to predation (e.g., by mink, raccoons, red fox), and scaup often attempt to renest if the initial nest fails (Afton, 1984; Bellrose, 1976). Annual mortality for juveniles is higher than that for adults, and adult female mortality exceeds adult male mortality (Smith, 1963; see table).

Similar species (from general references)

- The redhead (*Aythya americana*), a larger bay duck (48 cm), breeds on lakes and ponds in the northwestern United States and in midwestern Canada. They winter in coastal areas and the southern United States and Mexico. In summer, adult female and juvenile redheads consume predominantly animal matter (e.g., caddis flies, midges, water fleas, snails), while males include more plant materials in their diet.
- The canvasback (*Aythya valisineria*) is the largest bay duck (53 cm). They are common on lakes and ponds in the northern United States and southern Canada during the breeding season and along coastal areas of the United States during winter. Studies during the winter in North and South Carolina have found varying diets for canvasbacks, consuming mostly animal matter (e.g., clams); others eat only vegetation. In summer, adult female and juvenile canvasbacks eat predominantly animal material (e.g., caddis flies, snails, mayflies, midges), whereas adult males may eat predominantly vegetable material, particularly tubers of *Potamogeton*.
- The ring-necked duck (*Aythya collaris*) is similar in size (43 cm) to the lesser scaup and prefers freshwater wetlands. They are commonly seen on woodland lakes and ponds, but in winter also use southern coastal marshes. During the winter, ring-necked ducks eat mostly plant materials (81 percent) and a variety of animal matter (19 percent).
- The greater scaup (*Aythya marila*) (46 cm) is common in coastal areas and the Great Lakes during winter. They are omnivorous, eating 50 to 99 percent animal matter and the remainder plant foods during the winter.

General references

Allen (1986); Bartonek and Hickey (1969); Bellrose (1976); National Geographic Society (1987); Perry and Uhler (1982).

Lesser Scaup (*Aythya affinis*)

<i>Factors</i>	<i>Age/Sex/ Cond./Seas.</i>	<i>Mean</i>	<i>Range or (95% CI of mean)</i>	<i>Location or subspecies</i>	<i>Reference</i>	<i>Note No.</i>
Body Weight (g)	F preflightless	688		Manitoba, Canada	Austin & Fredrickson, 1987	1
	F flightless	647				
	F postflightless	693				
	F migratory	842				
	F	770	up to 950	United States	Nelson & Martin, 1953	
	M	860	up to 1,100			
Adult Body Fat (grams lipid: % of total body weight)	F preflightless	50.7 (7.4%)		Manitoba, Canada	Austin & Fredrickson, 1987	1
	F flightless	37.2 (5.7%)				
	F postflightless	46.5 (6.7%)				
	F migratory	188.1 (22.3%)				
Duckling Growth Rate	age in weeks	growth in g/day	(final body weight)	Utah or Canada	Sugden & Harris, 1972	2
	0-3	6.9	(190 g)			
	3-6	14	(485 g)			
	6-9	1.5	(516 g)			
	9-12	1.2	(542 g)			
Metabolic Rate (kcal/kg-day)	A F basal	83			estimated	3
	A M basal	81				
		90				
	A B resting 20 to 30°C	216		Canada	McEwan & Koelink, 1973	
	A F free-living	211	(102 - 457)		estimated	4
	A M free-living		(99 - 445)			
Food Ingestion Rate (g/g-day)	juveniles, both sexes: 1 - 5 weeks 6 - 12 weeks	dry matter intake/ wet body weight 0.162 0.077		Saskatchewan/captive: reared in large brooder and in outdoor pens	Sugden & Harris, 1972	5
Water Ingestion Rate (g/g-day)	A F A M	0.064 0.062			estimated	6
Inhalation Rate (m ³ /day)	A F A M	0.34 0.36			estimated	7

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Lesser Scaup

Lesser Scaup (*Aythya affinis*)

<i>Factors</i>	<i>Age/Sex/ Cond./Seas.</i>	<i>Mean</i>	<i>Range or (95% CI of mean)</i>		<i>Location or subspecies</i>	<i>Reference</i>	<i>Note No.</i>
Surface Area (cm ²)	A F A M	842 906				estimated	8
<i>Dietary Composition</i>	<i>Spring</i>	<i>Summer</i>	<i>Fall</i>	<i>Winter</i>	<i>Location/Habitat (measure)</i>	<i>Reference</i>	<i>Note No.</i>
(animal) midges snails grass shrimp (plant - seeds) bulrush (plant - vegetative) green algae				(60.9) 45.9 7.7 7.3 (36.1) 36.0 (3.0) 2.3	Louisiana/lakes, marshes (% dry weight; esophageal & proventricular contents)	Afton et al., 1991	
juveniles only: (animal) scuds phantom midges clam shrimps dragon/damselflies water bugs water mites caddis flies water beetles mayflies (plants)		(100) 1 ± 1 54 ± 8 30 ± 8 - 4 ± 3 8 ± 3 - 1 ± 1 2 ± 1 (trace)	(100) 57 ± 9 1 ± 1 2 ± 2 17 ± 8 11 ± 7 - 6 ± 5 4 ± 3 - (trace)		Northwest Territories/lake (% wet volume ± SE; esophageal contents)	Bartonek & Murdy, 1970	

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Lesser Scaup

Lesser Scaup (*Aythya affinis*)

<i>Dietary Composition</i>	Spring	Summer	Fall	Winter	Location/Habitat (measure)	Reference	Note No.			
adults only: (animal)	(91.8)		(90.5)		nw Minnesota: spring and fall migrations/lakes, marshes, pools (% dry weight; esophageal & proventricular contents)	Afton et al., 1991				
scuds (amphipods)	33.2		54.9							
dragonflies	-		2.4							
caddis flies	8.8		7.6							
midges	2.3		-							
other insects	4.9		-							
snails	31.9		10.2							
fingernail clams	6.0		5.1							
brook stickleback	-		4.1							
fathead minnow	-		5.0							
other fish	3.5									
(plants - seeds)	(6.0)		(9.4)							
(plants - vegetative)	(2.2)		(0.1)							
(animal)	(90.9)	(75.1)	(49.6)					Saskatchewan, Canada/shallow lakes (% dry weight; esophagus and proventriculus contents)	Dirschl, 1969	
scuds	66.0	9.8	42.5							
diptera	-	1.3	0.1							
leeches	12.0	23.7	1.6							
fingernail clams	12.7	25.7	-							
cyprinid fish	-	2.9	-							
caddis flies	0.2	1.6	1.9							
clam shrimps	-	3.1	0.5							
(plant - seeds)	(9.1)	(24.9)	(50.4)							
Nuphar variegatum	-	13.2	42.8							
other seeds	9.1	11.7	7.6							
<i>Population Dynamics</i>	<i>Age/Sex Cond./Seas.</i>	<i>Mean</i>	<i>Range</i>		<i>Location/Habitat</i>	<i>Reference</i>	<i>Note No.</i>			
Home Range Size (ha)	breeding	89 ± 6.5 SE			Manitoba, Canada	Hammel, 1973	9			

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Lesser Scaup

Lesser Scaup (*Aythya affinis*)

<i>Population Dynamics</i>	<i>Age/Sex Cond./Seas.</i>	<i>Mean</i>	<i>Range</i>	<i>Location/Habitat</i>	<i>Reference</i>	<i>Note No.</i>
Population Density (pairs/ha)	A B seasonal wetland	0.029	13.1 - 58.5	North Dakota/ prairie potholes	Kantrud & Stewart, 1977	10
	A B permanent wetland	0.061				
	A B island in lake	28.9				
Clutch Size		9.47 ± 0.18 SE	7 - 12	Saskatchewan/marsh island	Hines, 1977	
	2nd yr female	10.0 ± 0.2 SE	8 - 12	Manitoba/lake	Afton, 1984	
	4th yr female	12.1 ± 0.2 SE	11 - 14			
Clutches /Year		1, but often renest if lost		NS/NS	Afton, 1984	
Days Incubation		24.8	21 - 27	NS/NS	Vermeer, 1968	10
Age at Fledging (days)	B	65 ± 0.91 SE		Manitoba/captive	Lightbody & Ankney, 1984	
Percent Nests Hatching	1st yr female	26.3		Manitoba/lake	Afton, 1984	
	2nd yr female	22.2				
	3rd yr female	45.5		Saskatchewan/marsh islands	Hines, 1977	
		76				
Percent Broods Surviving	up to 20 days of age	67.5 ± 4.9 SE		Manitoba/lake	Afton, 1984	
Age at First Breeding	M	most in 2nd yr 1 - 2 years		NS/NS Manitoba/lake	Palmer, 1976 Palmer, 1976; Afton, 1984	
	F					
Annual Mortality Rates (percent)	juveniles	68 - 71		NS/NS	Smith, 1963	
	A males	38 - 52				
	A females	49 - 60				

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Lesser Scaup

Lesser Scaup (*Aythya affinis*)

Seasonal Activity	Begin	Peak	End	Location	Reference	Note No.
Mating/Laying	early June early May	early June	early July	Manitoba, Canada Montana	Afton, 1984 Ellig, 1955	10
Hatching	early July	mid-July	early August	NW Territory and Saskatchewan, Canada	Toft et al., 1984; Hines, 1977	
Molt (fall)	July		September	Manitoba, Canada	Austin & Fredrickson, 1987	
Migration spring	early February mid-April	March - April	May	departing United States arriving Manitoba, Canada	Bellrose, 1976 Afton, 1984	
fall	September mid-October	mid- November	mid-November December	Pacific flyway (s OR, n CA) arriving United States	Gammonley & Heitmeyer, 1990 Bellrose, 1976	

- 1 Four stages of feather molt evaluated.
- 2 Ducklings stopped growing at rate typical of wild birds around 6 weeks of age. By 12 weeks, they weighed approximately 200 g less than typical of wild scaup.
- 3 Estimated using equation 3-28 (Lasiewski and Dawson, 1967) and body weights from Nelson and Martin (1953).
- 4 Estimated using equation 3-37 (Nagy, 1987) and body weights from Nelson and Martin (1953).
- 5 Young ducklings maintained in 18 to 27°C brooder, then in outdoor pens with same temperature range. Metabolizable energy of amphipods (estimated to be 3.11 kcal/g dry wt), a typical scaup food, is similar to the commercial diet used in the experiment (3.09 kcal/g dry wt). Ducklings stopped growing as rapidly as would wild ducklings at about 6 weeks of age. For methods of estimating food ingestion rates for adult scaup, see Chapters 3 and 4.
- 6 Estimated using equation 3-15 (Calder and Braun, 1983) and body weights from Nelson and Martin (1953).
- 7 Estimated using equation 3-19 (Lasiewski and Calder, 1971) and body weights from Nelson and Martin (1953).
- 8 Estimated using equation 3-21 (Meeh, 1879 and Rubner, 1883, cited in Walsberg and King, 1978) and body weights from Nelson and Martin (1953).
- 9 Relatively small, highly overlapping, home ranges. Cited in Allen (1986).
- 10 Cited in Bellrose (1976).

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2.1.5. Osprey (*Pandion haliaetus*)

Order *Falconiformes*, Family *Accipitridae*. The only North American member of the subfamily Pandioninae, these large birds of prey have long narrow wings, a sharp hooked bill, and powerful talons. Osprey are found near freshwater or saltwater, and their diet is almost completely restricted to fish. They are adapted for hovering over the water and dive feet-first, seizing fish with their talons (Robbins et al., 1983). Once very rare owing to DDT accumulation in their food (1950's to early 1970's), osprey now are increasing in numbers. In the United States, there are five regional populations of osprey (in order of abundance): Atlantic coast, Florida and gulf coast, Pacific Northwest, western interior, and Great Lakes (Henny, 1983). In North America, osprey breed primarily in a wide band from coast to coast across Canada and the southern half of Alaska, where they are not restricted to coastal and Great Lake areas as they are in the United States. However, osprey are reported from all States during the fall and spring migrations (Henny, 1986).

Body size. The various subspecies of osprey around the world differ in size, and in general females are heavier than males (Poole, 1989a; see table). Osprey found in the United States are considered to be of the subspecies *carolinensis* and average 56 cm from bill tip to tail tip (Robbins et al., 1983) and weigh between 1.2 and 1.9 kg (see table).

Habitat. In the United States, the majority of osprey populations are associated with marine environments, but large inland rivers, lakes, and reservoirs also may support osprey (Henny, 1986, 1988b). Good nesting sites in proximity to open, shallow water and a plentiful supply of fish are the primary resources required for osprey success (Poole, 1989a). The tops of isolated and often dead trees and man-made structures are preferred nesting sites. Osprey often nest in colonies (Poole, 1989a).

Food habits. Osprey are almost completely piscivorous, although they have been observed on occasion taking other prey including birds, frogs, and crustaceans (Brown and Amadon, 1968). Their prey preferences change seasonally with the abundance of the local fish (Edwards, 1988; Greene et al., 1983). Osprey occasionally will pick up dead fish but only if fresh (Bent, 1937). Osprey are most successful catching species of slow-moving fish that eat benthic organisms in shallow waters and fish that remain near the water's surface (Poole, 1989a). Osprey consume all parts of a fish except the larger bones; later, bones and other undigestible parts are ejected in fecal pellets (Bent, 1937).

Molt. Juvenile plumage is fully developed by fledging at about 60 days of age (Henny, 1988b). Juveniles undergo a gradual molt to adult plumage at approximately 18 months of age (Brown and Amadon, 1968). For adults, the basic molt takes place in two phases; the first phase occurs primarily on the wintering grounds prior to spring migration. Completion of the molt occurs in the summer range prior to fall migration (Henny, 1988b).

Migration. Osprey are year-round residents in the most southern parts of their range (e.g., south Florida, Mexico) but are migratory over the rest of their range in the United States and Canada (Poole, 1989a). Studies of banded osprey have shown that the fall migration begins in late August in the north temperate zone, with adults and juveniles

from the eastern and central United States comprising a broad front flying south and then directly across open ocean to their wintering grounds in Central and South America (Poole, 1989a). Spring migration appears to follow the same routes with birds reaching, for example, the Chesapeake Bay area in mid-March (Reese, 1977) and Minnesota by the first half of April (Dunstan, 1973; Henny and Van Velzen, 1972). The majority of migrating osprey appear to follow the coastline, perhaps because they come from coastal colonies or because the coast offers abundant food (Poole, 1989a). After their first migration south, juveniles remain in their wintering grounds for about a year and a half, returning north to the breeding grounds as 2-year-olds (Henny and Van Velzen, 1972).

Breeding activities and social organization. Nonmigratory (i.e., year-round resident) populations breed during the winter; whereas migratory populations breed during the summer (Poole, 1989a). Monogamy is the general rule for osprey; breeding pairs remain together and return to the same nest site year after year (Fernandez and Fernandez, 1977; Henny, 1988b). Colonies of osprey occur in areas such as islands, reservoirs, or lakes that offer secure nesting sites and abundant food (Henny, 1986), but most osprey are solitary nesters, often separated from other nests by tens to hundreds of kilometers (Poole, 1989a). The female performs most of the incubation and relies completely on the male for food from just after mating until the young have fledged (Poole, 1989a). Van Daele and Van Daele (1982) found that ospreys at successful nests incubated 99.5 to 100 percent of the daylight hours; disturbance of the nest during this time can kill the eggs if the adults are kept from returning to the nest for some time. After hatching, the female is in constant attendance at the nest for the first 35 days but may perch nearby at intervals after that (Henny, 1988b). The female distributes the food delivered by the male by biting off pieces to feed to the young (Poole, 1989a). By 30 days, the nestlings have reached 70 to 80 percent of their adult weight and begin to be active in the nest (Poole, 1989a). The young fledge by age 60 to 65 days in nonmigratory populations and by about 50 to 55 days in migratory populations (Henny et al., 1991). After fledging, the young remain dependent on both parents for food usually for an additional 2 to 3 weeks (Poole, 1989a), but dependency can continue up to 6 weeks in the more southern populations (Henny, 1986).

Home range and resources. Osprey build large stick nests in the tops of tall trees or artificial structures such as buoys and radio towers (Poole, 1989a). In the Chesapeake Bay area, less than one third of the 1,450 breeding pairs built their nests in trees, while over half nested on channel markers and duck blinds, and the remainder on miscellaneous man-made structures (Henny et al., 1974). Osprey build their nest at the top of the chosen site, which can make it vulnerable to destruction from high winds (Henny, 1986). If not lost, the same nest often is used year after year, and it can become quite large (e.g., over 2 m tall and 1.5 m across) (Dunstan, 1973; Henny, 1988a). On islands where no predators are present, osprey will nest on the ground (Poole, 1989b). The distance osprey travel from their nests to forage (i.e., foraging radius) depends on the availability of appropriate nest sites near areas with sufficient fish; osprey will travel up to 10 to 15 km to obtain food (Van Daele and Van Daele, 1982).

Population density. Population density depends on the availability and distribution of resources and can be highly variable. Henny (1988a) reported as many as 1.9 nests per hectare in one of the largest osprey colonies in the western United States in 1899, with an

estimated 1.0 to 1.2 nests per hectare occupied that year. Lower densities on the order of 0.005 to 0.1 nests per hectare are more common (see table).

Population dynamics. Breeding data from many locations in the United States and Canada during the years 1950 to 1976 show low productivity (fewer than one chick fledged per active nest on average). Evidence indicates the cause to be egg-shell thinning that resulted from the ospreys' exposure to DDT that had bioaccumulated in fish (Henny and Anthony, 1989; Henny et al., 1977; Poole, 1989a). Thus, data from reproductive studies conducted during this time can only be used with this in mind (Spitzer et al., 1978).^a Because of their terminal position in the aquatic food chain, osprey can be a sensitive indicator of toxic contaminants that bioaccumulate (Henny et al., 1978; Henny, 1988b).

Osprey are only known to start a second clutch if the first one is destroyed (Poole, 1989a). Juveniles do not return to their place of birth until 2 years of age, and they do not breed until their third season (Henny and Van Velzen, 1972). Often, breeding is delayed until 4 to 7 years of age in areas such as the Chesapeake Bay, where good nesting sites are scarce (Poole, 1989b).

General references

Poole (1989a); Brown and Amadon (1968); Henny (1986); Henny (1988b).

^aIn the table beginning on the next page, data on the number fledged per active nest and the number fledged per successful nest are provided only for studies of populations that appeared to be unaffected by DDT.

Osprey (*Pandion haliaetus*)

<i>Factors</i>	<i>Age/Sex/ Cond./Seas.</i>	<i>Mean</i>	<i>Range or (95% CI of mean)</i>	<i>Location (subspecies)</i>	<i>Reference</i>	<i>Note No.</i>
Body Weight (g)	A F	1,568	1,250 - 1,900	NS	Brown & Amadon, 1968	1
	A M	1,403				
	A F courtship	1,880 ± 20 SE	se Massachusetts	Poole, 1984		
	A F incubation	1,925 ± 25 SE				
	A F late nestl.	1,725 ± 25 SE				
	A M courtship	1,480 ± 15 SE				
A M late nestl.	1,420 ± 15 SE	Maryland, Virginia	McLean, 1986			
F at fledging	1,510					
M at fledging	1,210					
Egg Weight (g)		72.2 ± 5.35 SD	66.0 - 81.3	North Carolina <i>(carolinensis)</i>	Whittemore, 1984	
Metabolic Rate (kcal/kg-day)	A F basal	69			estimated	2
	A M basal	71				
	A F free-living	181	(85 - 384)		estimated	3
	A M free-living	186	(87 - 395)			
Food Ingestion Rate (g/g-day)	A F courtship period	0.21		se Massachusetts	Poole, 1983	
Water Ingest. Rate (g/g-day)	A F	0.051			estimated	4
	A M	0.053				
Inhalation Rate (m ³ /day)	A F	0.578			estimated	5
	A M	0.531				
Surface Area (cm ²)	A F	1,353			estimated	6

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Osprey

Osprey (*Pandion haliaetus*)

<i>Dietary Composition</i>	Spring	Summer	Fall	Winter	Location/Habitat (measure)	Reference	Note No.
alewife smelt pollock winter flounder		32 5 53 10			Nova Scotia, Canada/ harbor, bay (% wet weight; observed captures)	Greene et al., 1983	7
starry flounder cutthroat trout		95 5			se Alaska/NS (% wet weight; observed captures, noting fish length)	Hughes, 1983	7
carp crappie		67 33			w Oregon/NS (% wet weight; observed captures, noting fish length)	Hughes, 1983	7
gizzard shad sunfish largemouth bass golden shiner	63 29 5 3				Florida/lake (% of prey caught; identified at nests)	Collopy, 1984	
brown bullhead salmonids northern squawfish yellow perch largescale sucker	37.7 20.8 19.3 11.6 10.6				Idaho/reservoir (% of fish caught; observed captures)	Van Daele & Van Daele, 1982	
Size of fish caught: < 10 cm 11 - 20 cm 21 - 30 cm 31 - 40 cm 41 + cm		3.3 42.1 46.7 6.6 1.3			Idaho/reservoir (% of fish in each size class; determined from remains at nest)	Van Daele & Van Daele, 1982	

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Osprey

Osprey (*Pandion haliaetus*)

<i>Population Dynamics</i>	<i>Age/Sex Cond/Seas</i>	<i>Mean</i>	<i>Range</i>	<i>Location/Habitat</i>	<i>Reference</i>	<i>Note No.</i>
Foraging Radius (km)	A M A B spring A B	1.7 10 3 to 8	0.7 - 2.7 > 1	Minnesota/lakes Nova Scotia/coastal nw California/coastal, bay	Dunstan, 1973 Greene et al., 1983 Koplin, 1981	
Population Density (nests/ha)	A B summer A B spring A B spring A B spring	1.9 0.028 0.10 0.005		Oregon/lake in 1899 only Florida/wetland North Carolina/reservoir North Carolina/lake	Henny, 1988a Eichholz, 1980 Henny & Noltemeier, 1975 Henny & Noltemeier, 1975	
Clutch Size		3.23 ± 0.03 SE 2.84 ± 0.07 SE 2.67 ± 0.07 SE 3.23 ± 0.09 SE 2.82	1 - 4	Atlantic Seaboard/NS Georgia, Florida/NS s California, n Mexico/NS ne United States/NS Idaho/river, lakes	Judge, 1983 Judge, 1983 Judge, 1983 Spitzer, 1980 Henny et al., 1991	
Clutches/Year		1		NS/NS	Poole, 1989a	8
Days Incubation		38.1 ± 3.2 SD	32 - 42 35 - 43	Baja California, Mexico/coastal islands Massachusetts/NS	Judge, 1983 Poole, 1989a	
Age at Fledging (days)	non-migr. pop. migratory pop.	62.5 ± 4.9 SD 54 ± 3.0 SD	52 - 76 48 - 59	Baja California, Mexico/coastal islands Maryland/Chesapeake Bay	Judge, 1983 Stotts & Henny, 1975	9 9
Number Fledge per Active Nest		1.16 1.34 1.58 1.92	0.79 - 1.47 (10 yrs) 1.17 - 1.89 (3 yrs)	N. Carolina/lake S. Carolina/lake Idaho/reservoir e United States/coastal	Whittemore, 1984 Henny & Noltemeier, 1975 Van Daele & Van Daele, 1982 Poole, 1984	

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Osprey

Osprey (*Pandion haliaetus*)

<i>Population Dynamics</i>	<i>Age/Sex Cond/Seas</i>	<i>Mean</i>	<i>Range</i>	<i>Location/Habitat</i>	<i>Reference</i>	<i>Note No.</i>
Number Fledge per Successful Nest		1.7		Baja California, Mexico/coastal islands	Judge, 1983	
		2.14		Idaho/river	Henny et al., 1991	
		1.83		Florida/lake	Collopy, 1984	
		1.79		Delaware/coastal bay	Henny et al., 1977	
		2.05		Montana/lake	Henny et al., 1991	
Age at Sexual Maturity	B B	3 yrs	3 - 5 yrs	New York, Massachusetts/NS North America/NS	Spitzer, 1980 Henny & Wight, 1969	10
Annual Mortality Rates (percent)	1st year	57.3		New York, New Jersey/NS	Henny & Wight, 1969	
	years 2 - 18	18.5 ± 1.8				
	J B	41		NS/NS	Spitzer, 1980	
	A B	15				
Average Longevity	if reach sex. maturity	4.8		NS/NS	Brown & Amadon, 1968	

<i>Seasonal Activity</i>	<i>Begin</i>	<i>Peak</i>	<i>End</i>	<i>Location</i>	<i>Reference</i>	<i>Note No.</i>
Mating	late April	May	mid-June	Delaware, New Jersey	Bent, 1937	
	early Dec. early January	May	late February early March	Minnesota Florida (nonmigratory) Baja California, Mexico (nonmigratory)	Dunstan, 1973 Poole, 1989a Judge, 1983	
Hatching	mid-March	early May	late May	Maryland, Virginia	Bent, 1937	
	late April February	mid-May	mid-June late April	New York/New England Baja California, Mexico (nonmigratory)	Bent, 1937 Judge, 1983	
Migration fall	late August	September	November	most of United States	Henny, 1986	11
	spring			Minnesota North Carolina	Dunstan, 1973 Parnell & Walton, 1977	

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Osprey

Osprey (*Pandion haliaetus*)

- 1 Late nestl. indicates late nestling stage of the breeding season. Cited in Poole (1989a).
- 2 Estimated using equation 3-28 (Lasiewski and Dawson, 1967) and body weights from Brown and Amadon (1968).
- 3 Estimated using equation 3-37 (Nagy, 1987) and body weights from Brown and Amadon (1968).
- 4 Estimated using equation 3-15 (Calder and Braun, 1983) and body weights from Brown and Amadon (1968).
- 5 Estimated using equation 3-19 (Lasiewski and Calder, 1971) and body weights from Brown and Amadon (1968).
- 6 Estimated using equation 3-21 (Meeh, 1879 and Rubner, 1883, cited in Walsberg and King, 1978) and body weights from Brown and Amadon (1968).
- 7 Percent wet weight of food ingested by free-flying osprey estimated by identifying species of fish captured (using binoculars), estimating the length of each fish captured by comparison with osprey, and using laboratory measures of weights and lengths of samples of these fish species.
- 8 Second clutch produced only if first is lost.
- 9 Nestlings in migratory populations fledge at an earlier age than nestlings in nonmigratory populations, such as those in Mexico and south Florida.
- 10 Cited in Henny (1988b).
- 11 Cited in Henny (1986).

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2.1.6. Red-Tailed Hawk (buteo hawks)

Order Falconiformes, Family Accipitridae. The family Accipitridae includes most birds of prey except falcons, owls, and American vultures. Buteo hawks are covered in this section.^b Buteo hawks are moderately large soaring hawks that inhabit open or semi-open areas. They are the most common daytime avian predators on ground-dwelling vertebrates, particularly rodents and other small mammals. They range in size from the broad winged hawk (41 cm bill tip to tail tip) to the ferruginous hawk (58 cm). Hawks egest pellets that contain undigestible parts of their prey, such as hair and feathers, that can be useful in identifying the types of prey eaten (bones usually are digested completely; Duke et al., 1987).

Selected species

The red-tailed hawk (*Buteo jamaicensis*) is the most common *Buteo* species in the United States (National Geographic Society, 1987). Breeding populations are distributed throughout most wooded and semiwooded regions of the United States and Canada south of the tundra (Adamcik et al., 1979), although some populations are found in deserts and prairie habitats. Six subspecies are recognized (Brown and Amadon, 1968). Nesting primarily in woodlands, red-tails feed in open country on a wide variety of small- to medium-sized prey.

Body size. Males of this medium-sized buteo (46 cm) weigh about 1 kg, and females are approximately 20 percent heavier than the males (see table). Otherwise, the sexes look alike (Brown and Amadon, 1968).

Habitat. Red-tails are found in habitats ranging from woodlands, wetlands, pastures, and prairies to deserts (Bohm 1978b; Gates, 1972; MacLaren et al., 1988; Mader, 1978). They appear to prefer a mixed landscape containing old fields, wetlands, and pastures for foraging interspersed with groves of woodlands and bluffs and streamside trees for perching and nesting (Brown and Amadon, 1968; Preston, 1990). Red-tails build their nests close to the tops of trees in low-density forests and often in trees that are on a slope (Bednarz and Dinsmore, 1982). In areas where trees are scarce, nests are built on other structures, occasionally in cactus (Mader, 1978), on rock pinnacles or ledges, or man-made structures (Brown and Amadon, 1968; MacLaren et al., 1988). In winter, night roosts usually are in thick conifers if available and in other types of trees otherwise (Brown and Amadon, 1968).

Food habits. Red-tails hunt primarily from an elevated perch, often near woodland edges (Bohm, 1978a; Janes, 1984; Preston, 1990). Small mammals, including mice, shrews, voles, rabbits, and squirrels, are important prey, particularly during winter. Red-tails also eat a wide variety of foods depending on availability, including birds, lizards, snakes, and large insects (Bent, 1937; Craighead and Craighead, 1956; Fitch et al., 1946). In general, red-tails are opportunistic and will feed on whatever species are most abundant

^bOther members of the family Accipitridae, eagles and the osprey, are covered in Sections 2.1.7 and 2.1.5, respectively.

(Brown and Amadon, 1968). Winter food choices vary with snow cover; when small mammals such as voles become unavailable (under the snow), red-tails may concentrate on larger prey, such as pheasants (Gates, 1972).

Molt. Juveniles molt into adult plumage in a gradual process from the spring (age about 14 months) to summer or early fall (Bent, 1937).

Migration. The more northerly red-tailed hawk populations are migratory while the more southerly are year-round residents (Bent, 1937).

Breeding activities and social organization. Red-tails lay one clutch per year consisting of one to three eggs, although a replacement clutch is possible if the initial clutch is lost early in the breeding season (Bent, 1937). Their nests are large and built of twigs (Bohm, 1978b). Both sexes incubate, but the male provides food for the female during incubation and the entire family following hatching (Brown and Amadon, 1968). The parents continue to feed their young after fledging while they are learning to hunt (Brown and Amadon, 1968).

Home range and resources. Red-tailed hawks are territorial throughout the year, including winter (Brown and Amadon, 1968). Trees or other sites for nesting and perching are important requirements for breeding territories and can determine which habitats are used in a particular area (Preston, 1990; Rothfels and Lein, 1983). Home range size can vary from a few hundred hectares to over 1,500 hectares, depending on the habitat (Andersen and Rongstad, 1989; Petersen, 1979). In a 10-year study in Oregon, Janes (1984) found that the size of red-tail territories and the location of boundaries between territories varied little from year to year, even though individual birds or pairs died and were replaced.

Population density. Population densities generally do not exceed 0.03 pairs per hectare, and usually are lower than 0.005 pairs per hectare (see Appendix). Populations in southern areas such as Florida can increase substantially in the winter with the influx of migrants from the more northerly populations (Bohall and Collopy, 1984).

Population dynamics. Beginning at 2 years of age, most red-tailed hawks attempt to breed, although the proportion breeding can vary by population and environmental conditions (Henny and Wight, 1970, 1972). Average clutch size varies regionally, tending to increase from east to west and from south to north (Henny and Wight, 1970, 1972). In a 10-year study of red-tails in Alberta, Canada, Adamcik et al. (1979) found that the breeding population of adults remained stable despite strong cyclical fluctuations in the density of their main prey, the snowshoe hare, over the years. The mean clutch size for the red-tail population, however, appeared to vary with prey density, from 1.7 to 2.6 eggs/nest (Adamcik et al., 1979). Over the course of the study, about 50 percent of observed nestling losses occurred within 3 to 4 weeks after hatching due to starvation. Most of the variance in yearly mortality of nestlings could be attributed to the amount of food supplied and the frequency of rain. Large raptors such as horned owls also can be important sources of mortality for red-tail nestlings in some areas (Adamcik et al., 1979).

Similar species (from general references)

- The ferruginous hawk (*Buteo regalis*), one of the larger buteos (58 cm), inhabits the dry open country of the western United States.
- The red-shouldered hawk (*Buteo lineatus*) is slightly smaller (53 cm) and feeds on snakes, frogs, crayfish, mice, and some small birds. Its range is east of the Rocky Mountains and in California, with moist mixed woodlands preferred.
- Swainson's hawk (*Buteo swainsoni*) is restricted to the open plains of the western United States. Although it is as large (53 cm) as the red-tail, it preys mostly on insects.
- The broad-winged hawk (*Buteo platypterus*) is one of the smaller buteos (41 cm) and preys on mice, frogs, snakes, and insects. It prefers woodlands and is found almost exclusively east of the Mississippi River.
- Harris' hawk (*Parabuteo unicinctus*) is similar in size (53 cm) to the red-tailed hawk but is restricted to the semiarid wood and brushlands of the southwest. This bird nests in saguaro, mesquite, and yucca and preys on rodents, lizards, and small birds.
- The rough-legged hawk (*Buteo lagopus*) is one of the larger buteos (56 cm). It winters throughout most of the United States in open country but breeds only in the high arctic of North America.
- The zone-tailed hawk (*Buteo albonotatus*) is slightly smaller (51 cm) than most buteos and feeds on rodents, lizards, fish, frogs, and small birds. It can be found in mesa and mountain country within its limited range between the southwest United States and Mexico.
- The short-tailed hawk (*Buteo brachyurus*) is the smallest buteo (39 cm) and can only be found in the southern tip of Florida in mixed woodland and grassland habitats.

General references

Brown and Amadon (1968); Craighead and Craighead (1956); Fitch et al. (1946); National Geographic Society (1987).

Red-Tailed Hawk (*Buteo jamaicensis*)

<i>Factors</i>	<i>Age/Sex/ Cond./Seas.</i>	<i>Mean</i>	<i>Range or (95% CI of mean)</i>	<i>Location</i>	<i>Reference</i>	<i>Note No.</i>
Body Weight (g)	A F	1,224		Michigan, Pennsylvania	Craighead & Craighead, 1956	1
	A M	1,028				
	A F	1,154		sw Idaho	Steenhof, 1983	
	A M	957				
	A F	1,235		Ohio	Springer & Osborne, 1983	
	A M	1,204				
	hatchling F	58				
	hatchling M	57				
juvenile F	1,149					
juvenile M	962					
Metabolic Rate (IO_2 /kg-day)	A B standard MR /spring	17.7 ± 5.9 SD		Michigan/metabolism chamber	Pakpahan et al., 1989	
Metabolic Rate (kcal/kg-day)	A F basal	73		California/mountains	estimated	2
	A M basal	77			Soltz, 1984	3
	A M breeding	109	(91 - 408)		estimated	4
	A F breeding	102				
A F free-living	192	(95 - 426)				
A M free-living	201					
Food Ingestion Rate (g/g-day)	A F winter	0.11		Michigan/captive outdoors	Craighead & Craighead, 1956	5
	A M winter	0.10				
	A M summer	0.086				
Water Ingestion Rate (g/g-day)	A F	0.055			estimated	6
	A M	0.059				
Inhalation Rate (m^3 /day)	A F	0.48			estimated	7
	A M	0.42				
Surface Area (cm^2)	A F	1,147			estimated	8
	A M	1,021				

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Red-Tailed Hawk

Red-Tailed Hawk (*Buteo jamaicensis*)

Dietary Composition	Spring	Summer	Fall	Winter	Location/Habitat (measure)	Reference	Note No.
summary of 10 years: snowshoe hare Richard's ground squirrel Franklin's ground squirrel voles & mice other mammals waterfowl ruffed grouse sharp-tailed grouse other grouse other birds		mean \pm SD 25.6 \pm 19 30.4 \pm 10 5.1 \pm 2 4.8 \pm 2 7.8 \pm 6 16.2 \pm 10 2.0 \pm 2 1.2 \pm 1 0.9 \pm 1 6.3 \pm 3			Alberta, Canada/ farm & woodlands (% wet weight of prey brought to chicks)	Adamcik et al., 1979	9
(mammals) Belding's ground squirrel mtn cottontail pocket gopher Townsend's ground squirrel (birds) <i>Alectoris graeca</i> western meadowlark (snakes) gopher snake	(78.5) 52.8 13.1 7.3 2.9 (8.5) 3.5 1.8 (13.1) 6.1				nc Oregon/ pasture and wheat fields (% wet weight of prey brought to nests; March to June)	Janes, 1984	9
ground squirrel rabbit pocket gopher other mammals gopher snake whiptail lizard birds		60.8 26.5 4.3 2.6 3.8 0.3 1.3			c California/foothills (% wet weight of prey brought to nests)	Fitch et al., 1946	9

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Red-Tailed Hawk

Red-Tailed Hawk (*Buteo jamaicensis*)

<i>Population Dynamics</i>	<i>Age/Sex Cond./Seas.</i>	<i>Mean</i>	<i>Range</i>	<i>Location/Habitat</i>	<i>Reference</i>	<i>Note No.</i>
Territory Size (ha)	A B spring	60 - 160		c California/foothills	Fitch et al., 1946	10
	A B winter	697 ± 316 SD	381 - 989	s Michigan/fields, woodlots	Craighead & Craighead, 1956	
	A B fall	1,770	957 - 2,465	Colorado/upland prairie, pinyon-juniper woodlands	Andersen & Rongstad, 1989	
Population Density	summer: A B	pairs/ha: 0.0017 - 0.0050		Colorado/open aspen	McGovern & McNurney, 1986	
	A B area a A B area b	0.0004 0.0012	0.0002 - 0.0005 0.0010 - 0.0013	s Michigan/fields, woodlots	Craighead & Craighead, 1956	
	A B	0.0012	0.0010 - 0.0015	Alberta, Canada/farm, woodlands	Adamcik et al., 1979	
	winter: B B	N/ha: 0.014		Toronto, Canada/mixed old fields	Baker & Brooks, 1981	
	B B	0.0015 ± 0.0003 SD	0.0012 - 0.0018	s Michigan/fields, woodlots	Craighead & Craighead, 1956	
Clutch Size		2.0 ± 0.77 SD 2.32 2.2 2.11 2.96	1 - 3 1.9 - 2.6 /10 yrs	c California/foothills Arizona/desert Alberta, Canada/farm, woodlands Florida/NS Oregon, Washington/NS	Fitch et al., 1946 Mader, 1978 Adamcik et al., 1979 Henny & Wight, 1972 Henny & Wight, 1970	
Clutches/Year		1			Bent, 1937	
Days Incubation		32		Alberta, Canada	Adamcik et al., 1979	

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Red-Tailed Hawk

Red-Tailed Hawk (*Buteo jamaicensis*)

<i>Population Dynamics</i>	<i>Age/Sex Cond./Seas.</i>	<i>Mean</i>	<i>Range</i>	<i>Location/Habitat</i>	<i>Reference</i>	<i>Note No.</i>
Growth Rate	to 1 week 1 to 2 weeks 2 to 3 weeks 3 to 4 weeks 4 to 5 weeks	20 g/day 34 g/day 39 g/day 26 g/day 10 g/day		Ohio/free-living, habitat NS	Springer and Osborne, 1983	11
Age at Fledging		45 to 46 days		California/foothills	Fitch et al., 1946	
Number Fledge per Active Nest	high prey low prey	1.47 ± 0.25 SE 1.15 1.9 1.2	0.28 - 1.90/ 10 yrs	Oregon/pasture Alberta, Canada/farm, woodlands Idaho/canyon, shrub steppe	Janes, 1984 Adamcik et al., 1979 Steenhof & Kochert, 1985	
Number Fledge per Successful Nest		2.12 1.85		north of 42°N latitude/ North America south of 42°N latitude/ North America	Henny & Wight, 1970 Henny & Wight, 1970	12 12
Age at Sexual Maturity	B	2 years		throughout range	Henny & Wight, 1970	
Annual Mortality Rates (percent)	J B 1st year A B J B 1st year A B	62.4 20.6 ± 1.3 SE 66.0 23.9 ± 2.2 SE		north of 42°N latitude/ North America south of 42°N latitude/ North America	Henny & Wight, 1970, 1972 Henny & Wight, 1970, 1972	13 13
Longevity			maximum 18 yrs	North America/NS	Henny & Wight, 1970, 1972	
<i>Seasonal Activity</i>	<i>Begin</i>	<i>Peak</i>	<i>End</i>	<i>Location</i>	<i>Reference</i>	<i>Note No.</i>
Mating	mid-February mid-April late March	early May	early April mid-May early April	Arizona Alberta Canada south Michigan	Mader, 1978 Luttich et al., 1971 Craighead & Craighead, 1956	

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Red-Tailed Hawk

Red-Tailed Hawk (*Buteo jamaicensis*)

<i>Seasonal Activity</i>	<i>Begin</i>	<i>Peak</i>	<i>End</i>	<i>Location</i>	<i>Reference</i>	<i>Note No.</i>
Hatching	late March mid-May late April	early June	early May mid-June early May	Arizona Alberta, Canada south Michigan	Mader, 1978 Luttich et al., 1971 Craighead & Craighead, 1956	
Fall Migration			mid-October late October late November	Montana, Alberta, Canada North Dakota Minnesota	Bent, 1937; Luttich et al., 1971 Bent, 1937 Bent, 1937	14
Spring Migration	late February mid-March early April	early March		south Michigan Maine, Montana Alberta, Canada	Craighead & Craighead, 1956 Bent, 1937 Luttich et al., 1971	15

- 1 Estimated from data provided by authors.
- 2 Estimated using equation 3-28 (Lasiewski and Dawson, 1967) and body weights from Craighead and Craighead (1956).
- 3 Estimated from time and energy budgets for breeding season only.
- 4 Estimated using equation 3-37 (Nagy, 1987) and body weights from Craighead and Craighead (1956).
- 5 Hawks maintained outdoors using falconer's techniques; fed lean raw beef supplemented with natural prey. Overall activity levels not described. Winter temperatures averaged 3 to 5°C and summer temperatures averaged 15°C during trials. Females weighed 1,218 g; males in winter weighed 1,147 g; males in summer weighed 855 g.
- 6 Estimated using equation 3-15 (Calder and Braun, 1983) and body weights from Craighead and Craighead (1956).
- 7 Estimated using equation 3-19 (Lasiewski and Calder, 1971) and body weights from Craighead and Craighead (1956).
- 8 Estimated using equation 3-21 (Meeh, 1879 and Rubner, 1883, as cited in Walsberg and King, 1978) and body weights from Craighead and Craighead (1956).
- 9 Percent biomass (wet weight) estimated from observations of prey brought to the nest (identified to species) and remains of prey found at the nests, using standard wet weights for each species of prey from other studies or measured in the lab.
- 10 Home range determined by 95 percent ellipse method; radio-tagged hawks, two of each sex.
- 11 Estimated from figure.
- 12 Summarizing data from several studies.
- 13 Summarizing banding recoveries prior to 1951.
- 14 Late departure dates.
- 15 Early arrival dates.

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2.1.7. Bald Eagle (eagles)

Order *Falconiformes*, Family *Accipitridae*. Eagles have long rounded wings, large hooked bills, sharp talons, and are the largest birds of prey in the United States. They swoop down on their prey at high speeds, and their diet varies by species and considerably by habitat. In most species, the male is smaller than the female, but otherwise the sexes are similar in appearance. This family also includes kites and hawks.

Selected species

The bald eagle (*Haliaeetus leucocephalus*), our national symbol, is a federally designated endangered species. Relatively common in Alaska, populations in the lower 48 States have been seriously diminished, although they are recovering in some areas. Bald eagles are most commonly sighted in coastal areas or near rivers or lakes. Bald eagles are primarily carrion feeders.

Body size. Females are significantly larger than males, but otherwise the sexes look alike (Brown and Amadon, 1968). Body size increases with latitude and is the sole basis by which the northern and southern subspecies are divided (Snow, 1973). Length from bill tip to tail tip averages 81 cm in the more northerly populations.

Habitat. Bald eagles generally are restricted to coastal areas, lakes, and rivers (Brown and Amadon, 1968), although some may winter in areas not associated with water (Platt, 1976). Preferred breeding sites include proximity to large bodies of open water and large nest trees with sturdy branches (often conifers) and areas of old-growth timber with an open and discontinuous canopy (Andrew and Mosher, 1982; Anthony et al., 1982; Grubb, 1980; Peterson, 1986). In an analysis of more than 200 nests, Grubb (1980) found 55 percent within 46 m of a shoreline and 92 percent within 183 m of shore. During migration and in winter, conifers often are used for communal roosting both during the day and at night, perhaps to minimize heat loss (Anthony et al., 1982; Stalmaster, 1980). Mature trees with large open crowns and stout, horizontal perching limbs are preferred for roosting in general (Anthony et al., 1982; Chester et al., 1990). Bald eagles reach maximum densities in areas of minimal human activity and are almost never found in areas of heavy human use (Peterson, 1986).

Food habits. Primarily carrion feeders, bald eagles eat dead or dying fish when available but also will catch live fish swimming near the surface or fish in shallow waters (Brown and Amadon, 1968). In general, bald eagles can be described as opportunistic feeders, taking advantage of whatever food source is most plentiful and easy to scavenge or to capture, including birds and mammals (Brown and Amadon, 1968; Green, 1985; Watson et al., 1991). In many areas, especially in winter, waterfowl, killed or injured by hunters, and shore birds are an important food source (Todd et al., 1982). Eagles forage in upland areas in the winter when surface waters are frozen over, consuming carrion including rabbits, squirrels, and dead domestic livestock such as pigs and chickens (Brown and Amadon, 1968; Harper et al., 1988). Bald eagles also have been known to steal food from other members of their own species as well as from hawks, osprey, gulls, and mergansers (Grubb, 1971; Jorde and Lingle, 1988; Sobkowiak and Titman, 1989). This

may occur when there is a shortage of a primary food source, such as fish, and an abundance of other prey such as waterfowl being used by other predatory birds (Jorde and Lingle, 1988). Some prey are important to a few populations; for example, in the Chesapeake Bay region, turtles are consumed during the breeding season (Clark, 1982), and at Amchitka Island in Alaska, sea otter pups are found regularly in bald eagle nests (Sherrod et al., 1975). In the Pacific Northwest during the breeding season, Watson et al. (1991) found that bald eagles hunted live prey 57 percent of the time, scavenged for 24 percent of their prey, and pirated 19 percent (mostly from gulls or other eagles). Because bald eagles scavenge dead or dying prey, they are particularly vulnerable to environmental contaminants and pesticides (e.g., from feeding on birds that died from pesticides, consuming lead shot from waterfowl killed or disabled by hunters) (Henny and Anthony, 1989; Harper et al., 1988; Lingle and Krapu, 1988). Bald eagles also are vulnerable to biomagnification of contaminants in food chains. For example, near Lake Superior (WI), herring gulls, which were consumed by over 20 percent of nesting bald eagle pairs, were found to be a significant source of DDE and PCB intake by the eagles (Kozie and Anderson, 1991). The gulls contained higher contaminant levels than the local fish because of their higher trophic level.

Molt. Adult eagles molt yearly. In northern populations, molting occurs from late spring to early fall; in southern populations, molting may be initiated earlier (McCullough, 1989). It is likely that the molt is not complete, and that some feathers are retained for 2 years. Young bald eagles generally molt into their adult plumage by their fifth year (McCullough, 1989).

Migration. Bald eagles migrate out of areas where lakes are completely frozen over in winter, but will remain as far north as the availability of open water and a reliable food supply allow (Brown and Amadon, 1968). Areas with ice-free waterways, such as the Columbia River estuary in Washington and Oregon, may support both resident and migratory populations in the winter (Watson et al., 1991). The far northern breeding populations migrate south for the winter and often congregate in areas with abundant food, particularly the Mississippi Valley and the northwestern States (Snow, 1973). Some populations of eagles that breed in southern latitudes (e.g., Arizona, Florida) show a reverse migration and migrate north in midsummer (following breeding), returning south in early autumn or winter (Brown and Amadon, 1968; Grubb et al., 1983).

Breeding activities and social organization. Bald eagles have been observed to nest successfully at 4 years of age, but most do not breed until at least their fifth year (Nye, 1983). Breeding pairs remain together as long as both are alive (Brown and Amadon, 1968). Large stick nests (approximately 1.5 m across and 0.6 m deep) are built near water and most often in a large tree, but sometimes on rocky outcrops or even on the ground on some islands (Brown and Amadon, 1968; Grubb, 1980). In the absence of disturbance, the same nest site may be used for many years (Nash et al., 1980). In Florida, eggs are laid in late autumn or winter, while over the rest of the eagle's range, mating and egg laying occur in spring (Brown and Amadon, 1968). Clutch sizes are larger in the north, and both sexes take responsibility for feeding the young (Brown and Amadon, 1968). Young fledge at about 10 to 12 weeks of age; after leaving the nest, they are still dependent on their parents for several weeks and often return to the nest for food (Sprunt et al., 1973). After nesting, large groups will often gather at sites with plentiful food

resources, such as along rivers following a salmon spawn (Fitzner and Hanson, 1979; Keister et al., 1987; McClelland, 1973).

Home range and resources. During the breeding season, eagles require large areas in the vicinity of open water, with an adequate supply of nesting trees (Brown and Amadon, 1968). Distance from human disturbance is an important factor in nest site selection, and nests have been reported to fail as a result of disturbance (Andrew and Mosher, 1982). During incubation and brooding, eagles show territorial defense of an area around the nest site. Following fledging, there is little need for nest defense, and eagles are opportunistic in their search for abundant sources of prey (Mahaffy and Frenzel, 1987). During winter, eagles roost communally in large aggregations and share a foraging home range. For example, Opp (1980) described a population of 150 eagles that fed on meadow voles in a 250-ha flooded field for a 4-week period. This group also established a communal night roost in the vicinity.

Population density. Because population density depends strongly on the configuration of the surface water bodies used for foraging, few investigators have published explicit density estimates on an area basis; most report breeding densities along a shoreline on a linear basis. During the breeding season, 0.03 to 0.4 pairs have been recorded per km shore (see table). Eagles migrating south from their summer territories in Canada have aggregated in communal roosts of up to 400 eagles in a 40-ha area (Crenshaw and McClelland, 1989). In the winter, communal roost sites may also contain large numbers of eagles. Opp (1980) described a group of 150 eagles that roosted and foraged together in the Klamath Basin (OR/CA), and communal night roosts of up to 300 eagles in Oregon in late winter.

Population dynamics. Not all adults in an area are part of the breeding population. Some pairs may establish territories and not breed, while others may not even pair. The percentage of adults breeding and the breeding success of those that do vary with local food abundance, weather, and habitat conditions (Hansen, 1987; Hansen and Hodges, 1985; McAllister et al., 1986). In past years, bioaccumulation of organochlorine pollutants reduced the reproductive success of bald eagles. Now, in many areas, these raptors are reproducing at rates similar to those prior to the widespread use of these pesticides (Green, 1985). Eagles lay one clutch per year, although replacement clutches may be laid upon loss of the initial one (Sherrod et al., 1987). Very little is known about mortality rates of bald eagles; Grier (1980) concluded from population models that adult survival is more important than reproductive rate to the continued success of bald eagle populations. In captivity, bald eagles have lived for up to 50 years (Snow, 1973), and one wild eagle, banded and recaptured in Alaska, was estimated to be almost 22 years old (Cain, 1986). Upon loss of an initial clutch, bald eagles may lay replacement clutches if sufficient time remains (Sherrod et al., 1987).

Similar species (from general references)

- The golden eagle (*Aquila chrysaetos*) is similar in size (81 cm) to the bald eagle, and its range encompasses all but the southeastern United States. Small mammals, snakes, birds, and carrion are primary prey items, and golden eagles prefer mountainous or hilly terrain.

General references

Brown and Amadon (1968); Green (1985); Peterson (1986); Stalmaster and Gessaman (1982, 1984).

Bald Eagle (*Haliaeetus leucocephalus*)

<i>Factors</i>	<i>Age/Sex/ Cond./Seas.</i>	<i>Mean</i>	<i>Range or (95% CI of mean)</i>	<i>Location or subspecies</i>	<i>Reference</i>	<i>Note No.</i>
Body Weight (g)	J F summer	5,089	4,359 - 5,756 3,524 - 4,568	Alaska	Imler & Kalmbach, 1955	1
	J M summer	4,014				
	A F	4,500		Florida	Wiemeyer, 1991 (pers. comm.)	
	A M	3,000				
	egg	120.6 ± 8.2 SD				
	egg	102.5 ± 17.9 SD	108 - 134	Wisconsin	Krantz et al., 1970 Krantz et al., 1970	
	at hatching	91.5 ± 5.2 SD	71 - 125	Florida	Bortolotti, 1984b	
	nestlings:					
	M 10 days	500 (est.)	3,575 - 4,500	Saskatchewan, Canada	Bortolotti, 1984a,b	2
	M 30 days	2,700 (est.)				
M 50 days	3,600 (est.)					
M 60 days	4,066 ± 35.1 SE					
F 10 days	500 (est.)	4,800 - 5,600	Saskatchewan, Canada	Bortolotti, 1984a,b	2	
F 30 days	3,000 (est.)					
F 50 days	4,600 (est.)					
F 60 days	5,172 ± 46.5 SE					
Metabolic Rate (kcal/kg-day)	free-living			Connecticut	Craig et al., 1988	3
	A winter	99				
	J winter	111				
	A F free-living	135	(62 - 290)		estimated	4
	A M free-living	143	(66 - 307)			

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Bald Eagle

Bald Eagle (*Haliaeetus leucocephalus*)

<i>Factors</i>	<i>Age/Sex/ Cond./Seas.</i>	<i>Mean</i>	<i>Range or (95% CI of mean)</i>	<i>Location or subspecies</i>	<i>Reference</i>	<i>Note No.</i>	
Food Ingestion Rate (g/g-day)	winter: B B salmon B B rabbit B B duck	0.092 ± 0.026 SD 0.075 ± 0.013 SD 0.065 ± 0.012 SD		Utah (captive)	Stalmaster & Gessaman, 1982		
	A B subadult B juvenile B	0.12 0.10 0.091		Washington (free-flying)	Stalmaster & Gessaman, 1984	5	
	A B juvenile B	0.12 0.14		Connecticut (free-flying)	Craig et al., 1988	6	
Water Ingestion Rate (g/g-day)	A F A M	0.035 0.037			estimated	7	
Inhalation Rate (m ³ /day)	A F A M	1.43 1.19			estimated	8	
Surface Area (cm ²)	A F A M	2,970 2,530			estimated	9	
<i>Dietary Composition</i>	<i>Spring</i>	<i>Summer</i>	<i>Fall</i>	<i>Winter</i>	<i>Location/Habitat (measure)</i>	<i>Reference</i>	<i>Note No.</i>
mallard American widgeon American coot other birds Chinook salmon sucker European carp other fish unaccounted				32 9 9 3 21 4 1 1 20	Washington/river (% biomass; prey remains found below communal roost)	Fitzner & Hanson, 1979	

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Bald Eagle

Bald Eagle (*Haliaeetus leucocephalus*)

<i>Dietary Composition</i>	Spring	Summer	Fall	Winter	Location/Habitat (measure)	Reference	Note No.
brown bullhead white sucker chain pickerel smallmouth bass white perch other fish black duck other birds mammals		24.8 19.5 20.1 3.8 3.6 4.9 3.0 13.5 6.8			Maine/inland river (% occurrence in pellets) samples from all seasons except winter	Todd et al., 1982	
(fish) channel catfish Sonora sucker carp other fish (birds) American coot great blue heron (mammals) desert cottontail jackrabbit rock squirrel (reptiles)		(57.6) 21.8 8.6 17.3 8.5 (14.1) 8.1 4.4 (28.1) 8.1 14.9 1.1 (0.2)			central Arizona/desert scrub, riparian (% biomass; prey observed brought to nest or found at nests)	Haywood & Ohmart, 1986	
pink salmon herring trout other fish other animals		15.5 32.0 4.5 24.0 24.0			Alaska/coastal (% frequency of occurrence; prey observed brought to the nest)	Ofelt, 1975	

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Bald Eagle

Bald Eagle (*Haliaeetus leucocephalus*)

<i>Population Dynamics</i>	<i>Age/Sex Cond./Seas.</i>	<i>Mean</i>	<i>Range</i>	<i>Location/Habitat</i>	<i>Reference</i>	<i>Note No.</i>
Territory Area (ha)	pair spring	3,494 ± 2,520 SD	1,821 - 6,392	Arizona/desert, riparian river	Haywood & Ohmhart, 1983	
Territory Length (km)	pair pair	3.5 15.8	1.4 - 7.2 11.1 - 26.6	Washington/SJ Islands; Grays Harbor	Grubb, 1980	
Territory Radius (km)	pair incubat. pair brooding	0.56 ± 0.18 SE 0.72 ± 0.21 SE		Minnesota/lake, woods	Mahaffy & Frenzel, 1987	
Winter Home Range (ha)	J B winter A B winter	1,830 ± 1,460 SD 1,880 ± 900 SD		Missouri/lake	Griffin & Baskett, 1985	
Foraging Distance (km)	B B winter	3 to 7		Connecticut/river	Craig et al., 1988	
Population Density (pair/km shore)	summer summer	0.38 0.035 0.026 0.045		se Alaska/riverine WY, ID, MT/ Yellowstone Continental Snake	Hansen, 1987 Swenson et al., 1986	
Clutch Size		2 2.3	1 - 3 1 - 4	NS/NS PA, DE, MD, NJ	Brown & Amadon, 1968 Schmid, 1966-67	
Clutches/Year		1		NS/NS	Sherrod et al., 1987	
Days Incubation		35	34 - 38	Maryland (captive)	Maestrelli & Wiemeyer, 1975	
Age at Fledging (days)	M F	79.9 ± 1.08 SE 83.0 ± 0.94 SE		Saskatchewan/lake	Bortolotti, 1989	
Number Fledge per Active Nest		1.01 1.28 0.90 1.14 1.00 ± 0.06 SE	0.58 - 1.22/10 yr 1.07 - 1.58/9 yr 0.76 - 1.14/7 yr 0 - 3	California/NS Montana/NS Washington/NS Florida/NS Alaska/NS	Henny & Anthony, 1989 Henny & Anthony, 1989 Henny & Anthony, 1989 McEwan & Hirth, 1979 Sprunt et al., 1973	

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Bald Eagle

Bald Eagle (*Haliaeetus leucocephalus*)

<i>Population Dynamics</i>	<i>Age/Sex Cond./Seas.</i>	<i>Mean</i>	<i>Range</i>	<i>Location/Habitat</i>	<i>Reference</i>	<i>Note No.</i>
Number Fledge per Successful Nest		1.65 ± 0.26 SD 1.35 ± 0.11 SD 2.2 1.64	1.22 - 1.48/6 yr 1 - 3	Arizona/desert scrub, river Washington/San Juan Island PA, DE, MD, NJ/NS ID, MT, WY/river, lake	Grubb et al., 1983 Grubb et al., 1983 Schmid, 1966-67 Swenson et al., 1986	
Age at Sexual Maturity	B	4	3 - 5	United States/NS	Nye, 1983	
Annual Mortality (percent)	A B fledging to 1 yr	5.4 89.3		Alaska/Amchitka Island	Sherrod et al., 1977	
Longevity	A B		up to 50 yrs	captivity	Snow, 1973	
<i>Seasonal Activity</i>	<i>Begin</i>	<i>Peak</i>	<i>End</i>	<i>Location</i>	<i>Reference</i>	<i>Note No.</i>
Mating/Laying	late September December late October February early March late March	late December late March	November late January March late April early April	Florida, Texas Arizona else United States MD, VA, DE WY, MT, ID Vancouver BC	Mager, 1977 Grubb et al., 1983 USFWS, 1989 LeFranc & Cline, 1983 Swenson et al., 1986 Brown & Amadon, 1968	10
Fledging	April early July	late July late August	May mid-August	else Louisiana WY, MT, ID else Alaska	Harris et al., 1987 Swenson et al., 1986 Hansen, 1987	
Fall Migration	early October late October November	June November December/January December	mid-December January	Arizona Montana else Oregon, n California else Alaska	Grubb et al., 1983 Crenshaw & McClelland, 1989 Keister et al., 1987 Hodges et al., 1987	
Spring Migration	late March early March	December April early April		Arizona else Oregon, n California WY, MT, ID Illinois	Grubb et al., 1983 Keister et al., 1987 Swenson et al., 1986 Sabine, 1981	

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Bald Eagle

Bald Eagle (*Haliaeetus leucocephalus*)

- 1 Cited in Maestrelli and Wiemeyer (1975) and Bortolotti (1984a); juveniles up to 3 years of age.
- 2 Estimated from Figure 4.
- 3 Daily energy budget for free-living eagles based on time-activity budgets and metabolic models; assuming 4.5 kg eagle.
- 4 Estimated using equation 3-37 (Nagy, 1987) and body weights from Imler and Kalmbach (1955).
- 5 Estimated from observed captures of preweighed salmon provided at feeding stations. Eagle body weight assumed to be 4.5 kg. Some feeding may have occurred elsewhere.
- 6 Estimate of food consumed based on observed feeding behaviors and an eagle body weight of 4.5 kg.
- 7 Estimated using equation 3-15 (Calder and Braun, 1983) and body weights from Imler and Kalmbach (1955).
- 8 Estimated using equation 3-19 (Lasiewski and Calder, 1971) and body weights from Imler and Kalmbach (1955).
- 9 Estimated using equation 3-21 (Meeh, 1879 and Rubner, 1883, as cited in Walsberg and King, 1978) and body weights from Imler and Kalmbach (1955).
- 10 Cited in Green, 1985.

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2.1.8. American Kestrel (falcons)

Order *Falconiformes*, Family *Falconidae*. Falcons are the more streamlined of the raptor species, with long pointed wings bent back at the wrists and large tails that taper at the tips. They consume many kinds of animals including insects, reptiles, small mammals, and birds. Falcons are found in a variety of habitats, from cities to the most remote areas. Strong fliers that achieve high speeds, falcons range in size from the American kestrel (27 cm bill tip to tail tip) to the peregrine falcon (41 to 51 cm).

Selected species

The American kestrel (*Falco sparverius*), or sparrow hawk, is the most common falcon in open and semi-open areas throughout North America. There are three recognized subspecies: *F. s. paulus* (year-round resident from South Carolina to Florida and southern Alabama), *F. s. peninsularis* (year-round resident of southern Baja California), and *F. s. sparverius* (widespread and migratory) (Bohall-Wood and Collopy, 1986). Predators of the kestrel include large raptors such as great horned owls, golden eagles, and red-tailed hawks (Meyer and Balgooyen, 1987).

Body size. Weighing slightly over one tenth of a kilogram, the kestrel is the smallest falcon native to the United States (Brown and Amadon, 1968). As for most raptors, females are 10 to 20 percent larger than males (Bloom, 1973; Craighead and Craighead, 1956). Kestrel body weights vary seasonally, with maximum weight (and fat deposits) being achieved in winter and minimum weights in summer (Bloom, 1973; Gessaman and Haggas, 1987).

Habitat. Kestrels inhabit open deserts, semi-open areas, the edges of groves (Brown and Amadon, 1968), and even cities (National Geographic Society, 1987). In several areas, investigators have found that male kestrels tend to use woodland openings and edges, while females tend to utilize more open areas characterized by short or sparse ground vegetation, particularly during the winter (Koplin, 1973, cited in Mills, 1976; Meyer and Balgooyen, 1987; Mills, 1975, 1976; Smallwood, 1987). In other areas, however, investigators have found no such differentiation (Toland, 1987; Sferra, 1984). In Florida, kestrels appear to prefer sandhill communities (particularly pine/oak woodlands); these areas provide high-quality foraging habitat and the majority of available nest sites (Bohall-Wood and Collopy, 1986). Kestrels are more likely to use habitats close to centers of human activities than are most other raptors (Fischer et al., 1984).

Food habits. Kestrels prey on a variety of small animals including invertebrates such as worms, spiders, scorpions, beetles, other large insects, amphibians and reptiles such as frogs, lizards, and snakes, and a wide variety of small- to medium-sized birds and mammals (Brown and Amadon, 1968; Mueller, 1987). Large insects, such as grasshoppers, are the kestrels' primary summer prey, although in their absence kestrels will switch to small mammals (Collopy, 1973) and birds (Brown and Amadon, 1968). In winter, small mammals and birds comprise most of the diet (Collopy and Koplin, 1983; Koplin et al., 1980). Kestrels usually cache their vertebrate prey, often in clumps of grass or in tree limbs and holes, to be retrieved later (Collopy, 1977; Mueller, 1987; Rudolph, 1982; Toland,

1984). Invertebrate prey usually are eaten immediately (Rudolph, 1982). In Florida, where small mammals are scarce and reptiles are abundant, lizards are an important component of the diet (Bohall-Wood and Collopy, 1987). Kestrels forage by three different techniques: using open perches from which to spot and attack ground prey, hovering in the air to spot ground prey, and catching insects on the wing (Rudolph, 1982, 1983).

Molt. Females begin their molt during incubation and complete it by the end of the breeding season. Males, who are responsible for capturing most of the prey for the family, do not begin their molt until near the end of the breeding season (Smallwood, 1988).

Migration. The American kestrel is a year-round resident over most of the United States, but is migratory over the northern-most portions of its range (National Geographic Society, 1987). Because of their late molt, males migrate and arrive at the wintering grounds later than females or immatures (Smallwood, 1988).

Breeding activities and social organization. Adult kestrels are solitary, except during the breeding season, and maintain territories even in winter (Brown and Amadon, 1968). Kestrels typically build their nests in tree cavities, but have used holes in telephone poles, buildings, or stream banks when tree cavities are not available (Brown and Amadon, 1968). Both parents participate in incubation, but the female performs most of the incubation, while the male provides her with food (Brown and Amadon, 1968). Following hatching, the male brings the majority of the prey to the nestlings (Brown and Amadon, 1968). After fledging, young kestrels remain dependent on their parents for food for at least 2 to 4 additional weeks (Lett and Bird, 1987). Fledglings often perch and socialize with their siblings prior to dispersal (Lett and Bird, 1987). In Florida, resident kestrels (*paulus* subspecies) maintain year-round pair bonds and joint territories. The resident pairs have a competitive advantage over winter migrants (*sparverius* subspecies) in their territories (Bohall-Wood and Collopy, 1986).

Home range and resources. Although some investigators have not noted territorial defense (e.g., Craighead and Craighead, 1956), Mills (1975) demonstrated that kestrels defend territories by introducing captured birds into other birds' territories. Winter foraging territories range from a few hectares in productive areas (e.g., in California) (Meyer and Balgooyen, 1987) to hundreds of hectares in less productive areas (e.g., Illinois, Michigan) (Craighead and Craighead, 1956; Mills, 1975). Summer breeding territories probably follow the same pattern (Craighead and Craighead, 1956).

Population density. Although much smaller than red-tailed hawks and bald eagles, reported kestrel breeding population densities can be similarly low (e.g., 0.0003 to 0.004 nests per hectare; see table).

Population dynamics. Kestrels are sexually mature in the first breeding season after their birth (Carpenter et al., 1987). Scarcity of suitable nesting cavities probably limits the size of kestrel populations in parts of the United States (Cade, 1982). Three to four young may fledge per nest per year, but mortality of juveniles in the first year is high (60 to 90 percent) (Craighead and Craighead, 1956; Henny, 1972). Adult mortality can be low (e.g., 12 percent per year) (Craighead and Craighead, 1956).

Similar species (from general references)

- The peregrine falcon (*Falco peregrinus*), a rare resident of woods, mountains, and coasts, preys almost exclusively on birds. Though uncommon, they can be found wintering in most states, but rarely breeding. These large falcons (38 cm) have been reintroduced in some areas in the United States and have nested in urban environments.
- The merlin (*Falco columbarius*), larger (30 cm) than the kestrel, can be found in a variety of habitats but nests in open woods or wooded prairies. Wintering along coasts and near cities of the Great Plains, it primarily eats birds.
- The prairie falcon (*Falco mexicanus*) also is larger (39 to 50 cm) than the kestrel and inhabits dry, open country and prairies. A year-round resident of the western United States, prairie falcons prey chiefly on birds and small mammals.

General references

Cade (1982); Craighead and Craighead (1956); National Geographic Society (1987); Brown and Amadon (1968).

American Kestrel (*Falco sparverius*)

<i>Factors</i>	<i>Age/Sex/ Cond./Seas.</i>	<i>Mean</i>	<i>Range or (95% CI of mean)</i>	<i>Location</i>	<i>Reference</i>	<i>Note No.</i>
Body Weight (g)	F fall	115 ± 8.6 SD		California, Imperial Valley	Bloom, 1973	
	F winter	132 ± 13 SD				
	M fall	103 ± 6.7 SD		California, Imperial Valley	Bloom, 1973	
	M winter	114 ± 7.8 SD				
	F laying/inc.	124		Utah	Gessaman & Haggas, 1987	
	F fall	127				
	F winter	138				
	M incubate	108		Utah	Gessaman & Haggas, 1987	
M fall	111					
M winter	119					
Metabolic Rate (kcal/kg-day)	F laying/inc.	414.4 ± 9.84 SE		Utah (free-living)	Gessaman & Haggas, 1987	1
	F fall	368.7 ± 17.0 SE				
	F winter	327.2 ± 5.72 SE				
	M incubate	337.6 ± 16.8 SE		Utah (free-living)	Gessaman & Haggas, 1987	1
	M fall	364.9 ± 26.9 SE				
	M winter	386.4 ± 9.41 SE				
	A F basal	134			estimated	2
A M basal	140					
A F free-living	333	(157 - 706)		estimated	3	
A M free-living	345	(162 - 733)				
Food Ingestion Rate (g/g-day)	A B winter (vert. prey) (invert. prey)	0.29 (0.18) (0.11)		nw California (free-living)	Koplin et al., 1980	4
	A M summer	0.31		Ohio (seminatural enclosure)	Barrett & Mackey, 1975	
Water Ingestion Rate (g/g-day)	A F	0.11			estimated	5
	A M	0.12				

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American Kestrel

American Kestrel (*Falco sparverius*)

<i>Factors</i>	<i>Age/Sex/ Cond./Seas.</i>	<i>Mean</i>	<i>Range or (95% CI of mean)</i>		<i>Location</i>	<i>Reference</i>	<i>Note No.</i>
Inhalation Rate (m ³ /day)	A F A M	0.089 0.079				estimated	6
Surface Area (cm ²)	A F A M	267 242				estimated	7
<i>Dietary Composition</i>	<i>Spring</i>	<i>Summer</i>	<i>Fall</i>	<i>Winter</i>	<i>Location/Habitat (measure)</i>	<i>Reference</i>	<i>Note No.</i>
invertebrates mammals birds reptiles other				32.6 31.7 30.3 1.9 3.5	California/open areas, woods (% wet weight of prey observed captured)	Meyer & Balgooyen, 1987	
vertebrates (primarily lizards) invertebrates	49 51				Florida/dry pine-oak woodlands (sandhill) (% wet weight of prey observed captured)	Bohall-Wood & Collopy, 1987	
Coleoptera other invertebrates frogs (<i>Rana aurora</i>) other herpetofauna <i>Microtus californicus</i> <i>Sorex vagrans</i> other mammals				10.8 14.2 8.0 12.2 30.2 9.4 11.5	California/hayfields, pasture (% wet weight of prey observed captured)	Collopy & Koplín, 1983	

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American Kestrel

American Kestrel (*Falco sparverius*)

<i>Population Dynamics</i>	<i>Age/Sex Cond./Seas.</i>	<i>Mean</i>	<i>Range</i>	<i>Location/Habitat</i>	<i>Reference</i>	<i>Note No.</i>
Territory Size (ha)	A F winter A M winter	31.6 ± 10.7 SD 13.1 ± 2.0 SD	18.7 - 42.0 9.7 - 14.8	California/open areas, woods	Meyer & Balgooyen, 1987	
	A B winter	154	< 452	Illinois/agricultural area	Mills, 1975	
	A B summer	202 ± 131 SD	41 - 500	Wyoming/grasslands, forests	Craighead & Craighead, 1956	
	A B summer	131 ± 100 SD	21 - 215	Michigan/woodlots, fields	Craighead & Craighead, 1956	
Population Density	pairs summer	0.0026 nests/ha 0.0004 nests/ha	0.0023 - 0.0031 0.0003 - 0.0006	Missouri/urban Missouri/rural	Toland & Elder, 1987 Toland & Elder, 1987	
	pairs summer	0.0035 pairs/ha		Wyoming/grasslands, forest	Craighead & Craighead, 1956	
	pairs summer	birds/ha: 0.0007 ± 0.00004 SD 0.0005 ± 0.0001 SD 0.0010 ± 0.0002 SD	0.0005 - 0.0012 0.0005 - 0.0006 0.0008 - 0.0011	s Michigan/fields, woodlots	Craighead & Craighead, 1956	
	B B fall A B winter A B spring					
Clutch Size		4.3		California/juniper, sagebrush	Bloom & Hawks, 1983	
		4 to 5	3 - 7	NS/NS	Brown & Amadon, 1968	
Clutches/Year		1		Quebec, Canada/captive	Carpenter et al., 1987	
Days Incubation		33.7 ± 0.33 SE	33 - 35	Maryland/captive	Porter & Wiemeyer, 1972	
		29 to 30		NS/NS	Brown & Amadon, 1968	
Age at Fledging		27.4 days	26 - 30 days	Maryland/captive	Porter & Wiemeyer, 1972	

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American Kestrel

American Kestrel (*Falco sparverius*)

<i>Population Dynamics</i>	<i>Age/Sex Cond./Seas.</i>	<i>Mean</i>	<i>Range</i>	<i>Location/Habitat</i>	<i>Reference</i>	<i>Note No.</i>
Number Fledge per Active Nest		3.1		California/juniper, sagebrush	Bloom & Hawks, 1983	
		3.8		Wyoming/grasslands, forest	Craighead & Craighead, 1956	
Number Fledge per Successful Nest		3.7		California/juniper, sagebrush	Bloom & Hawks, 1983	
Age at Sexual Maturity	B	1 yr		Quebec, Canada/captive	Carpenter et al., 1987	
Annual Mortality (percent)	A B J B	12 88		s Michigan, Wyoming/ open areas, woods	Craighead & Craighead, 1956	
	A B J B	46.0 ± 4.6 SE 60.7		North America/NS	Henny, 1972	
Longevity			up to 9 yrs	Quebec, Canada/captive	Carpenter et al., 1987	
<i>Seasonal Activity</i>	<i>Begin</i>	<i>Peak</i>	<i>End</i>	<i>Location</i>	<i>Reference</i>	<i>Note No.</i>
Mating/ Laying	early May mid-April early April	late May	late June early June mid-May	California central US northern Utah	Bloom & Hawks, 1983 Brown & Amadon, 1968 Gessaman & Haggas, 1987	
	mid-March		early June	Florida	Brown & Amadon, 1968	
Hatching	early June early May	late June	late July mid-June	California northern Utah	Bloom & Hawks, 1983 Gessamen & Haggas, 1987	
		early May		central Missouri	Toland & Elder, 1987	
Molt	mid-May		mid-September	northern Utah	Gessaman & Haggas, 1987	

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American Kestrel

American Kestrel (*Falco sparverius*)

<i>Seasonal Activity</i>	<i>Begin</i>	<i>Peak</i>	<i>End</i>	<i>Location</i>	<i>Reference</i>	<i>Note No.</i>
Migration fall spring	early September early March mid-April		early November	northern Utah south Michigan Wyoming	Gessaman & Haggas, 1987 Craighead & Craighead, 1956 Craighead & Craighead, 1956	

- 1 Investigators estimated values from time-activity budget studies of kestrels in the field and rates of energy expenditure during different activities measured in the laboratory.
- 2 Estimated using equation 3-28 (Lasiewski and Dawson, 1967) and body weights from winter measurements by Gessaman and Haggas (1987).
- 3 Estimated using equation 3-37 (Nagy, 1987) and body weights from winter measurements by Gessaman and Haggas (1987).
- 4 Authors observed prey captured daily, and estimated total wet-weight prey intake using measured or reported weights for identifiable prey and estimated weights for unidentifiable invertebrate prey (also, assumed kestrel weighed 119 g). Also, see Chapters 3 and 4 for methods by estimating food ingestion rates.
- 5 Estimated using equation 3-15 (Calder and Braun, 1983) and body weights from winter measurements by Gessaman and Haggas (1987).
- 6 Estimated using equation 3-19 (Lasiewski and Calder, 1971) and body weights from winter measurements by Gessaman and Haggas (1987).
- 7 Estimated using equation 3-21 (Meeh, 1879 and Rubner, 1883, cited in Walsberg and King, 1978) and body weights from winter measurements by Gessaman and Haggas (1987).

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American Kestrel

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2.1.9. Northern Bobwhite (quail)

Order Galliformes, Family Phasiadinae. Quail are ground-dwelling birds with short, heavy bills adapted for foraging on the ground for seeds and insects. Most species inhabit brush, abandoned fields, and open woodlands; some inhabit parklands. Quail and most other gallinaceous birds are poor flyers that seldom leave the ground and do not migrate. All species of this family gather in coveys (i.e., flocks of varying size) during some part of the year. Quail range in size from Montezuma's quail (22 cm bill tip to tail tip) to the mountain and Gambel's quail (28 cm); sexes are similar in size but differ in appearance.

Selected species

The northern bobwhite (*Colinus virginianus*) feeds mainly on seeds by gleaning on the ground and low vegetation. It ranges from southeastern Wyoming, east to southern Minnesota and across to southern Maine, south through the central and eastern United States to eastern New Mexico in the west and to Florida in the east (American Ornithologists' Union, 1983). It is the most widespread of the North American quail and used to be very common, particularly east of the Rocky Mountains. Over the past three decades, however, populations have been declining throughout its range (Brennan, 1991).

Body size. Northern bobwhite are average-sized quail (25 cm). Wild bobwhites typically weigh between 150 and 200 g depending on location and season (see table), while commercially bred stock usually exceed 200 g and may reach 300 g or more (Brenner and Reeder, 1985; Koerth and Guthery, 1991). Males and females are similar in size, and weights tend to increase with latitude and toward the west coast of the United States (Hamilton, 1957; Rosene, 1969; Roseberry and Klimstra, 1971). Females are heaviest in the spring and summer when they are laying eggs; males are lightest at this time of year (Hamilton, 1957; Roseberry and Klimstra, 1971). Juveniles tend to weigh slightly less than adults through winter (Hamilton, 1957; Roseberry and Klimstra, 1971). Koerth and Guthery (1987) found both males and females to maintain between 9 and 11 percent body fat (as a percentage of dry body weight) throughout the year in southern Texas; more northern populations may maintain higher body fat ratios, particularly just prior to breeding (McRae and Dimmick, 1982).

Habitat. During the breeding season, grasslands, idle fields, and pastures are the preferred nesting habitat, and bobwhite often nest in large clumps of grasses (Roseberry and Klimstra, 1984). Shade, open herbaceous cover, and green and growing vegetation are required for suitable nest sites (Lehmann, 1984). Bobwhites forage in areas with open vegetation, some bare ground, and light litter (Stoddard, 1931). Nearby dry powdery soils are important for dust bathing (Johnsgard, 1988). Shrubby thickets up to 2 m high are used for cover during midday (Schroeder, 1985). Although their range is extensive, northern bobwhite reproduce poorly in the arid western portions of their range and during droughts elsewhere (Schroeder, 1985). During the winter, they require wooded cover with understory for daytime cover, preferably adjacent to open fields for foraging (Yoho and Dimmick, 1972). They tend to roost at night in more open habitats with short and sparse vegetation (Schroeder, 1985). In the more northern latitudes, cover and food can be limited during the winter (Rosene, 1969). Changes in land use, primarily

the distribution of farms and farming methods, have eliminated large areas of bobwhite habitat in the last three decades (Brennan, 1991).

Food habits. Bobwhites forage during the day, primarily on the ground or in a light litter layer less than 5 cm deep (Rosene, 1969). Seeds from weeds, woody plants, and grasses comprise the majority of the adult bobwhite's diet throughout the year (Handley, 1931; Bent, 1932; Lehmann, 1984), although in winter in the south, green vegetation has been found to dominate the plant materials in their diet (Campbell-Kissock et al., 1985). Insects and other invertebrates can comprise up to 10 to 25 percent of the adults' diet during the spring and summer in more northerly areas and year-round in the south (Campbell-Kissock et al., 1985; Handley, 1931; Lehmann, 1984). Insects comprise the bulk of the chicks' diet; up to 2 or 3 weeks of age chicks may consume almost 85 percent insects, the remainder of the diet consisting of berries and seeds (Handley, 1931). Most insects consumed by bobwhite chicks are very small, less than 8 mm in length and 0.005 g (Hurst, 1972). Juvenile bobwhite, on the other hand, may consume only 25 percent insects, the remainder of their diet being fruit and seeds (Handley, 1931). Quail consume little grit. Korschgen (1948) found grit in only 3.4 percent of over 5,000 crops examined, and agreed with Nestler (1946) that hard seeds can replace grit as the grinding agent for northern bobwhite.

In some areas, bobwhites apparently can acquire their daily water needs from dew, succulent plants, and insects (Stoddard, 1931); in more arid areas or in times of drought, however, northern bobwhite need surface water for drinking (Johnsgard, 1988; Lehmann, 1984; Prasad and Guthery, 1986). Females need more water than males during the breeding season, and both sexes may require more water in the winter than in the summer when their diet is more restricted to seeds with low water content (Koerth and Guthery, 1990). Measurements on captive quail have indicated a daily water requirement of up to 13 percent of their body mass (see table); however, water intake requirements for free-ranging birds may be higher, perhaps 14 to 21 percent of body mass per day (Koerth and Guthery, 1990). In the absence of adequate water, females may fail to reproduce (Koerth and Guthery, 1991).

Dustbathing. Quail frequently dustbathe, although the reason for the behavior is debated.^c They scratch in dry dirt or dust, toss the dust up into their feathers, rub their head and sides in the dust, and then shake the dust from their plumage (Borchelt and Duncan, 1974). Experiments by Driver et al. (1991) indicate that ingestion of materials preened from feathers and direct dermal uptake can be significant exposure pathways for quail exposed to aerial application of pesticides. Dust bathing might, therefore, provide a significant exposure route for bobwhites using contaminated soils.

Molt. Juveniles attain adult plumage during their first fall molt at about 3 to 5 months of age (Hamilton, 1957; Stoddard, 1931). Adults undergo a complete prebasic

^cStoddard (1931) and others have suggested that dust bathing helps to control ectoparasites; Borchelt and Duncan (1974) suggest that dust bathing helps control the amount of oil on the quails' feathers.

molt in the late summer and fall into winter plumage; in spring, a limited renewal of feathers around the head and throat provides the breeding plumage (Bent, 1932).

Migration. The northern bobwhite is a year-round resident over its entire range but may disperse locally to a different cover type or altitude with the changing season (Lehmann, 1984). Most winter in wooded or brushy areas, returning to more open habitats in spring for the breeding season (Lehmann, 1984; Rosene, 1969). Populations nesting at higher elevations tend to move to lower ground where the winters are less severe (Stoddard, 1931). The more southerly populations may be more sedentary; in a study in Florida, northern bobwhite were found no further than 1 km from where they were banded, and 86 percent were found within 400 m from their banding site over a 1- to 5-year period (Smith et al., 1982).

Breeding activities and social organization. Northern bobwhite build nests on the ground in open woodlands or in or around fields used for foraging. Most nests are constructed in grassy growth near open ground, often in areas with scattered shrubs and herbaceous growth (Klimstra and Roseberry, 1975; Stoddard, 1931). Both the male and female scrape out a saucer-shaped depression in the ground 2 to 6 cm deep and 10 to 12 cm across, lining it with dead grasses from the previous year's growth (Bent, 1932; Rosene, 1969). They lay large clutches, 12 to 30 eggs, which one or both parents incubate for approximately 23 days (Lehmann, 1984; Simpson, 1976). As a general rule, clutch size and nest success both decrease as the season progresses (Roseberry and Klimstra, 1984). Family units, consisting of both the male and female as well as the offspring, sometimes remain intact through the summer, but more often, one or both parents are lost to predation (some females leave their brood to the male and begin another), and other pairs or individual adults may adopt chicks from other broods (Lehmann, 1984). By fall, northern bobwhites of all ages gather in larger coveys for the fall and winter. The quail remain in coveys until the next spring, when they disperse as mating season begins (Lehmann, 1984; Roseberry and Klimstra, 1984). Coveys of northern bobwhite tend to average 10 to 12 or 15 birds (up to 30) (Johnsgard, 1988; Lehmann, 1984; Rosene, 1969). When roosting in winter, the birds in a covey form a small circle on the ground under a tree or in thick brush, with heads facing outward and their bodies closely packed to conserve heat.

Home range and resources. In the breeding season, the bobwhite's home range includes foraging areas, cover, and the nest site and may encompass several hectares. Mated males and incubating females have the smallest spring and summer home ranges; bachelor males and post-nesting males and females have much larger foraging ranges (see table). Bobwhite tend to use a portion of their home range more intensively than the remainder of the range (Urban, 1972). In the fall and winter, the range of each bobwhite covey must include adequate open foraging areas and cover, typically shrubby or woody thickets (Rosene, 1969). Each covey may utilize an area of several hectares, although as in summer, there tend to be activity centers where the quail spend most of their time (Yoho and Dimmick, 1972).

Population density. Bobwhite density depends on food and cover availability and varies from year to year as well as from one location to another (Roseberry and Klimstra, 1984). Densities are highest at the end of the breeding season in the fall. In the

southeast, densities may reach values as high as 7.5 birds (adults and juveniles) per hectare, although average values of 2 to 3 may be more common in these areas (Guthery, 1988; Lehmann, 1984; Smith et al., 1982). Winter and spring densities between 0.1 and 0.8 birds per hectare have been recorded in the spring further north (Roseberry et al., 1979).

Population dynamics. Bobwhites attempt to rear one or two broods per year (up to three in the south) (Bent, 1932; CKWRI, 1991; Stanford, 1972b). Bobwhite clutch sizes are generally smaller in more southerly populations (Roseberry and Klimstra, 1984) and smaller as the breeding season progresses in any given locale (Lehmann, 1984; Simpson, 1976). Predation is a major cause of nest loss; once hatched, chicks leave the nest immediately to follow both or one parent (Lehmann, 1984; Roseberry and Klimstra, 1984). Juveniles can survive without parental care after about 6 weeks of age (Lehmann, 1984). They reach maturity by 16 weeks of age in the laboratory although they continue to gain weight through about 20 weeks (Moore and Cain, 1975), and they may require 8 to 9 months to mature in the wild (Johnsgard, 1988; Jones and Hughes, 1978). Adult mortality as well as juvenile mortality is high, with 70 to 85 percent of birds surviving less than 1 year (Brownie et al., 1985; Lehmann, 1984); thus, the bulk of the population turns over each year.

Similar species (from general references)

- California quail (*Callipepla californica*), also known as valley quail, are similar in size (25 cm) to the bobwhite and also gather in coveys during autumn and winter. They are common in open woodlands, brushy foothills, stream valleys, and suburbs, usually near permanent surface waters; however, their range is restricted largely to the western coastal States and Baja California.
- Gambel's quail (*Callipepla gambelii*) is larger (28 cm) than the bobwhite, and is a resident of the southwestern desert scrublands, usually near permanent surface waters. It also gathers in coveys in winter.
- The scaled quail (*Callipepla squamata*), similar in size (25 cm) to the bobwhite, is restricted to the mesas, plateaus, semidesert scrublands, and grasslands mixed with scrub, primarily of western Texas, New Mexico, and Mexico.
- Mountain quail (*Oreortyx pictus*) are found in the chapparal, brushy ravines, and mountain slopes of the west up to 3,000 m. These also are large quail (28 cm). During the fall, they gather in coveys and descend to lower altitudes for the winter.
- The Montezuma quail (*Cyrtonyx montezumae*), formerly known as the harlequin quail, is a small (22 cm), secretive resident of the southwest. This species is usually found in grassy undergrowth of juniper or oak-pine woodlands.

General references

Johnsgard (1988); Lehmann (1984); National Geographic Society (1987); Rosene (1969); Roseberry and Klimstra (1984); Stoddard (1931).

Northern Bobwhite (*Colinus virginianus*)

<i>Factors</i>	<i>Age/Sex/ Cond./Seas.</i>	<i>Mean</i>	<i>Range or (95% CI of mean)</i>	<i>Location or subspecies</i>	<i>Reference</i>	<i>Note No.</i>	
Body Weight (g)	A B fall	189.9 ± 3.28 SE		Kansas	Robel, 1969		
	A B winter	193.9 ± 4.56 SE					
	A B spring	190.0 ± 4.98 SE					
	A M winter	181		Illinois	Roseberry & Klimstra, 1971		
	A M summer	163					
	A F winter	183					
	A F summer	180					
	A M winter	161		west Rio Grande, Texas	Guthery et al., 1988		
	A M summer	154					
	A F winter	157					
	A F summer	157					
	at hatching	6.3		(weight gain:)	southwest Georgia/both captive and wild birds living in farms, woods, and thickets		Stoddard, 1931
	day 6	9 - 10		(0.5 - 0.75 g/day)			
day 10	10 - 13						
day 19	20 - 25	(1.5 g/day)					
day 32	35 - 45						
day 43	55 - 65	(1.75 g/day)					
day 55	75 - 85						
day 71	110 - 120	(1.75 - 2.0 g/day)					
day 88	125 - 150						
day 106	140 - 160						
J B fall	174.0 ± 3.49 SE		Kansas	Robel, 1969			
Body Fat (% dry weight)	A M winter	15.5 ± 2.8 SD		Tennessee	McRae & Dimmick, 1982		
	A M spring	8.8 ± 3.2 SD					
	A F winter	13.8 ± 2.7 SD					
	A F spring	12.7 ± 2.4 SD					
Body Fat (% dry weight) (continued)	A M winter	10.2 ± 0.6 SE	9.0 - 11.9	southern Texas/captive	Koerth & Guthery, 1987		
	A M spring	7.9 ± 0.2 SE	6.5 - 10.0				
	A F winter	10.6 ± 0.8 SE	8.3 - 19.9				
	A F spring	9.7 ± 0.3 SE	7.7 - 11.2				

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Northern Bobwhite

Northern Bobwhite (*Colinus virginianus*)

<i>Factors</i>	<i>Age/Sex/ Cond./Seas.</i>	<i>Mean</i>	<i>Range or (95% CI of mean)</i>	<i>Location or subspecies</i>	<i>Reference</i>	<i>Note No.</i>
Egg Weight (grams)		9.3 ± 0.3 SE 8.6	8.0 - 10.2	Texas southwest Georgia	Koerth & Guthery, 1991 Stoddard, 1931	
Metabolic Rate (kcal/kg-day)	A F nonbreed A F laying	183.3 243.9		Nebraska/captive	Case, 1982	1
	A M basal A F basal	129 125			estimated	2
	A M free-living A F free-living	320 311	(151 - 677) (147 - 659)		estimated	3
Food Ingestion Rate (g/g-day)	A B winter A B spring A B summer A B fall	0.093 ± 0.0032 SE 0.067 ± 0.0021 SE 0.079 ± 0.0061 SE 0.072 ± 0.0017 SE		southern Texas/captive	Koerth & Guthery, 1990	4
	(kcal/kg-day) A B winter A B fall A B spring	587 657 519		Kansas	Robel, 1969	5
Water Ingestion Rate (g/g-day)	A M summer A F summer	0.10 ± 0.023 SD 0.13 ± 0.037 SD		southern Texas/captive	Koerth & Guthery, 1990	
	A M summer A F summer	0.11 0.10			estimated	6
Inhalation Rate (m³/day)	A M summer A F summer	0.10 0.11			estimated	7
Surface Area (cm²)	A M summer A F summer	298 320			estimated	8

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Northern Bobwhite

Northern Bobwhite (*Colinus virginianus*)

<i>Dietary Composition</i>	Spring	Summer	Fall	Winter	Location/Habitat (measure)	Reference	Note No.
adults: (total plant foods) misc. seeds other seeds: legumes senna cultivated plants grasses sedges mast spurges fruits forage plants (total animal foods) grasshoppers bugs beetles	(87.2) 21.1 15.2 7.2 2.1 3.1 1.1 14.1 0.1 11.1 12 (12.8) 3.2 2.8 4.6	(78.7) 6.0 3.9 0.4 2.1 11.3 1.2 0.2 1.2 45.8 0.3 (19.6) 7.5 4.4 6.3	(79.7) 11.1 10.1 0.2 5.3 26.0 2.4 0.5 5.5 11.3 0.3 (20.3) 16.6 0.6 0.8	(96.8) 2.6 31.5 12.8 2.6 2.3 1.1 28.0 0.4 9.5 5.2 (3.2) 2.4 0.1 0.2	southeastern United States/NS (% volume; crop and gizzard contents)	Handley, 1931	
adults: seeds of weeds seeds of woody plants seeds of grasses cultivated grains, etc. greens insects	43.64 4.03 13.2 3.7 27.4 8.03	33.7 20.5 24.8 1.9 4.9 14.2	30.0 39.7 0.7 8.3 3.4 17.9	34.3 9.5 7.2 15.4 10.3 23.3	south Texas/semi-prairie, brushland (% dry volume; crop contents)	Lehmann, 1984	
adults: seeds of forbs seeds of grasses seeds/fruits of woody plants unidentified seeds green vegetation invertebrates		3.5 51.7 9.7 4.6 4.8 25.8	19.0 42.9 - - 1.8 36.2	12.0 4.9 1.4 2.3 72.4 6.5	southwest Texas/grasslands drought conditions (% wet volume; crop contents)	Campbell-Kissock et al., 1985	

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Northern Bobwhite

Northern Bobwhite (*Colinus virginianus*)

<i>Population Dynamics</i>	<i>Age/Sex/Cond./Seas.</i>	<i>Mean</i>	<i>Range or (95% CI of mean)</i>	<i>Location/Habitat</i>	<i>Reference</i>	<i>Note No.</i>
Percent Nests Successful		17.5	15.4 - 19.0	southwest Georgia/pine woods, farms	Simpson, 1976	
		32.6 ± 8.1 SD	21.0 - 52.8	south Illinois/agricultural	Roseberry & Klimstra, 1984	
Number Hatch per Successful Nest	spring/summer	12.2		south Texas/semiprairie, brush	Lehmann, 1984	
	March	20.0		southwest Georgia/pine woods, farms	Simpson, 1976	
	August	8.4				
Age at Sexual Maturity	B B	8 - 9 months 16 weeks		NS/NS (wild) South Carolina/lab	Johnsgard, 1988 Jones & Hughes, 1978	
Annual Mortality Rates (percent)	A M	78.8 ± 2.47 SE	64.7 - 94.8	Florida/open woods	Brownie et al., 1985	
	A F	85.3 ± 2.72 SE	68.4 - 98.6			
	J M	81.8 ± 2.46 SE	73.0 - 93.7			
	J F	87.2 ± 1.68 SE	67.9 - 95.8			
	B B	81		Illinois/agricultural	Roseberry & Klimstra, 1984	
	no hunting					
	B M	52		Florida/pine woods	Pollock et al., 1989	
	B F	56				
Longevity (months)	starting: B November B October	10.6 8.5		Texas/semiprairie, brush central Missouri/NS	Lehmann, 1984 Marsden & Baskett, 1958	9
<i>Seasonal Activity</i>	<i>Begin</i>	<i>Peak</i>	<i>End</i>	<i>Location</i>	<i>Reference</i>	<i>Note No.</i>
Mating/ Laying	March	May - June	August	Florida	Bent, 1932	
	mid-April April	mid-May - July	mid-August September	south Texas south Illinois	Lehmann, 1984 Roseberry & Klimstra, 1984	
Hatching	mid-March	May - June	mid-September	south Texas	Lehmann, 1984	
	late April	May - August	October	sw Georgia, northern Florida	Stoddard, 1931	
	early May	mid-June	October	Missouri	Stanford, 1972a	
	mid-May	June - August	early October	south Illinois	Roseberry & Klimstra, 1984	

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Northern Bobwhite

Northern Bobwhite (*Colinus virginianus*)

<i>Seasonal Activity</i>	<i>Begin</i>	<i>Peak</i>	<i>End</i>	<i>Location</i>	<i>Reference</i>	<i>Note No.</i>
Molt fall	August	September	October	NS	Bent, 1932	
spring	early February	March - April	early June	sw Georgia, northern Florida	Stoddard, 1931	

- 1 Metabolized energy requirements of farm-raised birds in captivity: (1) 7 weeks prior to laying (mean weight of hens = 194 g) and (2) during laying (mean weight of hens = 215 g).
- 2 Estimated using equation 3-28 (Lasiewski and Dawson, 1967) and summer body weights from Roseberry and Klimstra (1971).
- 3 Estimated using equation 3-37 (Nagy, 1987) and summer body weights from Roseberry and Klimstra (1971).
- 4 Diet of commercial game food with only 5 to 10 percent water content; maintained at temperature, humidity, and light cycle typical for Texas.
- 5 Gross energy intake calculated from the average volume of crop contents in shot birds, assuming a 1.5-hour retention period, 2.30 kcal/cm³ for the contents, and constant foraging throughout the daylight hours, which is likely to overestimate food intake.
- 6 Estimated using equation 3-15 (Calder and Braun, 1983) and body weights from Roseberry and Klimstra (1971).
- 7 Estimated using equation 3-19 (Lasiewski and Calder, 1971) and body weights from Roseberry and Klimstra (1971).
- 8 Estimated using equation 3-21 (Meeh, 1879 and Rubner, 1883, as cited in Walsberg and King, 1978) and body weights from Roseberry and Klimstra (1971).
- 9 Expected remaining longevity for those juvenile quail that survived to the month indicated.

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2.1.10. American Woodcock (woodcock and snipe)

Order Charadriiformes, Family Scolopacidae. These inland members of the sandpiper family have a stocky build, long bill, and short legs. However, their habitats and diet are distinct. Woodcock inhabit primarily woodlands and abandoned fields, whereas snipe are found in association with bogs and freshwater wetlands. Both species use their long bills to probe the substrate for invertebrates. The woodcock and snipe are similar in length, although the female woodcock weighs almost twice as much as the female snipe.

Selected species

The American woodcock (*Scolopax minor*) breeds from southern Canada to Louisiana throughout forested regions of the eastern half of North America. The highest breeding densities are found in the northern portion of this range, especially in the Great Lakes area of the United States, northern New England, and southern Canada (Gregg, 1984; Owen et al., 1977). Woodcock winter primarily in the southeastern United States and are year-round residents in some of these areas. Woodcock are important game animals over much of their range (Owen et al., 1977).

Body size. Woodcock are large for sandpipers (28 cm bill tip to tail tip), and females weigh more than males (Keppie and Redmond, 1988). Most young are full grown by 5 to 6 weeks after hatching (Gregg, 1984).

Habitat. Woodcock inhabit both woodlands and abandoned fields, particularly those with rich and moderately to poorly drained loamy soils, which tend to support abundant earthworm populations (Cade, 1985; Owen and Galbraith, 1989; Rabe et al., 1983a). In the spring, males use early successional open areas and woods openings, interspersed with low brush and grassy vegetation, for singing displays at dawn and dusk (Cade, 1985; Keppie and Redmond, 1985). Females nest in brushy areas of secondary growth woodlands near their feeding areas, often near the edge of the woodland or near a break in the forest canopy (Gregg, 1984). During the summer, both sexes use second growth hardwood or early successional mixed hardwood and conifer woodlands for diurnal cover (Cade, 1985). At night, they move into open pastures and early successional abandoned agricultural fields, including former male singing grounds, to roost (Cade, 1985; Dunford and Owen, 1973; Krohn, 1970). During the winter, woodcock use bottomland hardwood forests, hardwood thickets, and upland mixed hardwood and conifer forests during the day. At night, they use open areas to some degree, but also forested habitats (Cade, 1985). Diurnal habitat and nocturnal roosting fields need to be in close proximity to be useful for woodcock (Owen et al., 1977).

Food habits. Woodcocks feed primarily on invertebrates found in moist upland soils by probing the soil with their long prehensile-tipped bill (Owen et al., 1977; Sperry, 1940). Earthworms are the preferred diet, but when earthworms are not available, other soil invertebrates are consumed (Miller and Causey, 1985; Sperry, 1940; Stribling and Doerr, 1985). Some seeds and other plant matter may also be consumed (Sperry, 1940). Krohn (1970) found that during summer most feeding was done in wooded areas prior to entering fields at night, but other studies have indicated that a significant amount of food

is acquired during nocturnal activities (Britt, 1971, as cited in Dunford and Owen, 1973). Dyer and Hamilton (1974) found that during the winter in southern Louisiana, woodcock exhibited three feeding periods: early morning (0100 to 0500 hours) in the nocturnal habitat, midday (1000 to 1300 hours) in the diurnal habitat, and at dusk (1700 to 2100 hours) again in the nocturnal fields; earthworms and millipedes were consumed in both habitat types. Most of the woodcocks' metabolic water needs are met by their food (Mendall and Aldous, 1943, as cited in Cade, 1985), but captive birds have been observed to drink (Sheldon, 1967). The chicks leave the nest soon after hatching, but are dependent on the female for food for the first week after hatching (Gregg, 1984).

Molt. Woodcock molt twice annually. The prenuptial molt involves body plumage, some wing coverts, scapulars, and tertials and occurs in late winter or early spring; the complete postnuptial molt takes place in July or August (Bent, 1927).

Migration. Fall migration begins in late September and continues through December, often following the first heavy frost (Sheldon, 1967). The migration may take 4 to 6 weeks (Sheldon, 1967). Some woodcock winter in the south Atlantic region, while those that breed west of the Appalachian Mountains winter in Louisiana and other Gulf States (Martin et al., 1969, as cited in Owen et al., 1977). Woodcock are early spring migrants, leaving their wintering grounds in February and arriving on their northern breeding grounds in late March to early April (Gregg, 1984; Sheldon, 1967; Owen et al., 1977). Dates of woodcock arrival at their breeding grounds vary from year to year depending on the timing of snowmelt (Gregg, 1984). Sheldon (1967) summarizes spring and fall migration dates by States from numerous studies.

Breeding activities and social organization. From their arrival in the spring, male woodcock perform daily courtship flights at dawn and at dusk, defending a site on the singing grounds in order to attract females for mating (Owen et al., 1977; Gregg, 1984). Often several males display on a single singing ground, with each defending his own section of the area. Females construct their nests on the ground, usually at the base of a tree or shrub located in a brushy area adjacent to an opening or male singing ground (Gregg and Hale, 1977; McAuley et al., 1990; Owen et al., 1977). Females are responsible for all of the incubation and care of their brood (Trippensee, 1948). The young leave the nest soon after hatching and can sustain flight by approximately 18 days of age (Gregg, 1984).

Home range and resources. The home range of woodcocks encompasses both diurnal cover areas and nocturnal roosting areas and varies in size depending on season and the distribution of feeding sites and suitable cover. During the day, movements are usually limited until dusk, when woodcock fly to nocturnal roost sites. Hudgins et al. (1985) and Gregg (1984) found spring and summer diurnal ranges to be only 1 to 10 percent of the total home range. Movement on the nocturnal roost sites also is limited; however, during winter, woodcock are more likely to feed and move around at night (Bortner, pers. comm.). Singing males generally restrict their movements more than non-singing males, juveniles, and females (Owen et al., 1977).

Population density. The annual singing-ground survey conducted by the United States and Canada provides information on the population trends of woodcock in the

northern states and Canada during the breeding season (note from B. Bortner, U.S. Fish and Wildlife Service, Office of Migrating Bird Management, to Susan Norton, January 9, 1992). Gregg (1984) summarized results of several published singing-ground surveys and found estimates to vary from 1.7 male singing grounds per 100 ha in Minnesota (Godfrey, 1974, cited in Gregg, 1984) to 10.4 male singing grounds per 100 ha in Maine (Mendall and Aldous, 1943, cited in Gregg, 1984). Although this method is appropriate for assessing population trends, flushing surveys, telemetry, and mark-recapture are better methods for estimating woodcock densities because there are variable numbers of females and nonsinging males associated with active singing grounds (Dilworth, Krohn, Riffenberger, and Whitcomb pers. comm., cited by Owen et al., 1977). For example, Dwyer et al. (1988) found 2.2 singing males per 100 ha in a wildlife refuge in Maine, but with mark-recapture techniques, they found yearly summer densities of 19 to 25 birds per 100 ha in the same area.

Population dynamics. Woodcocks attempt to raise only a single brood in a given year but may renest if the initial clutch is destroyed (McAuley et al., 1990; Sheldon, 1967). In 12 years of study in Wisconsin, Gregg (1984) found 42 percent of all nests to be lost to predators and another 11 percent lost to other causes. Survival of juveniles in their first year ranges from 20 to 40 percent, and survival of adults ranges from 35 to 40 percent for males to approximately 40 to 50 percent for females (Dwyer and Nichols, 1982; Krohn et al., 1974). Derleth and Sepik (1990) found high adult survival rates (0.88 to 0.90 for both sexes) between June and October in Maine, indicating that adult mortality may occur primarily in the winter and early spring. They found lower summer survival rates for young woodcock between fledging and migration than for adults during the same months, with most losses of young attributed to predation.

Similar species (from general references)

- The common snipe (*Gallinago gallinago*) is similar in length (27 cm) to the woodcock, although lighter in weight. Snipe are primarily found in association with bogs and freshwater wetlands and feed on the various invertebrates associated with wetland soils. Snipe breed primarily in boreal forest regions and thus are found slightly north of the woodcock breeding range, with some areas of overlap in the eastern half of the continent. The breeding range of the snipe, however, extends westward to the Pacific coast and throughout most of Alaska, thus occupying a more extensive east-west range than the woodcock.

General references

Cade (1985); Dwyer et al. (1979); Dwyer and Storm (1982); Gregg (1984); National Geographic Society (1987); Owen et al. (1977); Sheldon (1967); Trippensee (1948).

American Woodcock (*Scolopax minor*)

<i>Factors</i>	<i>Age/Sex/ Cond./Seas.</i>	<i>Mean</i>	<i>Range or (95% CI of mean)</i>	<i>Location</i>	<i>Reference</i>	<i>Note No.</i>
Body Weight (g)	A M	176		throughout range	Nelson & Martin, 1953	
	A F	218				
	A M April	134.6 ± 2.9 SE		Maine	Dwyer et al., 1988	
	A M May	133.8 ± 5.8 SE				
	A M June	151.2 ± 9.5 SE				
	A M summer	145.9	127 - 165	central Massachusetts	Sheldon, 1967	
	J M summer	140.4	117 - 152			
	A F summer	182.9	162 - 216			
	J F summer	168.8	151 - 192			
	A M fall	169		Minnesota	Marshall (unpubl.)	1
J M fall	164					
A F fall	213					
J F fall	212					
	at hatching	13.0	9 - 16	Wisconsin	Gregg, 1984	
Egg Weight (g)	at laying near hatching	18 - 19 14 - 16		Wisconsin	Gregg, 1984	
Chick Growth Rate (g/day)	M F	5.1 6.2		Maine	Dwyer et al., 1982	
Metabolic Rate (kcal/kg-day)	A F basal	115		s Michigan	Rabe et al., 1983b	2
	A M basal	126			estimated	3
	A F basal	118				
	A F free-living	315		s Michigan	Rabe et al., 1983b	4
	A F nesting	553				
	A M free-living	313	(148 - 662)		estimated	5
	A F free-living	296	(140 - 627)			

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American Woodcock

American Woodcock (*Scolopax minor*)

<i>Factors</i>	<i>Age/Sex/ Cond./Seas.</i>	<i>Mean</i>	<i>Range or (95% CI of mean)</i>		<i>Location</i>	<i>Reference</i>	<i>Note No.</i>
Food Ingestion Rate (g/g-day)	A B winter (earthworm diet)	0.77	0.11 - 1.43		Louisiana (captive)	Stickel et al., 1965	
Water Ingestion Rate (g/g-day)	A M A F	0.10 0.10				estimated	6
Inhalation Rate (m ³ /day)	A M A F	0.11 0.13				estimated	7
Surface Area (cm ²)	A M A F	314 362				estimated	8
<i>Dietary Composition</i>	<i>Spring</i>	<i>Summer</i>	<i>Fall</i>	<i>Winter</i>	<i>Location/Habitat (measure)</i>	<i>Reference</i>	<i>Note No.</i>
earthworms Diptera Coleoptera Lepidoptera other animals plants		67.8 6.9 6.2 3.3 5.3 10.5			North America/NS (% volume; stomach contents)	Sperry, 1940	
earthworms beetle larvae grit (inorganic) other organic		58 10 31 1			Maine/fields (% wet weight; mouth esophagus, stomach, & proventriculus contents)	Krohn, 1970	9
earthworms other invertebrates				99+ <1	N Carolina/soybean fields (% wet weight; digestive tract)	Stribling & Doerr, 1985	
earthworms Coleoptera Hymenoptera				87 11 2	Alabama/NS (% volume; esophagus contents)	Miller & Causey, 1985	10

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American Woodcock

American Woodcock (*Scolopax minor*)

<i>Population Dynamics</i>	<i>Age/Sex Cond./Seas.</i>	<i>Mean</i>	<i>Range</i>	<i>Location/Habitat</i>	<i>Reference</i>	<i>Note No.</i>
Home Range Size (ha)	A M inactive A M active A M singing	3.1 (median) 73.6 (median) 10.5 (median)	0.3 - 6.0 38.2 - 171.2 4.6 - 24.1	Pennsylvania/mixed forests with shrubs and fields	Hudgins et al., 1985	
	B B summer A F with brood	32.4 ± 27.6 SD 4.5	7 - 98	Wisconsin/woods, open areas, brush	Gregg, 1984	
Population Density (birds/ha)	B B winter	3.38		North Carolina/agricultural: untilled soy stubble untilled corn stubble rebedded corn fields	Connors & Doerr, 1982	
	B B winter	0.20				
	B B winter	0.034				
	nests in spring	0.21 (nests/ha)		Pennsylvania/mixed pine and hardwoods, open fields Maine/second growth forest, meadows, and ponds	Coon et al., 1982 Dwyer et al., 1988	
	A M summer	0.035	0.026 - 0.046			
	A F summer	0.056	0.037 - 0.074			
J B summer	0.125	0.108 - 0.143				
B B summer	0.223	0.190 - 0.250				
Clutch Size		4	3 - 5	throughout range and habitats	Bent, 1927	
	1st clutch 2nd clutch	3.8 ± 0.42 SD 3.0 ± 0.67 SD		Maine/mixed forests, agricultural fields	McAuley et al., 1990	
Clutches/Year		1 but renest if 1st lost		throughout range and habitats	McAuley et al., 1990	
Percent Nests Hatching		about 50		Maine/mixed forests, fields	McAuley et al., 1990	
Days Incubation		19 - 21		NS/NS	Mendall & Aldous, 1943; Pettingill, 1936	11
Age at Fledging		18 - 19 days		Wisconsin/woods, open areas, brush	Gregg, 1984	

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American Woodcock

American Woodcock (*Scolopax minor*)

<i>Population Dynamics</i>	<i>Age/Sex Cond./Seas.</i>	<i>Mean</i>	<i>Range</i>	<i>Location/Habitat</i>	<i>Reference</i>	<i>Note No.</i>
Age at Sexual Maturity	M F	< 1 year 1 year		throughout range and habitats	Sheldon, 1967	
Annual Mortality Rates	A M east A M central J M east J M central A F east A F central J F east J F central	65 ± 5.2 SD 60 ± 15 SD 80 ± 4.8 SD 64 ± 12 SD 51 ± 7.3 SD 47 ± 9.6 SD 64 ± 7.7 SD 69 ± 9.4 SD		eastern and central United States/NS	Dwyer & Nichols, 1982	
<i>Seasonal Activity</i>	<i>Begin</i>	<i>Peak</i>	<i>End</i>	<i>Location</i>	<i>Reference</i>	<i>Note No.</i>
Mating/Laying	early February early April		mid-March	Texas Maine	Whiting & Boggus, 1982 Dwyer et al., 1982	
Hatching	early February late February late March mid-April	early May mid-May	early June	Louisiana Virginia Connecticut Massachusetts Maine	Pettingill, 1936 Pettingill, 1936 Pettingill, 1936 Sheldon, 1967 Dwyer et al., 1982	1 1 1
Molt		August to early September		NS/NS	Owen & Krohn, 1973	12
Migration						
spring	mid-February March	April	early March	leaving North Carolina arriving in northern range	Connors & Doerr, 1982 Gregg, 1984	
fall	October late September		December mid-December	arriving North Carolina leaving Canada	Sheldon, 1967 Owen et al., 1977	

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American Woodcock

American Woodcock (*Scolopax minor*)

- 1 As cited in Sheldon (1967).
- 2 Metabolic rate estimated by authors from equation of Aschoff and Pohl (1970).
- 3 Estimated using equation 3-28 (Lasiewski and Dawson, 1967) and summer body weights from Nelson and Martin (1953).
- 4 Estimate of free-living metabolism based on energy budget model. Metabolism during nesting estimated for peak needs during egg-laying.
- 5 Estimated using equation 3-37 (Nagy, 1987) and summer body weights from Nelson and Martin (1953).
- 6 Estimated using equation 3-15 (Calder and Braun, 1983) and summer body weights from Nelson and Martin (1953).
- 7 Estimated using equation 3-19 (Lasiewski and Calder, 1971) and summer body weights from Nelson and Martin (1953).
- 8 Estimated using equation 3-21 (Meeh, 1879 and Rubner, 1883, as cited in Walsberg and King, 1978) and summer body weights from Nelson and Martin (1953).
- 9 Grit comprised only 14 percent of total digestive tract contents volume.
- 10 Should provide a more accurate estimate of proportion of soft-bodied earthworms consumed than would including other portions of the digestive tract.
- 11 Cited in Trippensee (1948).
- 12 Cited in Owen et al. (1977).

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2.1.11. Spotted Sandpiper (sandpipers)

Order *Charadriiformes*, Family *Scolopacidae*. The family *Scolopacidae* includes numerous species of shorebirds, e.g., sandpipers, tattlers, knots, godwits, curlews, yellowlegs, willets, and dowitchers. Those known as sandpipers tend to be small with moderately long legs and bills. Most sandpipers forage on sandy beaches and mudflats; a few utilize upland areas. They feed almost exclusively on small invertebrates, either by probing into or gleaning from the substrate. Most species are highly migratory, breeding in arctic and subarctic regions and either wintering along the coasts or in southern latitudes and the southern hemisphere; therefore, many are only passage migrants throughout most of the United States. Scolapids range in size from the least sandpiper (11.5 cm bill tip to tail tip) to the long-billed curlew (48 cm).

Selected species

The spotted sandpiper (*Actitis macularia*) (19 cm) is a very common summer resident of freshwater and saltwater bodies throughout most of the United States. These sandpipers are most often encountered singly but may form small flocks. Most winter in the neotropics.

Body size. Females (approximately 50 g) are significantly larger than males (approximately 40 g) (Oring and Lank, 1986).

Habitat. Spotted sandpipers breed along the edges of bodies of water, usually in open habitats, from the northern border of the boreal forest across North America, south to the central United States (Oring and Lank, 1986). They require open water for bathing and drinking, semi-open habitat for nesting, and dense vegetation for breeding (Bent, 1929; Oring et al., 1983).

Food habits. In coastal areas, spotted sandpipers search the beach and muddy edges of inlets and creeks, wading less frequently than most sandpipers; inland they feed along the shores of sandy ponds and all types of streams, sometimes straying into meadows, fields, and gardens in agricultural areas (Bent, 1929). Their diet is composed primarily of terrestrial and marine insects (Bent, 1929). While adult flying insects comprise the bulk of the diet, crustaceans, leeches, molluscs, small fish, and carrion also are eaten (Oring et al., 1983). Young feed themselves immediately after hatching, concentrating on small invertebrates (Oring and Lank, 1986). During insect outbreaks, sandpipers will forage in wooded areas near water, and they have been observed eating eggs and fish on occasion (Oring, pers. obs.).

Molt. Partial prenuptial molt of body plumage occurs in March and April, while the postnuptial molt begins by August with the body feathers and ends anywhere from October to April with the loss of the primary flight feathers (Bent, 1929).

Migration. Spotted sandpipers generally migrate in small flocks or solitarily (National Geographic Society, 1987). They winter from southern United States to northern Chile, Argentina, and Uruguay (Oring and Lank, 1986), and breed across North

America, north from Virginia and southern California (National Geographic Society, 1987). In the spring, females arrive at the breeding grounds earlier than males (in one study, by about 2 weeks; Oring and Lank, 1982).

Breeding activities and social organization. The primary consideration for nesting sites is proximity to water, and spotted sandpipers have been known to build their ground nests in such diverse conditions as depressions in volcanic rock and strawberry patches (Bent, 1929). Spotted sandpipers are polyandrous (i.e., a single female lays eggs for multiple males), with males supplying most of the incubation and parental care (Oring, 1982). Thus reproduction is limited by the number of males present (Lank et al., 1985). Spotted sandpipers lay a determinate clutch of four eggs. Females may lay several clutches in a year, often a dozen eggs per season (Maxson and Oring, 1980). Egg laying begins between late May and early June in Minnesota (Lank et al., 1985), and males incubate after the third egg is laid (Oring et al., 1986). Females sometimes incubate and brood when another male is not available (Maxson and Oring, 1980). Parents brood small chicks and protect them with warning calls or by distracting or attacking predators (Oring and Lank, 1986).

Home range and resources. Although a variety of vegetation types are used, nests usually are placed in semi-open vegetation near the edge of a lake, river, or ocean (Oring et al., unpubl., as cited in Oring et al., 1983; McVey, pers. obs.). The suitability of nesting habitat varies from year to year in some locations due to levels of precipitation and predators (Oring et al., 1983).

Population density. Spotted sandpiper nesting densities have been studied well at only one location, on Little Pelican Island, Leech Lake, Minnesota. At this location, densities ranged from 4 to 13 females per hectare and 7 to 20 males per hectare over a 10-year period, depending on weather and other conditions (Oring et al., 1983).

Population dynamics. Females may lay one to six clutches for different males over one season (Oring et al., 1984), averaging 1.3 to 2.7 mates per year (Oring et al., 1991b). Female mating and reproductive success increase with age, but male success does not (Oring et al., 1991b). Lifetime reproductive success is most affected by fledging success and longevity for both males and females (Oring et al., 1991a).

Similar species (from general references)

- The solitary sandpiper (*Tringa solitaria*) is usually seen singly in freshwater swamps or rivers. Present over much of the United States during annual migrations, this average-sized sandpiper (18 cm) winters along the southeast and Gulf coasts.
- The western sandpiper (*Calidris mauri*) is a small sandpiper (13 cm), common on mudflats and sandbars, that winters on both the Atlantic and Pacific shores of the United States.

- The least sandpiper (*Calidris minutilla*), the smallest of this group (11 cm), is common in winter on salt marshes and muddy shores of rivers and estuaries in coastal areas across the United States.
- The semipalmated sandpipers (*Calidris pusilla*) are small birds (13 cm) seen in the United States primarily during migration and rarely wintering on Florida coasts.
- Most other members of the family *Scolopacidae* forage by gleaning.

General references

Oring and Lank (1986); Lank et al. (1985); National Geographic Society (1987); Oring et al. (1991a, 1991b).

Spotted Sandpiper (*Actitis macularia*)

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Spotted Sandpiper

<i>Factors</i>	<i>Age/Sex/ Cond./Seas.</i>	<i>Mean</i>	<i>Range or (95% CI of mean)</i>		<i>Location</i>	<i>Reference</i>	<i>Note No.</i>	
Body Weight (g)	A F spring A M spring	47.1 37.9	43 - 50 34 - 41		Minnesota island	Maxson & Oring, 1980		
Metabolic Rate (kcal/kg-day)	A F pre-breed	404 - 787			Minnesota	Maxson & Oring, 1980	1	
	A F laying	383 - 745						
	A F incubating	368 440						
	A M pre-breed	303						
	A M incubating	425						
	A M brooding	436	(202 - 937)		estimated	2		
	A F free-living A M free-living	460	(213 - 994)					
Food Ingestion Rate (g/g-day)							3	
Water Ingestion Rate (g/g-day)	A F A M	0.16 0.17				estimated	4	
Inhalation Rate (m³/day)	A F A M	0.039 0.033				estimated	5	
Surface Area (cm²)	A F A M	131 113				estimated	6	
<i>Dietary Composition</i>		Spring	Summer	Fall	Winter	Location/Habitat (measure)	Reference	Note No.
mayflies midges			✓ ✓			Minnesota/island in lake	Maxson & Oring, 1980	
<i>Population Dynamics</i>		Age/Sex Cond./Seas.	Mean	Range		Location/Habitat	Reference	Note No.
Territory Size (ha)			approx. 0.25			NS/NS	Maxson & Oring, 1980	

Spotted Sandpiper (*Actitis macularia*)

<i>Population Dynamics</i>	<i>Age/Sex Cond./Seas.</i>	<i>Mean</i>	<i>Range</i>	<i>Location/Habitat</i>	<i>Reference</i>	<i>Note No.</i>
Population Density (N/ha)	A F summer A M summer	10 13.9	3.8 - 12.5 7.5 - 20.0	Minnesota/island in lake	Oring et al., 1983	
Clutch Size		4	3 - 5	NS/NS	Bent, 1929; Oring et al., 1983	7
Clutches/Year			1 - 6	Minnesota/NS	Oring et al., 1983	
Days Incubation		18 to 24		NS/NS	Oring, unpublished	
Age at Fledging		approximately 18 days		NS/NS	Oring et al., 1991a	
Number Fledge per Nest That Hatches		1.83	0.58 - 2.76	Minnesota/island in lake	Oring et al., 1984	
Number Fledge per Successful Nest		2.58	1.67 - 2.91	Minnesota/island in lake	Oring et al., 1984	
Age at Sexual Maturity	F M	1 year 1 year		Minnesota/island in lake	Oring et al., 1983	
Annual Mortality Rates (percent)	F M	approx. 31 approx. 30		Minnesota/island in lake	Oring et al., 1983; Oring & Lank, 1982; Oring, unpublished	
Longevity	A F	3.7 years		Minnesota/island in lake	Oring et al., 1983	
<i>Seasonal Activity</i>	<i>Begin</i>	<i>Peak</i>	<i>End</i>	<i>Location</i>	<i>Reference</i>	<i>Note No.</i>
Mating	early May	late May - early June		Minnesota	Lank et al., 1985	
Hatching	early June	late June		Minnesota	Lank et al., 1985	

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Spotted Sandpiper

Spotted Sandpiper (*Actitis macularia*)

<i>Seasonal Activity</i>	<i>Begin</i>	<i>Peak</i>	<i>End</i>	<i>Location</i>	<i>Reference</i>	<i>Note No.</i>
Molt fall spring	August	March - April	October	NS	Bent, 1929 Bent, 1929	
Migration females males	late June early July	early - mid-July mid-July		Minnesota	Lank et al., 1985	

- 1 Estimated by authors; allometric model not specified.
- 2 Estimated using equation 3-37 (Nagy, 1987) and body weights from Maxson and Oring (1980).
- 3 See Chapters 3 and 4 for methods of estimating food ingestion rates; also see Section 4.1.3 and Table 4-4 for sediment ingestion rates for sandpipers.
- 4 Estimated using equation 3-15 (Calder and Braun, 1983) and body weights from Maxson and Oring (1980).
- 5 Estimated using equation 3-19 (Lasiewski and Calder, 1971) and body weights from Maxson and Oring (1980).
- 6 Estimated using equation 3-21 (Meeh, 1879 and Rubner, 1883, as cited in Walsberg and King, 1978) and body weights from Maxson and Oring (1980).
- 7 Spotted sandpipers are determinate layers, with a clutch size of four eggs. Clutches with fewer eggs are not complete or have lost eggs; larger clutches are the result of more than one female laying in a nest.

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Spotted Sandpiper

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2.1.12. Herring Gull (gulls)

Order *Charadriiformes*, Family *Laridae*. Gulls are medium- to large-sized sea birds with long pointed wings, a stout, slightly hooked bill, and webbed feet. They are abundant in temperate coastal areas and throughout the Great Lakes. Although gulls may feed from garbage dumps and landfills, most take natural prey. Gulls nest primarily in colonies, although some of the larger species also nest solitarily. Many populations migrate annually between breeding and wintering areas. North American gull species range in size from Bonaparte's gull (33 cm bill tip to tail tip) to the great black-backed gull (76 cm).

Selected species

The herring gull (*Larus argentatus*) (64 cm) has the largest range of any North American gull, from Newfoundland south to the Chesapeake Bay along the north Atlantic and west throughout the Great Lakes into Alaska. Along the Pacific coast, the similar-sized western gull (*L. occidentalis*) is the ecological equivalent of the herring gull. Both species take primarily natural foods, especially fish, although some individuals of both species forage around fishing operations and landfills (Pierotti, 1981, 1987; Pierotti and Annett, 1987). The increase in number of herring gulls in this century has been attributed to the increasing abundance of year-round food supplies found in landfills (Drury, 1965; Harris, 1970); however, birds specializing on garbage have such low reproductive success that they cannot replace themselves in the population (Pierotti and Annett, 1987, 1991). An alternative explanation of the species' expansion is that cessation of taking of gulls by the feather industry in the late 1800's has allowed gull numbers to return to pre-exploitation levels (Graham, 1975).

Body size. Adult females (800 to 1,000 g) are significantly smaller than males (1,000 to 1,300 g) in both the herring gull (Greig et al., 1985) and the western gull (Pierotti, 1981). Chicks grow from their hatching weight of about 60 to 70 g to 800 to 900 g within 30 to 40 days, after which time their weight stabilizes (Dunn and Brisbin, 1980; Norstrom et al., 1986; Pierotti, 1982). Norstrom et al. (1986) fitted chick growth rates to the Gompertz equation as follows:

$$BW = 997 e^{-e^{-(0.088(t - 14.8))}} \quad \text{for females, and}$$

$$BW = 1193 e^{-e^{-(0.075(t - 16.3))}} \quad \text{for males,}$$

where BW equals body weight in grams and t equals days after hatching. Adults show seasonal variation in body weight (Coulson et al., 1983; Norstrom et al., 1986).

Habitat. Nesting colonies of herring gulls along the northeastern coast of the United States are found primarily on sandy or rocky offshore or barrier beach islands (Kadlec and Drury, 1968). In the Great Lakes, they are found on the more remote, secluded, and protected islands and shorelines of the lakes and their connecting rivers (Weseloh, 1989). Smaller colonies or isolated pairs also can be found in coastal marshes (Burger, 1980a), peninsulas, or cliffs along seacoasts, lakes, and rivers (Weseloh, 1989), and occasionally in inland areas or on buildings or piers (Harris, 1964). Gulls are the most abundant seabirds

offshore from fall through spring, and are only found predominantly inshore during the breeding season in late spring and summer (Powers, 1983; Pierotti, 1988). Gulls forage predominantly offshore, within 1 to 5 km of the coast (Pierotti, 1988). In all seasons the number of birds feeding at sea outnumber those feeding inshore (data from Powers, 1983; Pierotti, pers. comm.). Inshore, herring gulls forage primarily in intertidal zones but also search for food in wet fields, around lakes, bays, and rock jetties, and at landfills in some areas (Burger, 1988). In Florida, herring gull presence at landfills is restricted to the winter months (December through April) and may consist primarily of first-year birds that migrated from more northerly populations (e.g., from the Great Lakes) (Patton, 1988).

Food habits. Gulls feed on a variety of foods depending on availability, including fish, squid, crustacea, molluscs, worms, insects, small mammals and birds, duck and gull eggs and chicks, and garbage (Bourget, 1973; Burger, 1979a; Fox et al., 1990; Pierotti and Annett, 1987). Gulls forage on open water by aerial dipping and shallow diving around concentrations of prey. At sea, such concentrations often are associated with whales or dolphins, other seabirds, or fishing boats (McCleery and Sibly, 1986; Pierotti, 1988). In the Great Lakes, concentrations of species such as alewife occur seasonally (e.g., when spawning) (Fox et al., 1990). Gulls also forage by stealing food from other birds and by scavenging around human refuse sites (e.g., garbage dumps, fish plants, docks, and seaside parks) (Burger and Gochfeld, 1981; 1983; Chapman and Parker, 1985). Individual pairs of gulls may specialize predominantly on a single type of food; for example, three quarters of a population of herring gulls in Newfoundland were found to specialize either on blue mussels, garbage, or adults of Leach's storm-petrel, with 60 percent of the specialists concentrating on mussels between 0.5 and 3 cm in length (Pierotti and Annett, 1987; 1991). Diet choices may change with the age and experience of adult birds as well as with availability of prey (Pierotti and Annett, 1987; 1991). Females take smaller prey and feed less on garbage than do males (Pierotti, 1981; Greig et al., 1985). For example, Fox et al. (1990) found females to feed more on smelt (100 to 250 mm) and males more on alewife (250 to 300 mm) in the Great Lakes region. Adult gulls sometimes attack and eat chicks of neighboring gulls or other species of seabird (Brown, 1967; Schoen and Morris, 1984). Juveniles up to 3 years of age forage less efficiently than adults (Greig et al., 1983; MacLean, 1986; Verbeek, 1977). In the Great Lakes, herring gulls' high consumption of alewife during their spawn may result in high exposures of the gulls to lipophilic contaminants that biomagnify (Fox et al., 1990).

Metabolism. Norstrom et al. (1986) have estimated an annual energy budget for free-living female herring gulls that breed in the Great Lakes and an annual energy budget for free-living juvenile herring gulls in the Great Lakes in their first year. Between September and March, the nonbreeding season, they estimate that adult females require 250 to 260 kcal/day. Following a dip in energy requirements to 210 kcal/day when the male feeds the female during courtship, the female's needs increase to peak at 280 kcal/day for egg production, then fall to approximately 210 kcal/day during incubation. The energy required to forage for food for the chicks is substantial, rising through July to peak in August at 310 to 320 kcal/day, then declining again until September when feeding chicks has ceased. These estimates compare well with those derived from Nagy's (1987) equation to estimate free-living metabolic rates for seabirds, except that the energy peaks required to produce eggs and to feed chicks are not included in Nagy's model. Readers interested in the metabolic rates of first-year herring gulls are referred to Norstrom et al. (1986). Ellis

(1984) provides an overview of seabird energetics and additional discussion of approaches and models for estimating metabolic rates of free-ranging seabirds.

Molt. Gull chicks are downy gray with dark brown spotting and molt into a dark-gray or brown mottled juvenile plumage. At the end of the first year, portions of the plumage have paled, and by the second year, gray plumage develops along the back and top of wings. By their third year, young gulls resemble dirty adults, and they acquire their full adult plumage by 4 years (Harrison, 1983; Kadlec and Drury, 1968). Adult gulls, at least in some populations, begin their primary feather molt during incubation and complete the molt by mid- to late fall (Coulson et al., 1983). They molt and replace the large body feathers from mid-summer to early fall (Coulson et al., 1983).

Migration. Herring gull populations along the northeast coast of North America tend to be migratory, while adult herring gulls of the Great Lakes are year-round residents. Along the western North Atlantic, most herring gulls arrive on their breeding grounds between late February and late April. They remain until late August or early September when they leave for their wintering grounds along the Atlantic and Gulf coasts or well offshore (Burger, 1982; Pierotti, 1988). Adult and older subadult herring gulls in the Great Lakes area are essentially nonmigratory (Mineau et al., 1984; Weseloh et al., 1990). Thus, in contrast to other fish-eating birds in the Great Lakes system that migrate south in the winter, herring gulls are exposed to any contaminants that may be in Great Lakes' fish throughout the year (Mineau et al., 1984). Postbreeding dispersal away from breeding colonies begins in late July and ends in August, with all ages traveling short distances. Great Lakes herring gulls less than a year old usually migrate to the Gulf or Atlantic coast (Smith, 1959; Mineau et al., 1984), traveling along river systems and the coast (Moore, 1976).

Breeding activities and social organization. Gulls nest primarily in colonies on offshore islands, and nest density is strongly affected by population size (Pierotti, 1981; 1982; 1987). Typically, males arrive at the breeding grounds first and establish territories. Both sexes build the nest of vegetation on the ground in areas that are sheltered from wind but may be exposed to the sun (Pierotti, 1981; 1982). Males feed females for 10 to 15 days prior to the start of egg laying (Pierotti, 1981). From the laying of the first egg until the chicks are 3 to 4 weeks old, one or both parents will be present at all times (Tinbergen, 1960). Males perform most territorial defense, females perform most incubation, and both parents feed the chicks until they are at least 6 to 7 weeks old (Burger, 1981; Pierotti, 1981; Tinbergen, 1960). All gulls are strongly monogamous; pair bonds can persist for 10 or more years and usually only are terminated by the death of a mate or failure to reproduce successfully (Tinbergen, 1960). Males may be promiscuous in populations with more females than males (Pierotti, 1981). Herring gull colonies often are found in association with colonies of other species, including other gulls (Bourget, 1973; Brown, 1967). In some nesting colonies, gulls attack chicks of neighboring gulls and other species (Brown, 1967; Schoen and Morris, 1984).

Home range and resources. During the breeding season, herring gulls defend a territory of several tens of square meters around the immediate vicinity of the nest (Burger, 1980b). Their daily foraging range depends on the availability of prey and on the foraging strategy, age, and sex of the gull. Using radiotelemetry on gulls in the Great Lakes, Morris

and Black (1980) demonstrated that some parents with chicks forage at specific locations within 1 km of the colony whereas other parents make extended flights to destinations across a lake more than 30 km away. Similarly, gulls that feed at sea may range tens of kilometers from their nest whereas gulls from the same colony feeding in the intertidal zone may travel less than 1 km (Pierotti and Annett, 1987; 1991). Males typically range farther than females and take larger prey items (Pierotti and Annett, 1987; 1991). At sea during the nonbreeding season, gulls may range hundreds of kilometers during a day (Pierotti, pers. comm.).

Population density. As described above, population density is determined by available nesting space, size of the breeding population, and quality of habitat. Small islands with good feeding areas nearby can have several hundred nests per hectare (Kadlec, 1971; Parsons, 1976b; Pierotti, 1982). In poor quality habitat, some pairs nest solitarily without another nest for several kilometers (Weseloh, 1989).

Population dynamics. Herring gulls and western gulls usually do not begin breeding until at least 4 years of age for males and 5 years of age for females (Burger, 1988; Pierotti, 1981; Pierotti, pers. comm.). Kadlec and Drury (1968) suggest that in a given year, 15 to 30 percent of adults of breeding age do not breed. Most breeding females produce three-egg clutches, but individuals in poor condition may lay only one or two eggs (Parsons, 1976a; Pierotti, 1982; Pierotti and Annett, 1987; 1991). Herring gulls will lay replacement eggs if all or a portion of their original clutch is destroyed (Parsons, 1976a). Hatching success appears to be influenced by female diet, with garbage specialists hatching a smaller percentage of eggs than fish or intertidal (mussel) specialists (Pierotti and Annett, 1987, 1990, 1991). Predation, often by gulls of the same or other species, also contributes to egg losses (Paynter, 1949; Harris, 1964; Davis, 1975). Many herring gull chicks that hatch die before fledging, most within the first 5 days after hatching (Harris, 1964; Kadlec et al., 1969; Brown, 1967). Adult mortality is low (around 10 percent per year), and some birds may live up to 20 years (Brown, 1967; Kadlec and Drury, 1968). Subadult birds exhibit higher mortality (20 to 30 percent per year) (Kadlec and Drury, 1968; Chabrzyk and Coulson, 1976).

Similar species (from general references)

- The western gull (*Larus occidentalis*) (64 cm), found on the Pacific coast of the United States, is the ecological equivalent of the herring gull and is similar in size (53 cm); males range from 1,000 to 1,300 g and females from 800 to 1,000 g (Pierotti, 1981).
- The glaucous gull (*Larus hyperboreus*) is larger (69 cm) than the herring gull and is the predominant gull breeding in the high arctic. Birds from Alaska are slightly smaller than birds from eastern Canada.
- The glaucous-winged gull (*Larus glaucescens*) is similar in size to the herring gull (66 cm) and is the primary breeding species north of the Columbia River. This species hybridizes extensively with the herring gull in Alaska.

- The California gull (*Larus californicus*) is smaller (53 cm) than the herring gull. This species breeds primarily in the Great Basin Desert and winters along the Pacific coast.
- The great black-backed gull (*Larus marinus*) is the largest species of gull (76 cm) in North America and breeds from Labrador to Long Island.
- The ring-billed gull (*Larus delawarensis*) is of average size (45 cm) and is the most common breeding gull in the Great Lakes and northern prairies.
- Franklin's gull (*Larus pipixcan*) is a small (37 cm), summer resident of the Great Plains.

General references

For general information: Harrison (1983); National Geographic Society (1987); Tinbergen (1960); Graham (1975). For discussion of diet: Burger (1988); Fox et al. (1990); Pierotti (1981); Pierotti and Annett (1987).

Herring Gull (*Larus argentatus*)

<i>Factors</i>	<i>Age/Sex Cond./Seas.</i>	<i>Mean</i>	<i>Range or (95% CI of mean)</i>	<i>Location</i>	<i>Reference</i>	<i>Note No.</i>
Body Weight (g)	A F spring A M spring	951 ± 88 SD 1,184 ± 116 SD		Lake Huron	Norstrom et al., 1986	
	A F summer A M summer	999 ± 90 SD 1,232 ± 107 SD	832 - 1,274 1,014 - 1,618	Newfoundland	Threlfall & Jewer, 1978	
	at hatching 10 days old 20 days old 30 days old	65 230 590 810	50 - 80 120 - 380 420 - 800 610 - 1,000	Maine	Dunn & Brisbin, 1980	
	30 days old 30 days old	964 ± 77 SD 818 ± 99 SD		Newfoundland/rocky island Newfoundland/grassy island	Pierotti, 1982	1
	Chick Growth Rate (g/day)	< 5 days 5-30 days	8.8 - 13.1 26.3 ± 6.5 SD		Newfoundland/island Newfoundland/island meadow Newfoundland/rocky island	Pierotti, 1982 Pierotti, 1982 Pierotti, 1982
	5-30 days 5-25 days	33.4 ± 4.7 SD 30.2 ± 1.75 SD	26.7 - 31.4	Maine/coastal island	Hunt, 1972	
Egg Weight (g)	3 egg clutch 2 egg clutch	87.2 85.7		New Brunswick	Herbert & Barclay, 1988	
	in 1983 in 1984	92.0 ± 5.9 SD 98.0 ± 8.0 SD		Lake Superior, Canada	Meathrel et al., 1987	
Metabolic Rate (kcal/kg-day)	A M basal A F basal	86 91			estimated	2
	A standard	99		laboratory	Lustick et al., 1978	
	A M free- living A F free- living	233 248	(84 - 646) (92 - 669)		estimated	3
	Also see text for a discussion of annual variation in free-living metabolic rate in herring gulls.					

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Herring Gull

Herring Gull (*Larus argentatus*)

<i>Factors</i>	<i>Age/Sex Cond./Seas.</i>	<i>Mean</i>	<i>Range or (95% CI of mean)</i>	<i>Location</i>	<i>Reference</i>	<i>Note No.</i>	
Food Ingestion Rate (g/g-day)	A M breeding	0.20		Newfoundland - diet of mussels	Pierotti & Annett, 1991	4	
	A F breeding	0.21					
	A M breeding	0.19		Newfoundland - diet of garbage	Pierotti & Annett, 1991	5	
	A F breeding	0.18					
Water Ingestion Rate (g/g-day)	A M	0.055			estimated	6	
	A F	0.059					
Inhalation Rate (m ³ /day)	A M	0.48			estimated	7	
	A F	0.41					
Surface Area (cm ²)	A M	1,150			estimated	8	
	A F	1,001					
<i>Dietary Composition</i>	<i>Summer</i>	<i>Summer</i>	<i>Summer</i>	<i>Summer</i>	<i>Location/Habitat (measure)</i>	<i>Reference</i>	<i>Note No.</i>
months:	Mid-May/ Mid-June	Mid-June/ Mid-July	Mid-July/ Mid-Aug.		Newfoundland/island	Haycock & Threlfall, 1975	
Mytilus edulis	30.9	0.9	9.1		(% occurrence in regurgitations and pellets)		
sea urchin	5.8	0.0	4.5				
fish	11.4	71.1	18.9				
Oceanodroma leucomorpha	22.4	7.0	15.9				
Fratercula arctica adults	5.8	0.0	1.5				
Fratercula, Uria chicks	0.0	3.5	9.1				
Larus sp. eggs	3.1	0.9	0.8				
Vaccinium angustifolium	-	-	9.9				
Gadus morhua offal	12.4	1.7	14.4				
assorted refuse	5.8	0.9	6.8				

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Herring Gull

Herring Gull (*Larus argentatus*)

<i>Dietary Composition</i>	Summer	Summer	Summer	Summer	Location/Habitat (measure)	Reference	Note No.
year: American smelt alewife other fish birds voles insects & refuse	1978 46.1 23.1 20.5 2.6 2.6 12.8	1979 18.4 73.7 0 2.6 2.6 0	1980 61.2 16.7 3.4 13.8 3.4 3.4	1981 57.8 23.4 3.1 6.2 9.4 0	Lake Ontario (% occurrence in regurgitations from and stomach contents of incubating adults)	Fox et al., 1990	
lake: fish insects offal, garbage gull chicks adult birds amphibians earthworms crayfish	Ontario 91.8 5.5 0.5 2.2 1.6 0.5 2.2 0	Erie 94.1 5.9 2.9 0 0 0 0 0	Huron 75.8 5.6 13.6 1.0 1.0 0 11.6 0.5	Superior 38.6 42.1 21.0 0 3.5 0 1.7 0	Great Lakes (% occurrence in boli regurgitated by chicks)	Fox et al., 1990	
snails crabs garbage offal worms other inverts. fish		3 14 27 5 23 28 unknown			CA,FL,NY,NJ,TX/ coastal (% of gulls feeding on items) offshore feeding on fish was not included in observations	Burger, 1988	
<i>Population Dynamics</i>	Age/Sex/Cond./Seas.	Mean	Range		Location/Habitat	Reference	Note No.
Foraging Radius (km)	A M A F	10 to 15 5 to 10	3 - 50 3 - 25		NS/coastal	Pierotti, pers. comm.	
Population Density (nests/ha)	summer summer	227 217 75	138 - 350		Massachusetts/coastal islands Newfoundland/island - rocky Newfoundland/island - grassy slope	Kadlec, 1971 Pierotti, 1982 Pierotti, 1982	

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Herring Gull

Herring Gull (*Larus argentatus*)

<i>Population Dynamics</i>	<i>Age/Sex/ Cond./Seas.</i>	<i>Mean</i>	<i>Range</i>	<i>Location/Habitat</i>	<i>Reference</i>	<i>Note No.</i>
Clutch Size		2.78	2.51 - 2.90 (over 8 sites)	New Jersey/salt marsh islands	Burger, 1979b	
		2.54	1 - 6 (per nest)	NE United States/coastal	Nisbet & Drury, 1984	
		2.38	2.3 - 2.8 (over 11 years)	Maine/coastal islands	Hunt, 1972	
		2.84 ± 0.44 SD		Lake Superior, Canada/ islands	Meathrel et al., 1987	
Clutches/Year		1	1 - 2*	(* if first eggs lost)	Burger, 1979a; Bourget, 1973	
Days Incubation		30.5 29	28 - 33	Holland/NS Newfoundland/island	Tinbergen, 1960 Pierotti, 1982	9
Age at Fledging (days)		51 43	35 - 44 to 56 - 61 31 to 52	Massachusetts/coastal island New Brunswick/island	Kadlec et al., 1969 Paynter, 1949	
Number Fledge per Active Nest	3 colonies	1.42	1.40 - 1.44	New Jersey/coastal	Burger & Shisler, 1980	
	6 colony-yrs	1.65	1.40 - 2.13	Lake Ontario/lakeshore	Mineau et al., 1984 (minimum and maximum are yearly means)	
	3 colony-yrs	1.78	1.62 - 2.10	Lake Erie/lakeshore		
	6 colony-yrs	2.19	2.16 - 2.25	Lake Huron/lakeshore		
Number Fledge per Successful Nest	3 colonies	1.80	1.79 - 1.80	New Jersey/coastal	Burger & Shisler, 1980	
Age at Sexual Maturity	F	5 years		throughout range/NS	Greig et al., 1983; Pierotti, pers. comm.	
	M	4 - 5 years				
	B	4.3 to 5.8	3 - 8	Scotland/coastal	Coulson et al., 1982	
Annual Mortality Rates (percent)	A B	8		New England/coastal	Kadlec & Drury, 1968	
	J B	22	17 - 33			
	A B	7.3		Scotland/coastal	Chabryzk & Coulson, 1976	

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Herring Gull

Herring Gull (*Larus argentatus*)

<i>Population Dynamics</i>	<i>Age/Sex/Cond./Seas.</i>	<i>Mean</i>	<i>Range</i>	<i>Location/Habitat</i>	<i>Reference</i>	<i>Note No.</i>
Longevity	A B	10	up to 30 years	NS/NS	Pierotti, pers. comm.	
<i>Seasonal Activity</i>	<i>Begin</i>	<i>Peak</i>	<i>End</i>	<i>Location</i>	<i>Reference</i>	<i>Note No.</i>
Mating/ Laying	late April early May early May early May	early May mid-May mid-May late May	early June early June mid-June end May	ne shore Lake Superior Maine New Jersey Newfoundland	Morris & Haymes, 1977 Bourget, 1973 Burger, 1977, 1979b Pierotti, 1982	
Hatching	May early June late June	mid - late May June mid-June late June	July end June mid-July	Great Lakes Massachusetts Newfoundland New Brunswick	Fox et al., 1990 Kadlec, 1971 Pierotti, 1982, 1987 Paynter, 1949	
Migration spring	February		late April	northwestern Atlantic populations	Burger, 1982	
fall	August		September			
Molt	June	July	August	Newfoundland	Pierotti, pers. comm.	

- 1 Weight of chicks from first egg laid in 1978 for the rocky island and in 1977 for the grassy area. In some years and some locations, chicks from the first egg were heavier than the rest, and at other times and locations, the first chick was lighter.
- 2 Estimated using equation 3-29 (Lasiewski and Dawson, 1967) and body weights from Threlfall and Jewer (1978).
- 3 Estimated using equation 3-38 (Nagy, 1987) and body weights from Threlfall and Jewer (1978).
- 4 Estimated using 11.2 meals of mussel consumed per day per pair, weight of 80 g per mussel meal of which half is shell and not included in ingestion rate, assuming that the female accounts for 46 percent of pair's energy requirement and the male accounts for 54 percent, and using the body weights of Threlfall and Jewer (1978).
- 5 Estimated using 4.2 meals of garbage consumed per day per pair, weight of 100 g per garbage meal, assuming that the female accounts for 46 percent of pair's energy requirement and the male accounts for 54 percent, and using the body weights of Threlfall and Jewer (1978).
- 6 Estimated using equation 3-15 (Calder and Braun, 1983) and body weights from Threlfall and Jewer (1978).
- 7 Estimated using equation 3-19 (Lasiewski and Calder, 1971) and body weights from Threlfall and Jewer (1978).
- 8 Estimated using equation 3-21 (Meeh, 1879 and Rubner, 1883, as cited in Walsberg and King, 1978) and body weights from Threlfall and Jewer (1978).
- 9 Beginning with first egg.

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2.1.13. Belted Kingfisher (kingfishers)

Order Coraciiformes, Family Alcedinidae. Kingfishers are stocky, short-legged birds with large heads and bills. They exist on a diet mostly of fish, which they catch by diving, from a perch or the air, head first into the water. They nest in burrows in earthen banks that they dig using their bills and feet.

Selected species

The belted kingfisher (*Ceryle alcyon*, formerly *Megaceryle alcyon*) is a medium-sized bird (33 cm bill tip to tail tip) that eats primarily fish. It is one of the few species of fish-eating birds found throughout inland areas as well as coastal areas. The belted kingfisher's range includes most of the North American continent; it breeds from northern Alaska and central Labrador southward to the southern border of the United States (Bent, 1940). Two subspecies sometimes are recognized: the eastern belted kingfisher (*Ceryle alcyon alcyon*), which occupies the range east of the Rocky Mountains and north to Quebec, and the western belted kingfisher (*Cercyle alcyon caurina*), which occupies the remaining range to the west (Bent, 1940).

Body size. The sexes are similar in size and appearance, although the female tends to be slightly larger (Salyer and Lagler, 1946). Bent (1940) reported that western populations are somewhat larger than eastern ones. Nestlings reach adult body weight by about 16 days after hatching, but then may lose some weight before fledging (Hamas, 1981).

Habitat. Belted kingfishers are typically found along rivers and streams and along lake and pond edges (Hamas, 1974). They are also common on seacoasts and estuaries (Bent, 1940). They prefer waters that are free of thick vegetation that obscures the view of the water and water that is not completely overshadowed by trees (Bent, 1940; White, 1953). Kingfishers also require relatively clear water in order to see their prey and are noticeably absent in areas when waters become turbid (Bent, 1940; Davis, 1982; Salyer and Lagler, 1946). White (1953) suggested that water less than 60 cm deep is preferred. They prefer stream riffles for foraging sites even when pools are more plentiful because of the concentration of fish at riffle edges (Davis, 1982). Belted kingfishers nest in burrows within steep earthen banks devoid of vegetation beside rivers, streams, ponds, and lakes; they also have been found to nest in slopes created by human excavations such as roadcuts and landfills (Hamas, 1974). Sandy soil banks, which are easy to excavate and provide good drainage, are preferred (Brooks and Davis, 1987; Cornwell, 1963; White, 1953). In general, kingfishers nest near suitable fishing areas when possible but will nest away from water and feed in bodies of water other than the one closest to home (Cornwell, 1963).

Food habits. Belted kingfishers generally feed on fish that swim near the surface or in shallow water (Salyer and Lagler, 1946; White, 1953; Cornwell, 1963). Davis (pers. comm. in Prose, 1985) believes that these kingfishers generally catch fish only in the upper 12 to 15 cm of the water column. Belted kingfishers capture fish by diving either from a perch overhanging the water or after hovering above the water (Bent, 1940). Fish

are swallowed whole, head first, after being beaten on a perch (Bent, 1940). The average length of fish caught in a Michigan study was less than 7.6 cm but ranged from 2.5 to 17.8 cm (Salyer and Lagler, 1946); Davis (1982) found fish caught in Ohio streams to range from 4 to 14 cm in length. Several studies indicate that belted kingfishers usually catch the prey that are most available (White, 1937, 1953; Salyer and Lagler, 1946; Davis, 1982). Diet therefore varies considerably among different water bodies and with season (see examples in Appendix). Although kingfishers feed predominantly on fish, they also sometimes consume large numbers of crayfish (Davis, 1982; Salyer and Lagler, 1946), and in shortages of their preferred foods, have been known to consume crabs, mussels, lizards, frogs, toads, small snakes, turtles, insects, salamanders, newts, young birds, mice, and berries (Bent, 1940). Parents bring surprisingly large fish to their young. White (1953) found that nestlings only 7 to 10 days old were provided fish up to 10 cm long, and nestlings only 2 weeks old were provided with fish up to 13 cm in length. After fledging, young belted kingfishers fed on flying insects for their first 4 days after leaving the nest, crayfish for the next week, and by the 18th day post-fledging, could catch fish (Salyer and Lagler, 1946).

Molt. The juvenile plumage is maintained through the winter, and young birds undergo their first prenuptial molt in the spring (between February and April) involving most of the body plumage (Bent, 1940). Adults have a complete postnuptial molt in the fall (August to October) (Bent, 1940).

Migration. This kingfisher breeds over most of the area of North America and winters in most regions of the continental United States (National Geographic Society, 1987). Although most northern kingfishers migrate to southern regions during the coldest months, some may stay in areas that remain ice-free where fishing is possible (Bent, 1940).

Breeding activities and social organization. During the breeding season, pairs establish territories for nesting and fishing (Davis, 1982); otherwise, belted kingfishers are solitary. They are not colonial nesters and will defend an unused bank if it lies within their territory (Davis, 1982). In migrating populations, the males arrive before the females to find suitable nesting territories (Davis, 1982). Kingfishers excavate their burrows in earthen banks, forming a tunnel that averages 1 to 2 m in length, although some burrows may be as long as 3 to 4 m (Hamas, 1981; Prose, 1985). The burrow entrance is usually 30 to 90 cm from the top of the bank (Bent, 1940; White, 1953) and at least 1.5 m from the base (Cornwell, 1963). Burrows closer to the top may collapse, and burrows too low may flood (Brooks and Davis, 1987). Burrows may be used for more than one season (Bent, 1940). Five to seven eggs are laid on bare substrate or on fish bones within the burrow (Hamas, 1981; White, 1953). Only one adult, usually the female, spends the night in the nest cavity; males usually roost in nearby forested areas or heavy cover (Cornwell, 1963). Both parents incubate eggs and feed the young (Bent, 1940). After fledging, the young remain with their parents for 10 to 15 days (Salyer and Lagler, 1946).

Home range and resources. During the breeding season, belted kingfishers require suitable nesting sites with adequate nearby fishing. During spring and early summer, both male and female belted kingfishers defend a territory that includes both their nest site and their foraging area (Davis, 1982). By autumn, each bird (including the young of the year)

defends an individual feeding territory only (Davis, 1982). The breeding territories (length of waterline protected) can be more than twice as long as the fall and winter feeding territories, and stream territories tend to be longer than those on lakes (Davis, 1982; Salyer and Lagler, 1946). Foraging territory size is inversely related to prey abundance (Davis, 1982).

Population density. Breeding densities of between two and six pairs per 10 km of river shoreline have been recorded, with density increasing with food availability (Brooks and Davis, 1987; White, 1936).

Population dynamics. Kingfishers are sensitive to disturbance and usually do not nest in areas near human activity (White, 1953; Cornwell, 1963). Kingfishers typically breed in the first season after they are born (Bent, 1940). Fledging success depends on food availability, storms, floods, predation, and the integrity of the nest burrow but can be as high as 97 percent (M. J. Hamas, pers. comm.). Dispersal of young occurs within a month of fledging (White, 1953). No data concerning annual survivorship rates were found.

Similar species (from general references)

- The green kingfisher (*Chloroceryle americana*) is smaller (22 cm) than the belted kingfisher and is only common in the lower Rio Grande Valley. It also is found in southeastern Arizona and along the Texas coast, usually during fall and winter.
- The ringed kingfisher (*Ceryle torquata*) is larger (41 cm) and resides in the lower Rio Grande Valley in Texas and Mexico.

General references

Bent (1940); Fry (1980); National Geographic Society (1987); Prose (1985); White (1953).

Belted Kingfisher (*Ceryle alcyon*)

<i>Factors</i>	<i>Age/Sex/ Cond./Seas.</i>	<i>Mean</i>	<i>Range or (95% CI of mean)</i>	<i>Location or subspecies</i>	<i>Reference</i>	<i>Note No.</i>
Body Weight (g)	A B	148 ± 20.8 SD	125 - 215	Pennsylvania	Powdermill Nature Center (unpubl.) Brooks & Davis, 1987	1
	A B	136 ± 15.6 SE		Pennsylvania		
	A B	158 ± 11.5 SE		Ohio		
	at hatching	10 - 12		Minnesota		
	at fledging	148 ± 13.3 SE		Pennsylvania		
	at fledging	169 ± 11.9 SE		Ohio		
Nestling Growth Rate (g/day)		5 to 6		Pennsylvania, Ohio/streams	Brooks & Davis, 1987	2
Metabolic Rate (kcal/kg-day)	A B basal	132	(154 - 693)		estimated	3
	A B free-living	327			estimated	4
Food Ingestion Rate (g/g-day)	A B	0.50	1.0 - 1.75	northcentral lower Michigan	Alexander, 1977	5
	nestlings			Nova Scotia	White, 1936	
Water Ingestion Rate (g/g-day)	A B	0.11			estimated	6
Inhalation Rate (m ³ /day)	A B	0.094			estimated	7
Surface Area (cm ²)	A B	280			estimated	8

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Belted Kingfisher

Belted Kingfisher (*Ceryle alcyon*)

<i>Dietary Composition</i>	Spring	Summer	Fall	Winter	Location/Habitat (measure)	Reference	Note No.
trout non-trout fish crustacea insects amphibians birds and mammals unidentified		17* 29 5 19 27 1 2			lower Michigan/lake (% wet weight; stomach contents) *data from spring and fall also	Alexander, 1977	
trout other game & pan fish (e.g., perch, centrarchids) forage fish (e.g., minnow, stickleback, sculpins) unidentified fish crayfish insects		30 13 15 1 41 < 1			Michigan/trout streams (% wet volume; stomach contents)	Salyer & Lagler, 1946	
salmon fry salmon (1-yr-old) salmon (2-yr-old) trout sticklebacks killifish suckers		11 42 1 15 30 < 1 < 1			Nova Scotia/riparian - streams (% of total number of prey; fecal pellets)	White, 1936	
crayfish cyprinids (minnows) (stonerollers) (unidentified) other fish		13 76 (13) (38) (26) 10			southwest Ohio/creek (% of total number of prey brought to nestlings)	Davis, 1982	

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Belted Kingfisher

Belted Kingfisher (*Ceryle alcyon*)

<i>Population Dynamics</i>	<i>Age/Sex/ Cond./Seas.</i>	<i>Mean</i>	<i>Range</i>	<i>Location/Habitat</i>	<i>Reference</i>	<i>Note No.</i>
Territory Size (km shoreline)	early summer - breeding pairs:	2.19 ± 0.56 SE		Pennsylvania/streams	Brooks & Davis, 1987	
		1.03 ± 0.28 SE		Ohio/streams	Brooks & Davis, 1987	
	late summer - nonbreeding individuals:	1.03 ± 0.22 SE		southwest Ohio/streams	Davis, 1980	
		0.39 ± 0.093 SE		southwest Ohio/streams	Davis, 1980	
Population Density (pair/km shore)	A B summer	0.11 - 0.19		Pennsylvania/streams	Brooks & Davis, 1987	
	A B summer	0.6		Nova Scotia/streams	White, 1936	
Clutch Size		5.8 ± 0.7 SE		Pennsylvania/streams	Brooks & Davis, 1987	
		6.8 ± 0.4 SE		Ohio/streams	Brooks & Davis, 1987	
Clutches/Year		1		Pennsylvania, Ohio/streams	Brooks & Davis, 1987	9
		1		Minnesota/lake	Hamas, 1975	
Days Incubation		22		Minnesota/lake	Hamas, 1975	
Age at Fledging		28 days		NS/NS	Bent, 1940	
Number Fledge per Active Nest		4.5 ± 1.9 SE		Pennsylvania/streams	Brooks & Davis, 1987	
		5.3 ± 2.2 SE		Ohio/streams	Brooks & Davis, 1987	
Age at Sexual Maturity		1 year		throughout range	Bent, 1940	

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Belted Kingfisher

Belted Kingfisher (*Ceryle alcyon*)

<i>Seasonal Activity</i>	Begin	Peak	End	Location	Reference	Note No.
Mating	April	April to May	early July	Minnesota	Hamas, 1975	
Hatching	May	June early June	late July	Minnesota Nova Scotia	Hamas, 1975 White, 1936	
Molt fall spring	August February		October April	NS NS	Bent, 1940 Bent, 1940	
Migration fall departures			mid-October mid-November mid-December	Maine NY, SD, WI, NE Massachusetts, New Jersey	Bent, 1940 Bent, 1940 Bent, 1940	
spring arrivals	late February mid-March early April			PA, RI, MO NY, CT, IL, WI Maine, Nova Scotia	Bent, 1940 Bent, 1940 Bent, 1940	

- 1 Cited in Dunning (1984).
- 2 Brooks and Davis (1987) reported fledging weights of 149 and 169 g for two populations. Given a hatching weight of about 10 g and 28 days required to fledge, on average, chicks must gain 5 to 6 g per day. Hamas (1981) found gains of approximately 8.5 g per day until day 18, and a loss of approximately 4.5 g per day until fledging.
- 3 Estimated using equation 3-28 (Lasiewski and Dawson, 1967) and body weights from Powdermill Nature Center (unpubl.).
- 4 Estimated using equation 3-37 (Nagy, 1987) and body weights from Powdermill Nature Center (unpubl.).
- 5 Estimated by author.
- 6 Estimated using equation 3-15 (Calder and Braun, 1983) and body weights from Powdermill Nature Center (unpubl.).
- 7 Estimated using equation 3-19 (Lasiewski and Calder, 1971) and body weights from Powdermill Nature Center (unpubl.).
- 8 Estimated using equation 3-21 (Meeh, 1879 and Rubner, 1883, as cited in Walsberg and King, 1978) and body weights from Powdermill Nature Center (unpubl.).
- 9 They are known to renest up to three times if clutches are lost early (Bent, 1940).

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2.1.14. Marsh Wren (wrens)

Order *Passeriformes*, Family *Troglodytidae*. Wrens are small insectivorous birds that live in a variety of habitats throughout the United States. They have long, slender bills adapted for gleaning insects from the ground and vegetation. Most species are migratory, although some populations are year-round residents.

Selected species

The marsh wren (*Cistothorus palustris*) is a common bird inhabiting freshwater cattail marshes and salt marshes. Marsh wrens breed throughout most of the northern half of the United States and in coastal areas as far south as Florida; they winter in the southern United States and into Mexico, particularly in coastal areas. Marsh wrens eat mostly insects, and occasionally snails, which they glean from the surface of vegetation. This species was formerly known as the long-billed marsh wren (*Telmatodytes palustris*).

Body size. Although wrens are small (13 cm bill tip to tail tip; about 10 g body weight), males tend to be about 10 percent heavier than females (see table). Body weight varies seasonally; in Georgia, where marsh wrens are resident throughout the year, they tend to be heavier in the spring and summer than in the fall and winter (Kale, 1965).

Habitat. Marsh wrens inhabit freshwater and saltwater marshes, usually nesting in association with bulrushes, cattails, and sedges or on occasion in mangroves (Welter, 1935; Bent, 1948; Kale, 1965; Verner, 1965). Standing water from several centimeters to nearly a meter is typical of the areas selected (Bent, 1948). Permanent water is necessary to provide a food supply of insects necessary to maintain the birds and as a defense against predation (Verner and Engelsens, 1970). Deeper water and denser vegetation are associated with reduced predation rates (Leonard and Picman, 1987).

Food habits. Marsh wrens consume aquatic invertebrates, other insects, and spiders, which they glean from the water surface, on stems and leaves of emergent vegetation, and the marsh floor (Kale, 1965; Welter, 1935). They sometimes also feed by flycatching (Welter, 1935). The insect orders most commonly taken include Coleoptera (both adults and larvae), Diptera (adults and larvae), Hemiptera (juveniles and adults), Lepidoptera (larvae most commonly fed to nestlings); and Odonata (newly emerged) (Bent, 1948; Kale, 1964). When feeding the young, at first the parents bring mosquito adults and larvae, midges, larval tipulids, and other small insects (Welter, 1935). As the young mature, the parents bring larger insects such as ground beetles, diving beetles, long-horned beetles, caterpillars, dragonflies, and sawflies to the nestlings (Welter, 1935). In a population in Georgia, spiders (usually 1 to 3 mm in size, sometimes 12 to 15 mm), small crabs (5 to 7 mm), small snails (1 to 3 mm), and insect eggs also were consumed and fed to nestlings (Kale, 1965). Thus, organisms that are aquatic for all or part of their lives are an important component of the diet of marsh wren adults and nestlings.

Migration. Marsh wrens are year-round residents in some southern and coastal maritime regions where marshes do not freeze. Most migratory wrens breed throughout the northern half of the United States through southern Canada and winter in Mexico and

the southern half of the United States (Bent, 1948; Verner, 1965; American Ornithologists' Union, 1983; National Geographic Society, 1987).

Breeding activities and social organization. Many populations of marsh wren are polygynous, with some males mating with two, occasionally three, females in a season, while the remaining males have one mate or remain bachelors. For example, Leonard and Picman (1987) found 5 to 11 percent bachelor males, 41 to 48 percent monogamous males, 37 to 43 percent bigamous males, and 5 to 12 percent trigamous males in two marshes in Manitoba, Canada. Similarly, Verner and Engelsen (1970) found 16 percent bachelors, 57 percent monogamous, and 25 percent bigamous males in eastern Washington state. In contrast, Kale (1965) found most males to be monogamous through 4 years of study in Georgia.

Males arrive at the breeding marshes before the females to establish territories that include both nest sites and foraging areas (Kale, 1965; Verner, 1965; Welter, 1935). Males build several nests in their territories throughout the breeding season (Kale, 1965; Verner, 1965). The female usually only adds lining material to a nest of her choice, although some may help construct the breeding nest (Kale, 1965). Breeding nests are oblong in shape, with a side opening, and are woven of cattails, reeds, and grasses and lashed to standing vegetation, generally 30 cm to 1 m above standing water or high tide (Bent, 1948; Verner, 1965). Incubation lasts approximately 2 weeks, as does the nestling period (Kale, 1965; Verner, 1965). After fledging, one or both parents continue to feed the young for about 12 days (Verner, 1965). Many populations typically rear two broods per year, although some may rear three (Kale, 1965; Verner, 1965). In the more monogamous populations, both parents regularly feed young, but in the more polygynous ones, the females may provide most of the food, with males assisting only toward the end of the nestling period (Leonard and Picman, 1988; Verner, 1965).

Home range and resources. Marshes smaller than 0.40 ha usually are not used by breeding marsh wrens (Bent, 1948). Average male territory size for a given year and location can range from 0.006 to 0.17 ha, depending on the habitat and conditions of the year (see table). Also, there is a trend in polygynous populations for polygynous males to defend larger territories than monogamous males or males that end up as bachelors (Verner and Engelson, 1970; Verner, 1964; Kale, 1965).

Population density. Because the species is polygynous, there may be more females than males inhabiting breeding marshes. Population density varies with the suitability and patchiness of the habitat. Densities as high as 120 adult birds per hectare have been recorded (Kale, 1965).

Population dynamics. Clutch size and number of clutches per year vary with latitude and climate (see table). In some populations, marsh wrens commonly destroy eggs and kill the nestlings of other pairs of their own species and other marsh-nesting passerines (Orians and Wilson, 1964; Picman, 1977; Welter, 1935). Fledging success depends strongly on nest location; nests over deeper water are less vulnerable to predation (Leonard and Picman, 1987). Of nests lost to all causes, Leonard and Picman (1987) found 44 percent due to mammalian predators, 27 percent due to other wrens, 11 percent due to weather, 8 percent due to nest abandonment, and 13 percent unknown. The

annual mortality of adults is lower than that of first-year birds. Both sexes of this species usually commence breeding in the first year following hatching (Kale, 1965).

Similar species

- The sedge wren (*Cistothorus platensis*, formerly known as the short-billed marsh wren) nests locally in wet meadows or shallow sedge marshes and hayfields in the northeastern United States, wintering primarily in the southeastern United States. It is slightly smaller (11 cm) than the marsh wren.

Note: None of the other wren species inhabit marshes, although all forage by gleaning insects from vegetation and other surfaces. Wrens that inhabit moist woodlands and open areas are listed below.

- The house wren (*Troglodytes aedon*) (12 cm) breeds throughout most of the United States, into southern Canada. It inhabits open habitats with brush and shrubs and is found in orchards, farmyards, and urban gardens and parks.
- The winter wren (*Troglodytes troglodytes*) (10 cm) breeds in southern Canada, where it nests in dense brush, especially along moist coniferous woodlands. It winters primarily in the southeastern United States, where it inhabits many types of woodlands.
- The Carolina wren (*Thryothorus ludovicianus*) (14 cm) is nonmigratory and can be found in both summer and winter in the eastern United States as far north as northern Delaware and as far west as Oklahoma. It inhabits moist woodlands and swamps and wooded suburban areas.
- Bewick's wren (*Thryomanes bewickii*) (13 cm) is more common in western States than the house wren and is declining east of the Mississippi. It is found in brushland, stream edges, and open woods.

General references

Kale (1965); Gutzwiller and Anderson (1987); Leonard and Picman (1987); Verner (1965), National Geographic Society (1987).

Marsh Wren (*Cistothorus palustris*)

<i>Factors</i>	<i>Age/Sex/ Cond./Seas.</i>	<i>Mean</i>	<i>Range or (95% CI of mean)</i>	<i>Location or subspecies</i>	<i>Reference</i>	<i>Note No.</i>
Body Weight (g)	F breeding	10.6 ± 0.99 SD	9.0 - 13.5 10.5 - 13.5	New York	Tintle (unpubl.)	1
	M breeding	11.9 ± 0.72 SD		Georgia	Kale, 1965	2
	A F	9.4 ± 1.1 SD	New York, Minnesota/fresh marshes	Welter, 1935	3	
	A M	10.6 ± 0.7 SD				
	J B	9.4 ± 1.6 SD				
nestling: day 1	1.1					
day 3	2.1					
day 5	4.7					
day 7	6.8					
day 9	10.0					
day 11	10.6					
day 13	11.3					
at fledging	8.84 ± 0.70 SD	Georgia	Kale, 1965			
Egg Weight (g)		1.14 ± 0.10 SD		Georgia	Kale, 1965	
Metabolic Rate (IO ₂ /kg-day)	A B basal	91.2		Georgia (captive)	Kale, 1965	4
	A B near basal	113				5
	A B light activity	169				6
Metabolic Rate (kcal/kg-day)	A B basal	444		Georgia (captive)	Kale, 1965 Kale, 1965	7
	A B near basal	557 ± 115 SD				8
	A B light activity	788 ± 115 SD			9	
	A B free-living	880 ± 90 SD			10	
	A F free-living	1,209			(571 - 2,563)	estimated
A M free-living	1,174	(554 - 2,486)				

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Marsh Wren

Marsh Wren (*Cistothorus palustris*)

<i>Factors</i>	<i>Age/Sex/ Cond./Seas.</i>	<i>Mean</i>	<i>Range or (95% CI of mean)</i>		<i>Location or subspecies</i>	<i>Reference</i>	<i>Note No.</i>
Food Ingestion Rate	A B free-living	1,155 ± 130 SD kcal/kg-day			Georgia (captive)	Kale, 1965	12
	A B free-living	0.67 g/g-day			Georgia (captive)	estimated from Kale, 1965	13
	A F free-living A M free-living	0.99 g/g-day 0.96 g/g-day				estimated	14
Water Ingestion Rate (g/g-day)	A F	0.28				estimated	15
	A M	0.26					
Surface Area (cm ²)	A F	45				estimated	16
	A M	48					
<i>Dietary Composition</i>	<i>Spring</i>	<i>Summer</i>	<i>Fall</i>	<i>Winter</i>	<i>Location/Habitat (measure)</i>	<i>Reference</i>	<i>Note No.</i>
Hymenoptera		17.3		12.4	Georgia/salt marsh (% wet volume; stomach contents)	Kale, 1965	17
Homoptera		13.0		40.1			
Coleoptera		11.6		12.6			
Lepidoptera		14.6		2.9			
Diptera		8.9		7.7			
Hemiptera		5.4		10.0			
Orthoptera		5.6		0.8			
spiders		15.1		6.2			
other arthropods (crabs, amphipods)		1.8		0.9			
molluscs (snails)		3.5		4.0			
other (insect eggs, undetermined, etc.)		4.5		3.3			

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Marsh Wren

Marsh Wren (*Cistothorus palustris*)

<i>Population Dynamics</i>	<i>Age/Sex/Cond./Seas.</i>	<i>Mean</i>	<i>Range</i>	<i>Location/Habitat</i>	<i>Reference</i>	<i>Note No.</i>
Territory Size (ha)	A M spring	0.0060 ± 0.0014 SD 0.0156 ± 0.0050 SD 0.0085 ± 0.0042 SD		Georgia/salt marsh 1, 1958 Georgia/salt marsh 2, 1958 Georgia/salt marsh 2, 1959	Kale, 1965	
	A M spring	0.17 ± 0.021 SE	0.0242 - 0.360	west Washington/fresh mixed-species marsh	Verner, 1965	
	A M spring	0.07 ± 0.06 SD		Manitoba/fresh cattail marsh	Leonard & Picman, 1986	
Population Density	spring: pairs/ha	48.3 ± 5.3 SD	45.1 - 56.2	Georgia/salt marsh (4 years)	Kale, 1965	
	males/ha	8.5 16.9		west Washington/fresh mixed-species marsh (2 areas)	Verner, 1965	
	males/ha	3.7 ± 0.5 SD	3.4 - 4.3	Manitoba/fresh mixed-species marsh (3 years)	Leonard & Picman, 1987	
Clutch Size		4.5	3 - 5	Georgia/salt marsh	Kale, 1965	
		6.0 ± 0.19 SD	4 - 8	east Washington/fresh pond-margin marsh	Verner, 1965	
		5.8 ± 0.8 SD		Manitoba/fresh cattail marsh	Leonard & Picman, 1987	
Clutches/Year		1 - 2	0 - 3	Georgia/salt marsh	Kale, 1965	
		2	0 - 2	east Washington/fresh pond- margin marsh	Verner, 1965	
		2 - 3	0 - 3	west Washington/fresh mixed-species marsh	Verner, 1965	
Days Incubation		13.1	12 - 14	Georgia/salt marsh	Kale, 1965	
		15.1	13 - 16	west Washington/fresh marsh	Verner, 1965	

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Marsh Wren

Marsh Wren (*Cistothorus palustris*)

<i>Population Dynamics</i>	<i>Age/Sex/Cond./Seas.</i>	<i>Mean</i>	<i>Range</i>	<i>Location/Habitat</i>	<i>Reference</i>	<i>Note No.</i>
Age at Fledging	B B	12 - 13 14	10 - 15 11 - 16	Georgia/salt marsh Washington/fresh marshes	Kale, 1965 Verner, 1965	
Number Fledge per Active Nest		3.4 ± 3.4 SD		Manitoba/fresh mixed marsh	Leonard & Picman, 1987	
Number Fledge per Successful Nest		4.5 ± 1.3 SD 5.1 ± 1.2 SD		Manitoba/fresh mixed-species marsh Manitoba/fresh cattail marsh	Leonard & Picman, 1987 Leonard & Picman, 1987	
Age at Sexual Maturity	B B	1 year 1 year		Manitoba/fresh marsh Washington/fresh marsh	Leonard & Picman, 1987 Verner, 1971	
Annual Mortality Rates (percent)	A B J B	32 70		Georgia/salt marsh	Kale, 1965	
<i>Seasonal Activity</i>	<i>Begin</i>	<i>Peak</i>	<i>End</i>	<i>Location</i>	<i>Reference</i>	<i>Note No.</i>
Mating/Laying	April mid-April late March late May	May - June April - May	mid-August early July mid-July early August	Georgia eastern Washington (Turnbull) western Washington (Seattle) New York	Kale, 1965 Verner, 1965 Verner, 1965 Welter, 1935	
Hatching	early May mid-April		mid-July early August	eastern Washington (Turnbull) western Washington (Seattle)	Verner, 1965 Verner, 1965	
Migration fall spring	September April	May mid-March (nonmigratory)	late October June	New York, Minnesota New York, Minnesota eastern Washington (Turnbull) western Washington (Seattle)	Welter, 1935 Welter, 1935 Verner, 1965 Verner, 1965	

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Marsh Wren

Marsh Wren (*Cistothorus palustris*)

- 1 As cited in Dunning (1984).
- 2 Collection dates not specified. Resident population; presumably averaged from birds captured throughout the year.
- 3 Estimated from Welter's (1935) growth curve based on 50 nestlings.
- 4 Measured by oxygen respirometry; lowest value of metabolism of postabsorptive wrens resting in the dark (but not at night) at temperatures within the thermoneutral zone.
- 5 Measured by oxygen respirometry; birds not postabsorptive, but resting in a dark box at temperatures within the thermoneutral zone.
- 6 Measured by oxygen respirometry; birds somewhat active in their cage.
- 7 Estimated from oxygen consumption, for conditions, see note 3.
- 8 Estimated from oxygen consumption, for conditions, see note 4.
- 9 Estimated from oxygen consumption, for conditions, see note 5.
- 10 Estimated from measured daily food intake, excretory losses, assimilation, and respiration for active birds in small cages (173 weekly determinations total). Because of the birds' high activity levels, Kale (1965) considered the measure representative of free-living birds.
- 11 Estimated using allometric equation 3-36 (Nagy, 1987) and body weights from Kale (1965).
- 12 Measured daily food intake of birds in cages and measured caloric content of diet provided. Because of the birds' high activity levels, Kale (1965) considered the measure representative of free-living birds.
- 13 Estimated from Kale's (1965) measured daily food intake (see note 11) assuming 5.62 kcal/gram (dry weight) insects, a 70 percent assimilation efficiency, and a 67 percent water content for insects.
- 14 Estimated from free-living metabolic rate estimated from Nagy's (1987) equation 3-36 (see note 10) assuming the same parameters described in note 12. These predicted food ingestion rates (>0.95 g/g-day) for free-living birds exceed the value estimated for Kale's (1965) caged birds (0.67 g/g-day); however, the latter does not include metabolic requirements of searching for food, reproduction, or unusual thermoregulatory demands.
- 15 Estimated using equation 3-15 (Calder and Braun, 1983) and body weights from Kale (1965).
- 16 Estimated using equation 3-21 (Meeh, 1879 and Rubner, 1883, as cited in Walsberg and King, 1978) and body weights from Kale (1965).
- 17 Summer column represents combination of spring and summer data; winter column represents combination of fall and winter data.

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Marsh Wren

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2.1.15. American Robin (thrushes)

Order Passeriformes, Family Muscicapidae, Subfamily Turdinae. Thrushes are common, medium-sized birds that eat worms, insects, and fruit. They live in a variety of habitats, including woodlands, swamps, suburbs, and parks. Most thrushes build nests of mud and vegetation on the ground or in the crotches of trees or shrubs; bluebirds nest in holes in trees and posts or in nest boxes. This group forages primarily on the ground and in low vegetation by probing and gleaning. Some thrushes are neotropical migrants while others reside year-round in North America. Thrushes range in size from the eastern and western bluebirds (18 cm from bill tip to tail tip) to the American robin (25 cm). Male and female plumages are similar in most thrushes, although in some species, such as the bluebirds, the males are more brightly colored.

Selected species

The American robin (*Turdus migratorius*) occurs throughout most of the continental United States and Canada during the breeding season and winters in the southern half of the United States and in Mexico and Central America. The breeding range of the robin has expanded in recent times with the increasing area covered by lawns and other open habitats (Howell, 1942; Martin et al., 1951; James and Shugart, 1974).

Body size. The sexes are similar in size and appearance. Their size varies slightly geographically; the smallest robins are found in the eastern United States and along the Pacific coast, and the largest ones occur in the Rocky Mountains, northern Great Plains, and northern deserts (Aldrich and James, 1991).^d The size of robins tends to increase with latitude in eastern North America but does not in western North America (Aldrich and James, 1991). Fledglings attain adult size at approximately 6 weeks of age (Howell, 1942).

Habitat. Access to fresh water, protected nesting sites, and productive foraging areas are important requirements for breeding robins (Speirs, 1953). Breeding habitats include moist forests, swamps, open woodlands, orchards, parks, and lawns. Robins forage on the ground in open areas, along habitat edges, or the edges of streams; they also forage above ground in shrubs and within the lower branches of trees (Paszkowski, 1982; Malmborg and Willson, 1988). Nests in wooded areas are usually near some type of opening such as the forest edge or a treefall gap (Young, 1955; Knupp et al., 1977). During the nonbreeding season, robins prefer moist woods or fruit-bearing trees and shrubs (Robbins et al., 1983). In the fall, flocks of migratory robins are often found along forest edges or clearings where fruits are most plentiful (Baird, 1980).

Food habits. Robins forage by hopping along the ground in search of ground-dwelling invertebrates and by searching for fruit and foliage-dwelling insects in shrubs and low tree branches (Malmborg and Willson, 1988; Paszkowski, 1982). In the months preceding and during the breeding season, robins feed mainly (greater than 90 percent volume) on invertebrates and on some fruits; during the remainder of the year, their diet

^dBased on linear measurements of museum study skins.

consists primarily (over 80 to 99 percent by volume) of fruits (Martin et al., 1951; Gochfeld and Burger, 1984; Wheelwright, 1986). Robins eat a wide variety of both plant and animal foods; in a compilation of diet records collected throughout the United States and southern Canada, Wheelwright (1986) found that robins consumed fruits from 51 genera and invertebrates from 107 families. Commonly eaten fruits include plums, dogwood, summac, hackberries, blackberries, cherries, greenbriers, raspberries, and juniper (Martin et al., 1951; Wheelwright, 1986); common invertebrates include beetles, caterpillars, moths, grasshoppers, spiders, millipedes, and earthworms (Martin et al., 1951; Wheelwright, 1986; Paszkowski, 1982). Wheelwright (1986) has compiled seasonal changes in the proportion of plants and invertebrates consumed by robins in three different sections of the United States (see table). Wheelwright (1986) also has summarized the average occurrence of fruits of various plant families in the stomachs of robins by month for these sections. Martin et al. (1951) have summarized the occurrence of fruits of various plant families in more specific areas of the United States (see Appendix).

Wheelwright (1986) found no differences between the sexes in the proportion or types of invertebrates and fruits eaten. Very young robins (up to at least 35 days of age) feed almost entirely on insects and other invertebrates (Howell, 1940). Older juveniles tend to eat a higher proportion of fruit and easy-to-capture prey than adults (Gochfeld and Burger, 1984; Wheelwright, 1986). In a given area, robins often show food preferences: a population in central New York seemed to prefer northern arrowwood and spice bush fruits over most other plants (Wheelwright, 1988); in Illinois, a group ate predominantly frost grapes and Virginia creeper in the late summer and fall (Malmborg and Willson, 1988).

During seasons when fruits dominate the diet, robins may need to consume quantities in excess of their body weight to meet their metabolic needs each day (see table). Robins as well as other fruit-eating birds exhibit a low digestive efficiency for fruits; Karasov and Levey (1990) estimated the metabolizable energy coefficient (MEC) (i.e., the proportion of food energy that actually is assimilated) for robins eating a mixed fruit diet to be only 55 percent, perhaps because of the low retention time of the digested matter in the gut (Levey and Karasov, 1992). The short retention time might actually be an adaptation to eating fruit because large quantities of fruit must be processed to obtain an adequate protein intake. In contrast, when eating insects, robins (as well as other bird species) exhibit a higher digestive efficiency of approximately 70 percent (Levey and Karasov, 1989). Moreover, the energy content of insects tends to be higher than that of most fruits, particularly on a wet-weight basis (see Chapter 4). Thus, during the spring when robins are consuming insects, they should consume a smaller amount relative to their body weight than when eating fruits (Chapter 4 provides approaches that can be used to estimate insect ingestion rates for robins).

Molt. Postjuvenile and postbreeding (prebasic) molts occur from late July to October (Wheelwright, 1986; Sharp, 1990). During this molt, robins are consuming largely fruits and other plant materials, which contain limited proteins. This may contribute to larger fruit consumption rates at this time. During the prebreeding (prealternate) molt, robins are feeding primarily on insects and other invertebrates (letter

from N.T. Wheelright, Department of Biology, Bowdoin College, Brunswick, ME, to Sue Norton, March 18, 1992).

Migration. Most robins nesting in the northern United States and Canada winter in the Gulf Coast States and the Carolinas (Speirs, 1953; Dorst, 1962, as cited in Henny, 1972). Wintering robins are most abundant between 30 and 35 degrees N latitude (Speirs, 1953). Robin flocks migrate during the day (Robbins et al., 1983); most northern robins leave their breeding grounds from September to November and return between February and April (Howell, 1942; Young, 1951; Fuller, 1977).

Breeding activities and social organization. The onset of the breeding season is later at higher latitudes (approximately 3 days for each additional degree in the east) and altitudes, but mating and egg laying generally occur in April or May (James and Shugart, 1974; Knupp et al., 1977). Males arrive on the breeding grounds before females to establish territories; females pair with established males, usually for the duration of the breeding season (Young, 1951). The female primarily builds the nest out of mud, dried grass, weedy stems, and other materials, constructing it on horizontal limbs, tree-branch crotches, within shrubs, or on any one of a number of man-made structures with horizontal surfaces (Howell, 1942; Klimstra and Stieglitz, 1957). First clutches usually contain three or four eggs; later clutches tend to contain fewer eggs (Young, 1955). The female does all of the incubating, which continues for 10 to 14 days following the laying of the second egg (Klimstra and Stieglitz, 1957; Young, 1955). Both males and females feed the nestlings (Young, 1955). Following fledging, the brood often divides, with the male and female each feeding half of the fledglings for another 2 weeks (Weatherhead and McRae, 1990). Females may start another brood before the current one is independent, leaving the male to feed all of the fledglings (Young, 1955). After reaching independence, juveniles often form foraging flocks in areas of high food availability (Hirth et al., 1969).

Early in the breeding season, robins often roost communally. Males can continue to use these roosts throughout the breeding season, whereas females stop once they begin incubating eggs (Howell, 1940; Pitts, 1984). As fall approaches and their diet turns more toward fruits, robins in many areas begin to roost communally again and may join other species, such as common grackles and European starlings, in large roosts (Morrison and Caccamise, 1990).

Home range and resources. During the breeding season, male robins establish breeding territories, which the female helps to defend against other robins. Nonetheless, the territories of different pairs often overlap where neither pair can establish dominance (Young, 1951). Most foraging during the breeding season is confined to the territory, but adults sometimes leave to forage in more productive areas that are shared with other individuals (Howell, 1942; Young, 1951; Pitts, 1984). In some prime nesting areas (e.g., dense coniferous forest), where robin densities are high, territories are small and the birds might often forage elsewhere (Howell, 1942). Adult robins often return to the same territory in succeeding years (Young, 1951). During the nonbreeding roosting period, robins are likely to return to the same foraging sites for many weeks and to join roosts within 1 to 3 km of these foraging areas (Morrison and Caccamise, 1990).

Population density. Nesting population density varies with habitat quality. Densely forested areas that provide well-protected nest sites have been found to support high densities of nesting robins; however, the relatively small territories found in these areas might not be used as much for foraging as those containing open areas (Howell, 1942). In the nonbreeding season, robins often join single- or mixed-species roosts that can include tens of thousands of birds (Morrison and Caccamise, 1990). Wintering robins are most common in pine or oak pine communities of the southeastern and southcentral United States, and decrease in abundance in drier, less forested areas westward (Speirs, 1953).

Population dynamics. Robins first attempt to breed the year after they hatch (Henny, 1972) and will raise multiple broods in a season (Howell, 1942). Predation is often a major source of mortality for both eggs and nestlings (Knupp et al., 1977; Klimstra and Stieglitz, 1957). Approximately half of the adult birds survive from year to year (Farner, 1949; Henny, 1972); the average longevity of a robin that survives to its first January is from 1.3 to 1.4 years (Farner, 1949).

Similar species (from general references)

- The wood thrush (*Hylocichla mustelina*), which is smaller than the robin (18 cm), co-occurs with the robin in some woodland habitats but is only present in the eastern United States. This species nests primarily in the interiors of mature forests and has been decreasing in abundance over the past decade as forested habitats in North America become increasingly fragmented (Robbins et al., 1989; Terborgh, 1989). This species is also primarily a summer resident, wintering in Florida and the neotropics.
- The hermit thrush (*Catharus guttatus*) is found in coniferous and mixed woodlands at northerly latitudes or high elevations and winters primarily in the southern half of the United States. This species is also significantly smaller (15 cm) than the robin.
- Swainson's thrush (*Catharus ustulatus*) is present in the western and northeastern United States during the summer months, wintering in the neotropics. It is also smaller than the robin (16 cm).
- The varied thrush (*Ixoreus naevius*) occurs in moist coniferous forests of the Pacific Northwest. This bird is similar in size (21 cm) to the robin.

General references

Howell (1942); Young (1955); National Geographic Society (1987); Robbins et al. (1983); Sharp (1990).

American Robin (*Turdus migratorius*)

<i>Factors</i>	<i>Age/Sex/ Cond./Seas.</i>	<i>Mean</i>	<i>Range or (95% CI of mean)</i>	<i>Location or subspecies</i>	<i>Reference</i>	<i>Note No.</i>
Body Weight (g)	A B all seas.	77.3 ± 0.36 SE	63.5 - 103	Pennsylvania	Clench & Leberman, 1978	1
	A M nonbreed. A F nonbreed.	86.2 ± 6.1 SD 83.6 ± 6.4 SD		New York	Wheelwright, 1986	
	A M breeding A F breeding	77.4 80.6		New York	Wheelwright, 1986	
	nestlings: at hatching	5.5		New York/forest	Howell, 1942	
	day 2	12.6				
day 4	24.3	4.1 - 6.7				
day 6	39.4	8.4 - 17.5				
day 8	50.9	17.9 - 32.3				
day 10	55.2	32.5 - 45.9				
day 14	55.0	42.0 - 59.3				
		49.0 - 63.2				
		51.8 - 58.2				
Egg Weight (g)		6.26	4.6 - 8.4	New York	Howell, 1942	
Metabolic Rate (kcal/kg-day)	A B basal	259	(336 - 1,513)	Kansas	estimated	2
	- B existence	344			Hazelton et al., 1984 (estimate)	3
	A B free-living	713			estimated	4
Food Ingestion Rate (kcal/kg-day)	A B free-living	1,070 ± 220 SD	760 - 1,330	Kansas	Hazelton et al., 1984	5
Food Ingestion Rate (g/g-day)	B B free-living	0.89 ± 0.73 SD		California	Skorupa & Hothem, 1985	6
	- B free-living	1.52 ± 0.25 SD	1.22 - 1.96	Kansas	Hazelton et al., 1984	7
Water Ingestion Rate (g/g-day)	A B	0.14			estimated	8

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American Robin

American Robin (*Turdus migratorius*)

<i>Factors</i>	Age/Sex/ Cond./Seas.	Mean	Range or (95% CI of mean)		Location or subspecies	Reference	Note No.
Surface Area (cm ²)	A B	198				Walsberg & King, 1978	9
	A B	182				estimated	10
<i>Dietary Composition</i>	Spring	Summer	Fall	Winter	Location/Habitat (measure)	Reference	Note No.
nestlings/fledglings: earthworms sowbugs spiders millipedes short-horned grass- hoppers beetles lepidopteran larvae ants unidentified animal grass (all parts) mulberries honeysuckle seeds unidentified plants		15.0 1.7 2.3 3.1 4.9 11.6 24.7 3.2 5.2 19.5 3.2 2.4 4.2			south central New York/forest (% wet weight; stomach contents) (age of robins ranged from 3 to 35 days after hatching; presence of grass is likely to be accidental - carried along with prey)	Howell, 1942	
adults: fruit invertebrates	7 93	68 32	92 8	83 17	eastern United States (% volume; stomach contents)	Wheelwright, 1986	11
adults: fruit invertebrates	8 92	41 59	76 24	73 27	central United States (% volume; stomach contents)	Wheelwright, 1986	11
adults: fruit invertebrates	17 83	29 71	63 37	70 30	western United States (% volume; stomach contents)	Wheelwright, 1986	11

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American Robin

American Robin (*Turdus migratorius*)

<i>Population Dynamics</i>	<i>Age/Sex Cond./Seas.</i>	<i>Mean</i>	<i>Range</i>	<i>Location/Habitat</i>	<i>Reference</i>	<i>Note No.</i>
Territory Size (ha)	spring A B	0.42	0.12 - 0.84	Tennessee/campus	Pitts, 1984	12
	A B	0.11		New York/dense conifers /unspecified forest	Howell, 1942	
	A B	0.21				
Foraging Home Range (ha)	summer, adults feeding: nestlings fledglings	0.15 ± 0.021 SE 0.81 ± 0.13 SE		Ontario/deciduous forest	Weatherhead & McRae, 1990	
Population Density (pairs/ha)	spring A B	1.98 ± 0.48 SD	1.39 - 2.54	Tennessee/campus	Pitts, 1984	
	A B	8.6		New York/dense conifers /unspecified forest	Howell, 1942	
	A B	4.9				
Clutch Size		3.17 3.45 ± 0.59 SD	1 - 5 1 - 5	Illinois/suburban Wisconsin/park	Klimstra & Stieglitz, 1957 Young, 1955	
Clutches/Year		2	1 - 3	New York/forest	Howell, 1942	
Days Incubation		12.5 ± 0.14 SE	10 - 14	Wisconsin/park	Young, 1955	13
Age at Fledging (days)	B	13.4 ± 0.13 SE		Wisconsin/park	Young, 1955	
Number Fledge per Breeding Pair		5.6		Wisconsin/park	Young, 1955	
		3.9		New York/forest	Howell, 1942	
		1.5 ± 0.45 SE		Ontario/deciduous forest	Weatherhead & McRae, 1990	
Number Fledge per Successful Nest	five areas	2.9	2.4 - 3.4 (over 5 areas)	Wisconsin/park	Young, 1955	
		2.5 ± 0.15 SD		Maine/forest	Knupp et al., 1977	

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American Robin

American Robin (*Turdus migratorius*)

<i>Population Dynamics</i>	<i>Age/Sex Cond./Seas.</i>	<i>Mean</i>	<i>Range</i>	<i>Location/Habitat</i>	<i>Reference</i>	<i>Note No.</i>
Age at Sexual Maturity	B	1 year		NS	Henny, 1972	
Annual Mortality Rates (percent)	A B J B	51 ± 0.5 SE 78 - 82		North America	Henny, 1972	
Longevity (years)	after Jan. 1 of first year	1.3 - 1.4	up to 9	North America	Farner, 1949	
<i>Seasonal Activity</i>	<i>Begin</i>	<i>Peak</i>	<i>End</i>	<i>Location</i>	<i>Reference</i>	<i>Note No.</i>
Mating/Laying	early April late April early May	mid-April late May	late April mid-July early July	Illinois south central New York n Maine	Klimstra & Stieglitz, 1957 Howell, 1942 Knupp et al., 1977	
Hatching	early May early May mid-May mid-April early June			west: California, New Mexico east: VA, WV, DC, NY northeast: VT, NH, CT Kentucky Colorado	James & Shugart, 1974 James & Shugart, 1974 James & Shugart, 1974 James & Shugart, 1974 James & Shugart, 1974	
Molt fall		July & August		North America	Wheelwright, 1986	
Migration fall	mid-Sept.	mid-October	early November early November	migrating through Minnesota leaving New York	Fuller, 1977 Howell, 1942	
spring	February mid-March		March mid-April	arriving New York arriving Wisconsin	Howell, 1942 Young, 1951	

1 As cited in Dunning (1984).

2 Estimated using equation 3-27 (Lasiewski and Dawson, 1967) and body weights from Clench and Leberman (1978).

3 Hazelton et al. (1984) estimate using Kendeigh's (1969) equations for a 55-g bird.

4 Estimated using equation 3-36 (Nagy, 1987) and body weights from Clench and Leberman (1978).

American Robin (*Turdus migratorius*)

- 5 Estimated kcal consumed in feeding trials. Diet consisted of paired offerings of fruit (to test preferences) over a 2-day period, 12 trials per pairing. Fruit included strawberries (2.29 kcal/g), cherries (4.34 kcal/g), green grapes (2.59 kcal/g), and purple grapes (5.85 kcal/g). Mean weight of the birds = 55 g.
- 6 Based on gizzard contents of robins caught foraging in vineyards; diet 85 percent (wet weight) grapes, 11.5 percent invertebrates, and 4.5 percent other plants. Mean weight of the birds = 82.3 g.
- 7 Based on same study described in note 5 and estimated weights of fruits consumed.
- 8 Estimated using equation 3-15 (Calder and Braun, 1983) and body weights from Clench and Leberman (1978).
- 9 Beak surface area 3.1 cm²; leg surface area 14.0 cm².
- 10 Estimated using equation 3-21 (Meeh, 1879 and Rubner, 1883, as cited in Walsberg and King, 1978) and body weights from Clench and Leberman (1978).
- 11 The U.S. Biological Survey and U.S. Fish and Wildlife Service records on which this study is based have several limitations: more birds were collected in agricultural and suburban than natural areas; seasons and time of day of collection were convenient to the collectors; quickly digested foods such as earthworms and other soft-bodied insects are underrepresented.
- 12 Birds nesting in high densities in dense coniferous forest probably foraged elsewhere more of the time than did birds with larger territories in less dense forests.
- 13 Also included data from Howell (1942) (Ithaca, New York) in calculations.

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