

*Circus
cyaneus*

Northern Harrier

FRENCH:
*Busard Saint-Martin*SPANISH:
Aguilucho pálido,
Gavilán rastrero,
Gavilán sabanero

The Northern Harrier (called the Hen Harrier in Europe and Asia) is a slender, white-rumped, medium-sized, and low-flying raptor of upland grasslands and fresh- and saltwater marshes. The only representative in North America of the cosmopolitan genus *Circus*, the Northern Harrier breeds throughout North America and Eurasia. It is the most northerly breeding and most broadly distributed of all harriers and is a long-distance migrant throughout much of its range. Its degree of sexual dimorphism in plumage and its propensity for polygyny are exceptional among birds of prey.

Like most other harriers, the Northern Harrier nests on the ground, usually in tall, dense clumps of vegetation, either alone or in loose colonies. Most males are monogamous or simultaneously bigamous,

The Birds of North America

Life Histories for
the 21st Century

although some males pair with up to five mates in a season. In North America, the frequency of polygyny is influenced more strongly by the abundance of food in spring than by a female-biased sex ratio. Females incubate eggs and brood offspring, and males provide the bulk of food for their mates and nestlings.

This raptor forages on the wing, capturing a wide range of prey, mainly small- and medium-sized mammals and birds, while coursing low and buoyantly over the ground. Unlike other hawks, it frequently relies

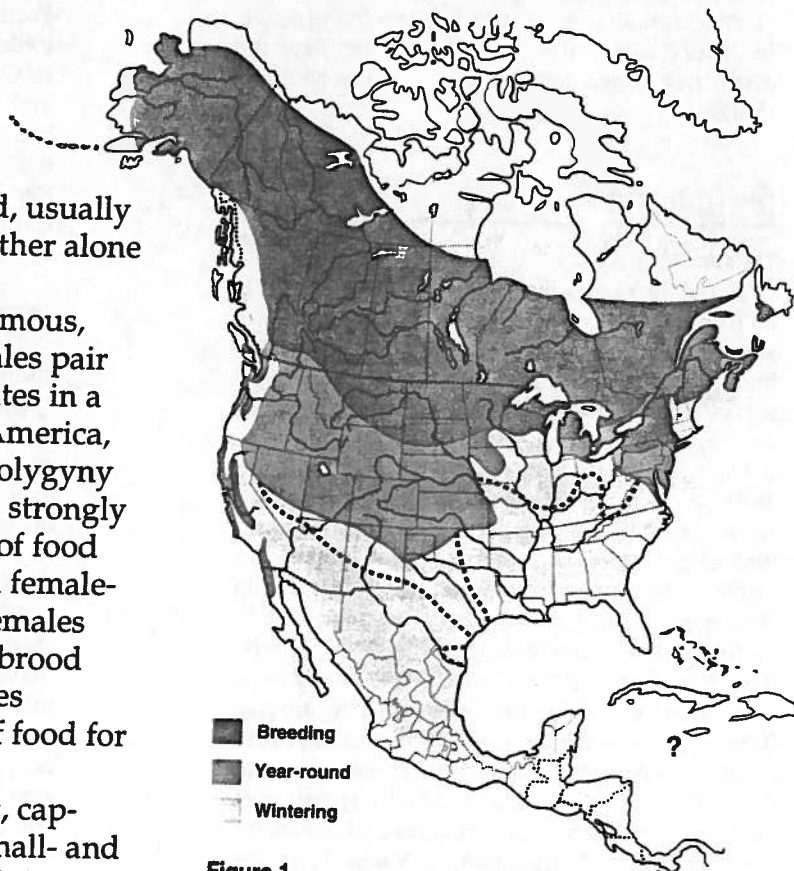
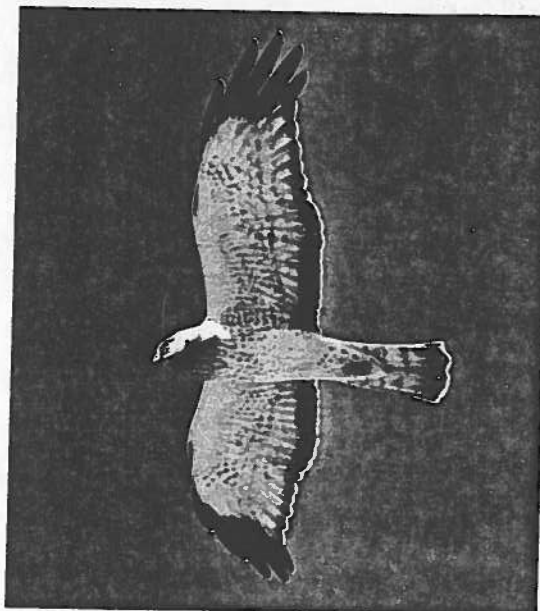


Figure 1. Distribution of the Northern Harrier in North America. This species breeds locally south to the dotted line and also breeds in the eastern and western Palearctic; see text for details.

heavily on auditory cues, as well as visual ones, to capture prey. Annual breeding numbers and productivity are strongly influenced by the availability of the species' principal prey in spring, usually microtine voles. In winter, individuals roost communally on the ground.

DISTINGUISHING CHARACTERISTICS

A strongly sexually dimorphic hawk of slim body, long wings and tail, and long, slender legs. Females about 50% heavier and 12.5% larger than males. Adult male gray above, lighter below, and with black wing-tips; adult female brown above and buffy with brown streaks below. Subadults similar to adult female but darker brown above and russet below (the russet not occurring in Eurasian forms). Both sexes have a distinctive white rump patch. Owl-like appearance of the face due to a facial ruff similar in structure and function to that found in most owls. Northern Harrier's narrower wings and slimmer tail distinguish it from the light-morph Rough-legged Hawk (*Buteo lagopus*). Northern Harrier usually seen in open habitats flying slowly low over the ground with a series of heavy flaps and distinctive buoyant, tilting glides, wings held in a shallow V.

DISTRIBUTION

THE AMERICAS

Breeding range. Figure 1. Widely but locally distributed in North America, breeding from n. Alaska and Canada (primarily south of tundra, including central Quebec, Maritime Provinces and s. Newfoundland) south to n. Baja Peninsula, Mexico (Howell and Webb 1995), and east to s. Nevada, s. Utah (Walters 1983), n. New Mexico (Hubbard 1978), n. Texas, s. Kansas (Kansas Breeding Bird Atlas unpubl. data), central Iowa (Iowa Breeding Bird Atlas unpubl. data), central Wisconsin (Robbins 1990), s. Michigan (Brewer et al. 1991), n. Ohio (Peterjohn 1989), s. Pennsylvania (Brauning 1992), se. Virginia (Virginia Breeding Bird Atlas unpubl. data, Hands et al. 1989, Bildstein and Collopy 1990, Serrentino 1992) and probably in ne. North Carolina. Rare and erratic breeder or summer resident south of this area. Absent or rare breeder in many states of the conterminous U.S. (Fig. 1), including portions of the Northeast (e.g., ne. Connecticut and Rhode Island north through e. Vermont and s. Maine; Laughlin and Kibbe 1985, Adamus 1987, Veit and Petersen 1993, Bevier 1994), and in mountainous or desert regions of the west coast (e.g., much of California, Small 1994; w. Oregon, Gilligan et al. 1994; w. Washington, Washington Breeding Bird Atlas

unpubl. data; and coast range of British Columbia, Campbell et al. 1990). May be absent over much of interior w. Ontario (Cadman et al. 1987). See Demography and Populations: population status.

Winter range. Winters primarily from s. Canada south through the conterminous U.S., Central America, and Caribbean islands (Fig. 1; Root 1988, Bildstein and Collopy 1990). Usual southern limit is Panama, rarely Andes Mtns. of Colombia and Venezuela (Ridgely and Gwynne 1989). Most birds occupy w. and s. U.S., also Mexico; fewer through Central America. Christmas Bird Count data suggest particularly high densities in parts of w. Texas, Oklahoma, New Mexico, California, and n. Utah (Root 1988). Absent from higher elevations of the Appalachian, Ozark, and Rocky mountains. Absent or rare in Wyoming, the Dakotas, w. Minnesota, and w. Iowa. In Mexico, widespread common winter resident, except in southeastern two-thirds of the Yucatán Peninsula and e. Chiapas, where species is a transient migrant (Howell and Webb 1995). In Central America, absent or very rare in Belize, n. Guatemala, and e. Honduras. Farther south, a rare transient and winter resident, most numerous on Pacific slope of Nicaragua, Costa Rica, and Panama (Stiles and Skutch 1989, Ridgely and Gwynne 1989). In Caribbean, winters regularly in Cuba (Garrido and Kirkconnell 1993), Bahamas (not all islands; Brudenell-Bruce 1975), uncommon in Cayman I., irregular and rare winter visitor to e. Dominican Republic (Dod 1981), rare in Puerto Rico and Virgin I. (Raffaella 1989), vagrant throughout the Lesser Antilles (Evans 1990); status in Jamaica uncertain.

OUTSIDE THE AMERICAS

Occurs throughout Europe and Asia (*Circus cyaneus cyaneus*); breeds in Eurasia from Portugal to Lapland, east to n. China, Russia, Siberia, and Kamchatka Peninsula. In winter, south to n. Africa and tropical Asia (Cramp and Simmons 1980, del Hoyo et al. 1995). Reports of North American individuals in Europe are rare and dubious (Thorpe 1988).

HISTORICAL CHANGES

In 1800s, numbers likely increased in response to clearing of eastern forests for timber and agriculture. In twentieth century, no recent broad-scale changes in distribution, although extensive local population declines have occurred throughout the breeding range due to losses of wetlands, undisturbed grasslands, and native prairies. See Demography and Populations: population status, below.

FOSSIL HISTORY

In ne. Mexico, fossils detected in samples from 11,000 to 27,000 years before present (ybp), but not in samples from 27,000 to 45,000 ybp (Steadman et al. 1994). Recorded as fossil from Pleistocene of

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Oregon and California (Brodkorb 1964). Subfossil from a late prehistoric site (ca. A.D. 1300) associated with human settlement in se. New Mexico (Emslie et al. 1992). In Middle Missouri Valley, SD, subfossils abundant and widespread among 51 archaeological sites; most associated with the period A.D. 900–1700, fewer after that time (Parmalee 1977). Subfossils recorded from sites in California, Utah, and Arizona (Brodkorb 1964).

SYSTEMATICS

Birds from North America belong to *Circus cyaneus hudsonius*, a large subspecies (Cramp and Simmons 1980). Compared to *C. c. cyaneus* (Eurasian subspecies), adult male *C. c. hudsonius* has darker bars on tail and possesses ventral bars; adult female a lighter brown above and below (Nieboer 1973, Scharf and Hamerstrom 1975). Juvenile *C. c. hudsonius* less streaked and more russet below than juvenile *C. c. cyaneus*.

C. c. hudsonius may be conspecific with Cinnereous Harrier (*C. cinereus*) of central and s. South America, although Cinnereous Harrier is smaller than Northern Harrier. The genus *Circus* is thought to have originated in the Palearctic, or at least Old World, colonizing North America over the Bering Strait, probably early in the Pleistocene. Northern Harrier probably developed in North America in postglacial times, then reinvaded the Palearctic via the Bering Strait (Nieboer 1973).

MIGRATION

NATURE OF MIGRATION IN THE SPECIES

Partial, but often long-distance (>1,500 km, especially in northern portions of range), migrant; known to undertake flights of >125 km over water (Kerlinger 1989). Most individuals migrate alone (Beske 1982, Kerlinger 1989). Occasionally soars on migration, but usually engages in active flapping flight. Movement is associated (although less so than in other raptors; Allen et al. in press) with low atmospheric pressure and approach of a cold front, which induces rising air and southerly winds. Flies in front of an atmospheric low in spring, behind in fall (Haugh and Cade 1966). Beske (1982) reported daily movements by migrating juveniles of 14–106 km. Hunts on migration.

TIMING AND ROUTES OF MIGRATION

Fall. Timing of departure from breeding grounds not well quantified. Observations from hawk-watch sites along migration routes in the Great Lakes region and e. Pennsylvania indicate an exceptionally

protracted (about 3 mo) fall passage, between mid-Aug and late Nov (see Fig. 4). Timing of fall migration is slightly earlier, and duration of passage apparently shorter, at sites in Rocky Mtns. and Great Basin than at sites in e. U.S. and coastal California (Haugh 1972, Binford 1979, Bildstein et al. 1984, Duncan 1986, Hoffman et al. 1992).

Earliest and latest dates of migration at Hawk Mtn., PA, are 7 Aug and 26 Dec, respectively. Mean dates (\pm SD) of passage for 25, 50, and 75% of the annual flight are 24 Sep \pm 5.7 d, 13 Oct \pm 6.2 d, and 28 Oct \pm 5.3 d, respectively. Rate of passage peaks at 0.51 individuals/hour in the last half of Oct, when the chance of seeing at least 1 individual/day is 86% at Hawk Mountain Sanctuary (Bednarz et al. 1990, Allen et al. in press, Hawk Mountain Sanctuary unpubl. data).

Migrants appear on Caribbean islands (e.g., Cuba, Puerto Rico) in Oct and in s. Central America in mid-Oct. Adult females precede adult males, and juvenile males precede juvenile females, although there is considerable overlap within and among sites (Haugh 1972, Bildstein et al. 1984, Duncan 1986). Juveniles precede adults by about 30 d (Bildstein et al. 1984).

Appears to follow leading lines (e.g., shoreline) less than other migrant falconiforms, and relative occurrence at traditional hawk-watch sites is often low. In mid-w. and e. North America, migrating Northern Harriers have been a small (<4%) but relatively consistent component of both coastal and inland hawk-watch sites in fall. Fall numbers are disproportionately higher on Atlantic Coast (e.g., at Cape May, NJ, about 1,700/yr) compared with inland observation sites (about 265–730/yr; Titus and Fuller 1990). At most migration-observation sites in w. North America, Northern Harriers make up 1–2% of total raptors recorded (Binford 1979, Hoffman et al. 1992).

Band recoveries and radiotelemetry data suggest that birds banded in mid-w. U.S. migrate south and southeast, with those moving through s. Ontario moving south-southwest and those through n. Great Plains moving south-southeast, south, and southwest (Mueller and Berger 1969, Duncan 1986). Thus, most migrants from the Great Lakes region apparently winter east of the Mississippi River (Hussell and Brown 1992).

Spring. Spring migration not well studied. In Central America and Mexico, most spring migrants observed in Mar. In U.S., winter territories are abandoned and communal roosts disbanded in late Feb and early Mar. Like fall migrants, spring migrants exhibit a protracted migration period, without a well-defined temporal peak (see Fig. 4). At Sandia Mtns., NM, 95% of migrants observed between 22 Feb and 4 May (median 8 Apr; Hoffman et al. 1992). At Derby Hill, NY, annual mean date of passage 25 Feb–25 May, with most birds observed mid-Mar to

late Apr (Smith and Muir 1978). At Grimsby, ON, most migrants observed between 21 Mar and 15 May (Hussell and Brown 1992). In New Brunswick and Manitoba, birds arrive on breeding grounds from late Mar through Apr (Haugh 1972, RBM). In s. Alaska, most migrants are observed between late Apr and early May (Swem 1985). In spring migration, adults precede juveniles, and males precede females (Hamerstrom 1969, Haugh 1972, Bildstein and Hamerstrom 1980). See also Bildstein 1988.

In central New Mexico and at 4 sites in ne. U.S., Northern Harriers made up about 2% of all raptors observed in spring (Smith and Muir 1978, Titus and Fuller 1990, Hoffman et al. 1992). In n. British Columbia, s. Yukon Territory, and Alaska, this was the most abundant raptor observed (40% of 314 [Mindell and Mindell 1984] and 61% of 1,391 [Swem 1985]).

MIGRATORY BEHAVIOR

From Kerlinger 1989, except where noted. In New York and New Jersey, migrates at low altitudes (primarily 500–900 m) on days when soaring conditions are good, descending to lower altitudes with westerly winds. During ridge-gliding flight in Pennsylvania and New Jersey, most flights solely gliding or glide-and-flapping. Mean air speed 12.9 ± 0.8 (SE) m/s; mean ground speed 10.8 ± 1.5 (SE) m/s. During fall in central New York, where leading lines are lacking, migrates via thermal soaring and interthermal gliding. Mean interthermal air speed 18.7 ± 1.2 (SE) m/s; mean ground speed 19.4 ± 2.5 (SE) m/s. Soaring in thermals the most common means of gaining altitude during migration. Mean rate of climb using thermal soaring 3.0 ± 1.1 (SE) m/s.

At most hawk-watch sites, migrating Northern Harriers are most frequent between 0800 and 1200 h, with numbers declining throughout remainder of day (Swem 1985, Hoffman et al. 1992, but see Haugh and Cade 1966). Unlike most raptors, migrating Northern Harriers fly in light rain and snow (Haugh and Cade 1966, KLB).

In Wisconsin, fledglings left natal area alone, not with siblings or parents. Occasionally soared with 1–2 conspecifics for brief periods. Migration was slow, with movements interrupted by the establishment of temporary (2- to 3-wk) home ranges. Did not migrate at night. Hunting on migration concentrated after sunrise and before sunset (Beske 1982).

CONTROL AND PHYSIOLOGY

Less affected by the passage of cold fronts than other raptors migrating past Hawk Mountain Sanctuary, PA (Allen et al. in press). Physiological data needed.

HABITAT

BREEDING RANGE

Open wetlands, including marshy meadows; wet, lightly grazed pastures; old fields; freshwater and brackish marshes; also dry uplands, including upland prairies, mesic grasslands, drained marshlands, croplands, cold desert shrub-steppe, and riparian woodland. Populations in mid-w. U.S. and ne. North America breed predominantly in wetland habitats; in w. U.S., proportionately more in upland (dry) habitats (Apfelbaum and Seelbach 1983, Simmons and Smith 1985). In both wetland and upland areas, densest populations typically associated with large tracts of undisturbed habitats dominated by thick vegetation growth (Apfelbaum and Seelbach 1983, Toland 1986b, Kanrud and Higgins 1992). Breeds up to (rarely) >2,400 m.

SPRING AND FALL MIGRATION

Few data. Fledglings migrating southeast from central Wisconsin regularly established temporary home ranges in freshwater marshes (Beske 1982). Seen in both open wetlands and uplands during migration.

WINTER RANGE

A variety of open habitats dominated by herbaceous cover, including deserts, coastal sand dunes, pasturelands, croplands, dry plains, upland and lowland grasslands, old fields, estuaries, open-habitat flood plains, and salt- and freshwater marshes (Temeles 1986, Bildstein 1987, Collopy and Bildstein 1987). Most concentrated populations are restricted to areas with low vegetation, especially the semiarid scrub and shrub-steppe (cold desert) habitats of the Great Basin and grasslands of s. Great plains. West of 100th meridian, northern limit of wintering distribution is coincident with areas where temperature drops below -15°C (Root 1988). In e. U.S., limits of range coincides with dense deciduous and coniferous forest, which it does not occupy. Avoids higher elevations of Appalachian and Ozark mountains.

FOOD HABITS

FEEDING BEHAVIOR

Main foods taken. Summer: small- and medium-sized mammals, primarily rodents, birds (chiefly passerines and small waterbirds), reptiles, and frogs. Winter: in northern part of range, almost exclusively *Microtus* voles; in southern part, mammals and birds. In southeastern coastal marshes devoid of mammals, takes passerines and waterbirds (Collopy and Bildstein 1987).

Microhabitat for foraging. Forages over open

habitats, e.g., prairies, shrub-steppe uplands, marshes. Frequency of use of certain habitats appears related to a combination of prey biomass and vegetative cover (Preston 1990). Areas of short vegetation, e.g., heavily grazed pasture and harvested fields, are underused, whereas idle and abandoned (often wet) fields with vegetative cover are used more than expected (Linner 1980, Bildstein 1987, Preston 1990). Males prefer more open habitats than females; differences are related to (1) use of different prey species (males take more birds than females do; Bildstein 1987); (2) the smaller homeranges of females relative to those of males, which results in female "preference" for habitats surrounding nest sites (Martin 1987); and (3) female exclusion of males from preferred hunting habitats during winter (Temeles 1986). Females hunt more in taller and denser vegetation than males do (Bildstein 1987, Temeles 1987).

Food capture and consumption. Virtually always hunts on the wing, coursing low (<5 m) over ground with a buoyant, gliding flight; flaps intermittently. Most pursuits are short temporally and spatially, and close to ground. Sometimes uses the cover of vegetation and terrain to surprise prey. Frequently follows distinct routes, e.g., ditches (Bildstein 1987). Known to subdue large prey by drowning (Bildstein 1988). Owl-like facial ruff and facial structures facilitate prey detection by sound, even in absence of visual cues (Fig. 2; Rice 1982).

Uses 4 types of hunting flights: (1) gliding: prolonged, nonstationary, nonpowered flight; (2) transect flight: rather straight-line powered flight, with <5 sharp (>30°) turns/min; (3) quartering: powered flight to and fro over short distances, with >5 sharp turns/min; and (4) border-following: powered flight within 5 m of land- or vegetation-type edges, e.g., fencerows (Bildstein 1987). In Ohio in winter, about 58% of time spent in transect flight, 22% quartering, and 20% border-following (Bildstein 1987). Uses 4 types of pounces: (1) hook pounce: preceded by a sharp (>270°) turn with a radius of ≤1.5 m; (2) hover pounce: preceded by a 1- to 3-s hover; (3) straight pounce: without prior changing of flight direction or speed; and (4) slow pounce: low-velocity repeated strikes at vole nests. Proportion of each type of hunting flight and pounce used varies among age and sex classes, habitats, vegetation height, and prey classes (Bildstein 1987, Collopy and Bildstein 1987, Temeles 1987).

In breeding season, hunting activity generally evenly distributed throughout daylight period, although there may be modest temporal "peaks" in midmorning, afternoon, and evening (e.g., Smith and Murphy 1973, Linner 1980). In Davis, CA (E. J. Temeles in litt.), concentrates hunting in early morning and evening to avoid midday heat (37°C).



Figure 2. Owl-like facial discs of the Northern Harrier help it to locate prey acoustically. Drawing by Tony Henneberg.

In Idaho (Martin 1987), males observed hunting within 30 min of sunrise. Virtually all male prey deliveries between 0530 and 1900 h, with peaks between 0900 and 1200 h. Females observed hunting between 0600 and 2120 h. Diurnal pattern of foraging females similar to that of males. In se. Washington in winter (Van Horn 1979), hunting flight highest mid- to late afternoon (sexes pooled). In areas with dense concentrations of larger *Buteo* hawks, avoids hunting during activity peaks of the latter (Bildstein 1987).

In New Brunswick (Barnard 1983), breeding males reduce foraging activity on calm, warm to hot days; individuals drastically reduce hunting activity during periods of moderate and heavy rains, increase hunting activity above normal during period following rainfall. In winter, less active on windless days than during periods of light and moderate winds, although high winds may keep birds on the ground (Bildstein 1987). May cease hunting for about 40–50 min following prey consumption, apparently due to a food-processing constraint (Temeles 1989a, b). See also Breeding: parental care, below.

Prey-capture success highly variable (5–35% of pounces successful; Temeles 1986, Toland 1986a, Bildstein 1987, Collopy and Bildstein 1987, RBM), depending on habitat, prey type, and age or sex class of individual harrier. Success rates typically decline with agility of prey (e.g., amphibians and reptiles 74%, small mammals 34%, birds 14%; Toland 1986a, but see Collopy and Bildstein 1987). Adult males tend to be more successful than females, and juveniles less successful than adults (Toland 1986a, Bildstein 1987), although confounding effects of habitat and prey types may obfuscate any differences among age and sex classes (e.g., Collopy and Bildstein 1987). Among wintering Northern Harriers feeding on voles in British Columbia, prey-capture success higher with snow cover (49% ± 11 SE) than without

(2% \pm 2; Temeles and Wellicome 1992). In s. U.S. in saltwater marshes, where Northern Harriers captured birds exclusively, individuals pounced 3 times as frequently, but had one-third the per-pounce hunting success, as did individuals hunting mainly cotton rats (*Sigmodon hispidus*) in freshwater marshes (Collopy and Bildstein 1987).

In breeding season, intraspecific food-robbery rare (Simmons et al. 1986b, RBM). In winter, prey robbery an uncommon but regular hunting technique (Bildstein 1987). See Behavior: social and interspecific behavior, below.

Large items, especially birds, are plucked and eaten, usually on the ground but sometimes on elevated perches. Smaller items swallowed whole. Small birds usually beheaded, bewinged, and befooted; small mammals sometimes eviscerated. Small mammals consumed in 197 s ($n = 22$), passerines in 1,400 s ($n = 7$; Bildstein 1987). When disturbed by conspecifics during feeding, Northern Harrier usually defends prey; when disturbed by larger *Buteos*, quickly yields prey.

DIET

Broad, with pronounced annual, seasonal, and geographical variation, influenced by local prey abundance and availability.

Winter. Most data from pellets collected at communal roosts (pellets underestimate frequency of large prey in diet; Bildstein 1987). Birds wintering in northern part of range feed almost exclusively on *Microtus* voles (84–93% by frequency); also mice (deer mouse [*Peromyscus maniculatus*] and house mouse [*Mus musculus*]; 1–4%), shrews (Soricidae; 1–3%), rabbits (*Sylvilagus*; <5%), and passerine birds (e.g., meadowlarks [*Sturnella* spp.], Northern Cardinal [*Cardinalis cardinalis*], and Song Sparrow [*Melospiza melodia*]; 1–9%) (Bildstein 1987). Few quantitative food studies from s. U.S., and none from Mexico in winter. In s. U.S., mostly mammals (58% in Arkansas [Preston 1990] and 85% in Mississippi [Jackson et al. 1972]), particularly cotton rat and house mouse; also harvest mice (*Reithrodontomys* spp.), rice rat (*Oryzomys palustris*), shrews, and passerine birds (e.g., meadowlarks and Northern Cardinal). Proportion of passerine birds in diet higher in southern than in northern portion of winter range (>15% by frequency vs. <10%, respectively), but quite variable between studies; e.g., 16% in Mississippi (Jackson et al. 1972), 42% in Arkansas (Preston 1990).

Breeding season. See Appendix 1. A variety of small mammals, reptiles, amphibians, and birds, the last including many recently fledged and ambulatory precocial young, and species not typically taken as adults (Barnard et al. 1987, KLB). Throughout North America, some insects, including

beetles (Coleoptera), grasshoppers, crickets, and locusts (Orthoptera), consumed in small amounts; frequently taken by recently fledged young (KLB). Vertebrate prey have masses ranging from about 7 to 1,000 g; average geometric mean prey mass 51.4 g (range 42.8–60.2, $n = 7$ studies); average food niche breadth index 3.96 (1.37–10.32, $n = 7$ studies; Marti et al. 1993).

FOOD SELECTION AND STORAGE

Opportunistic predator, with prey choice apparently limited only by size, formidability, and availability of prey. Wounded or otherwise sickly prey sometimes taken (Bildstein 1987). In the breeding season, females may capture heavier prey than males, including virtually all large, non-passerine bird prey (Barnard 1983, Toland 1985a, RBM). In New Brunswick, males deliver to nests significantly more passerine bird prey than females do (MacWhirter 1985).

In breeding season, temporal shifts in prey selection are typical. In New Brunswick, shifts from meadow voles in spring to juvenile passerines and frogs in midseason (MacWhirter 1985). Shift corresponds to increases in availability of passerine prey (Barnard et al. 1987).

In New Brunswick, food niche breadth index inversely correlated with abundance of voles in summer (RBM). Captures proportionately more adult and fledgling passerines in years of low vole abundance than in years of high vole abundance (MacWhirter 1985).

Breeding males and females known to cache and retrieve supplemental food (Simmons et al. 1987, RBM). Caching not detected among wintering birds in Ohio (Bildstein 1987).

NUTRITION AND ENERGETICS

Few data. In fall-winter, a female in captivity consumed 100 g/d (beef); in spring-summer, a male in captivity consumed 42 g/d; these values were 19.0 and 12.1% of body mass, respectively (Craighead and Craighead 1956). In pre-hatch period, males provide their mates with 3 items, or about 95 g/d (Simmons et al. 1986a, RBM). Among free-ranging, *C. c. cyaneus* wintering in the Netherlands, gross biomass intake 187 g/d (Raptor Group RUG/RIJP 1982). See Behavior: locomotion, below.

In New Brunswick (MacWhirter 1994), food consumption rates vary among broods, but female nestlings eat more (127.4 g/d, or 4.77 kg/nestling period) than males do (117.6 g/d, or 3.90 kg/nestling period). In the postfledging period, net food consumption rates (mean = 102.9 g/d) and the total amounts of food consumed (mean = 2.54 kg) by the sexes are similar. Over the entire period of parental care, females and males receive 7.18 kg (or

113.4 g/d) and 7.37 kg (or 124.6 g/d), respectively. Thus, prior to independence, each surviving offspring consumes about 245 prey (averaging 32 g each; RBM).

No data on energy assimilation efficiency. In order of decreasing caloric value per unit wet mass: birds, mammals, reptiles, and amphibians (Golley 1960, Cummins and Wuycheck 1971, Bird et al. 1982).

METABOLISM AND TEMPERATURE REGULATION

No data.

DRINKING, PELLET-CASTING, AND DEFECATION

Drinks in captivity (KLB). In captivity, single bird on ad libitum diet of small passerines and ground squirrels (*Spermophilus* spp.) produced 8 pellets in 149 h (Errington 1930b). In winter, average prey per pellet varies locally from 0.5 to 3.2 (median 1.3, $n = 5$ studies; Craighead and Craighead 1956, Jackson et al. 1972, Holt et al. 1987). Mean pellet mass (\pm SD) from roosts in Michigan and Massachusetts 0.9 g ($n = 450$; Craighead and Craighead 1956) and 2.9 ± 0.93 g ($n = 180$; Holt et al. 1987). In Massachusetts, mean (\pm SD) pellet length 36.9 ± 9.22 mm, mean bone mass per pellet 0.50 ± 0.335 g ($n = 180$). Percentage bone per pellet averages 17–18% (Holt et al. 1987).

Uric acid of Northern Harrier is chalky white; excreta green and pelletlike. No data on defecation rates.

SOUNDS

VOCALIZATIONS

Especially vocal near the nest. In courtship display, both sexes utter *kek*, *quik*, or *ek* notes in rapid series (Bildstein 1988). Distress (or Threat) Call is a more urgent, high-pitched *kek* or *ke*, again uttered in rapid succession (Figs. 3a and b). This call occurs when female is disturbed at the nest by ground predators, raptors, humans, or approaching ungulates, and often attracts her mate, which joins in calling (Bildstein 1988). Also given in flight when being mobbed by passerines. In winter, given by territory owners while "escorting" intruders out of the territory, and by individuals at communal roosts in response to ground and aerial intruders (Bildstein 1976, Bildstein and Collopy 1985, Temeles 1987). Induces flight in birds roosting nearby (Bildstein 1976). Distress Call more narrow-banded and nasal-sounding in males than in females.

During the breeding season, females issue Food Call, a piercing, descending scream, *eeyah eeyah* (Fig. 3c), which may be repeated for minutes, almost always in the presence of mate and apparently in an

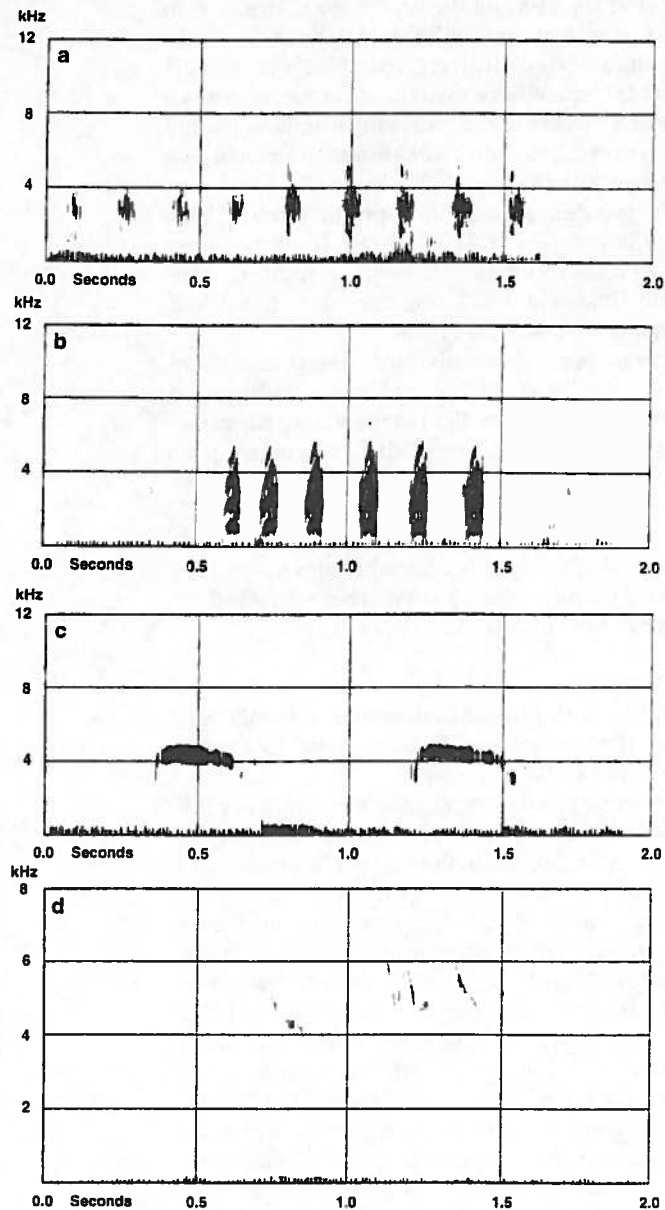


Figure 3. Vocalizations of the Northern Harrier: (a) male Distress Call (Borror Laboratory of Bioacoustics [BLB] #17965); (b) female Distress (or Threat) Call (BLB #17965); (c) female Food Call (BLB #17968); (d) female Feeding Chuckle Call (BLB #17967). Recorded by RBM at Tantramar Marsh, NB. Sonograms prepared with the assistance of the Borror Laboratory of Bioacoustics, Ohio State University.

effort to induce food transfers, hunting by the male, or to "solicit" copulation. Food Call is sometimes given by individuals attempting to rob prey from conspecifics; also by recently fledged young in pursuit of parents returning to the nest site with prey, and of siblings with recently transferred prey. In winter, territorial females give Food Call while on the ground in response to intruders (Temeles 1990a).

Same call heard during evening display flights at communal roosts (Bildstein 1988). Prey-carrying males emit a barely audible, chuckling *purrduk* when passing low over their nest, which solicits the female from the nest (Simmons et al. 1987).

Upon arriving with food at the nest, female utters a soft, high-frequency Feeding Chuckle Call (Fig. 3d), which appears to summon and orient nestlings for feeding bout. Young nestlings have several Begging Calls, including a weak, but monotonous *peep* (same call given from unhatched egg; RBM) and a rather variable, but shaky, *preeeii* (Bildstein 1988). Nestlings will emit Begging Calls in response to seeing parents fly overhead, or when female utters Food Call within about 150 m of nest (RBM). Nestlings produce a series of *chit* notes, referred to as a "pain" or "discomfort chitter" (F. Hamerstrom pers. comm.), which become more emphatic with increasing age. Once young fledge, vocabulary begins to sound like that of their parents.

NONVOCAL SOUNDS

None reported.

BEHAVIOR

LOCOMOTION

Walking, hopping, climbing, etc. Occasionally walks or hops short distances while retrieving prey, collecting nesting material, or retrieving nestlings that have strayed from the nest (see Breeding: parental care, below). Climbing not reported.

Flight. Typically flies slowly, low over the ground with a series of heavy flaps and distinctive buoyant, tilting glides, with wings held in a strong dihedral; sometimes hovers briefly. Occasionally soars. Has low wing-loading and high wing length-to-width ratios for a diurnal raptor (see Measurements, below). These features, along with wing-slotting, prominent alulas, and pronounced camber, enhance aerodynamic efficiency and the conservation of power, particularly at low flight speeds (Thompson-Hanson 1984). Estimated minimum metabolic cost of flight of female (5.12 Watts [J/s, =W]) is 70% higher than that of male (3.02 W; Temeles 1986). In Netherlands in winter, power output at minimum-cost flight-speed about 5.6 and 4.7 W for *C. c. cyaneus* females and males, respectively. Metabolic energy expenditure for flight approximately 98 kJ/h and 82 kJ/h for females and males, respectively (Raptor Group RUG/RIJP 1982).

Estimates of flight speed while hunting: 32 ± 15 (SD) km/h (Bildstein 1987), 37 (range 19–56) km/h (Trautman 1944). In Ohio, transect flight (see Food Habits: feeding, above, for a description of flight types) fastest (mean approximately 35.5 km/h),

border-following (mean approximately 29.4 km/h) intermediate, and quartering flight slowest (mean approximately 19.5 km/h); in general, males fly faster (mean approximately 38 km/h) than females or juveniles (28–30 km/h), regardless of flight type (Bildstein 1987). Males have shorter wings and lower wing-loading than females do (Nieboer 1973) and appear more agile in flight (Temeles 1986). E. J. Temeles (in litt.) observed a male Northern Harrier pursue a male Sharp-shinned Hawk (*Accipiter striatus*), and another evict a Prairie Falcon (*Falco mexicanus*) from its territory; the harrier outclimbed the falcon. Also see Migration: migratory behavior, above.

Swimming and diving. Rare and usually incidental to drowning of prey (Bildstein 1988).

SELF-MAINTENANCE

Preening, head-scratching, stretching, bathing, anting, etc. Preening typically done with considerable use of uropygial gland. Scratches head with toes, occasionally in flight. Stretches 1 wing and leg to side, balancing on the other leg. Breeding females bathe in ditches; females on winter territories bathe during rainstorms by sitting on fenceposts and stretching wings while facing into the rain (E. J. Temeles in litt., RBM). Bathes almost daily in captivity if fresh water provided.

Sleeping and roosting. No quantitative data on sleeping. Captive birds spend considerable portion of day roosting on 1 leg with eyes closed. Brooding females observed closing eyes for <10 min (RBM). In breeding season, adults and fledglings roost on ground, alone. For roosting in nonbreeding season, see Social and Interspecific Behavior, below.

Daily time budget. Species is diurnal. Daily time budget varies considerably as a function of weather and breeding activity. Even so, birds appear to be active for about 14–15 h during the breeding season and from 30 min after dawn to 30 min before dusk in winter. In spring, pre-laying female spends about 1 wk in "egg-laying lethargy," preening, with little flying and no prey captures (Simmons et al. 1987); male provides virtually all food for female (and later, offspring) from pre-laying to early nestling stage, about 60 d (Martin 1987, RBM). In incubation and early nestling period, male spends 68% (62–76%, $n = 3$) of daytime flying, chiefly hunting (Bildstein 1982). In Idaho (Martin 1987), breeding males were in flight 52% of time (6.75 h/d, with 20%, or 2.6 h/d spent hunting); much time (46%) spent loafing; total time flying and time spent foraging peaked while females brooded (68% total time flying, or 8.8 h/d; 34%, or 4.4 h/d, hunting).

In an agricultural area of California, wintering adult females foraged 6–16% and perched 47–85% of daily active period (Temeles 1989a). In a freshwater

marsh in Florida and a saltwater marsh in S. Carolina, birds spent 27 and 34%, respectively, of the time in hunting flight (Collopy and Bildstein 1987). In Ohio in winter (Bildstein 1987), 74% of 1,013 Northern Harriers sighted on roadside surveys were flap-sailing when first sighted, 5% soaring, and 21% perched; adult males were most active in early morning and late afternoon, whereas the reverse was true for unsexed juveniles. Adult females were most active in midmorning. See also Food Habits: feeding, above.

AGONISTIC BEHAVIOR

See Spacing, Social and Interspecific Behavior, and Predation, below. Females dominant to males at artificial feeding stations and at communal roosts (RBM, KLB).

SPACING

Territoriality. In breeding season, not strongly territorial, except near the nest, where both sexes are intolerant of conspecifics, chiefly those of the same sex and unrelated fledglings of either sex. Territorial interactions most frequent during courtship and incubation periods, then wane as season progresses, yet intrusions by neighbors into nest area always lead to vigorous pursuit (Errington 1930a, Martin 1987, Simmons et al. 1987).

Territorial behavior by females takes the form of leg-lowering, escorting flight, and talon grappling (Bildstein and Collopy 1985, Barnard and Simmons 1986). Males assert territoriality by leg-lowering, only to males, and sky-dancing (see Sexual Behavior, below), mainly to females (Simmons et al. 1987). Transient spring migrants may perform aerial displays over territories (Hamerstrom 1969). Leg-lowering and escorting flight involve slow, low-level, close (2–40 m), and parallel flights by birds along the common border of their territories. Wings held in an exaggeratedly high angle; tarsi are extended fully, talons exposed and may be clasped together. The participants repeatedly glide to the ground in displays lasting up to 7 min (Barnard and Simmons 1986). Borders often defined by vegetation changes or height differences, fence lines, or topographic features (Errington 1930a, Martin 1987). Northern Harriers use high-speed pursuit and stooping when defending nest site against conspecific intruders.

In New Brunswick, monogamous male territories approximately 110 ha in size; areas defended by females smaller (approximately 10 ha; Simmons 1983). In Idaho, by contrast, males defend an area of only 0.8 ha (Martin 1987).

In winter, adult females defend territories against conspecific and some heterospecific intruders. Consequently, males are excluded from preferred

foraging areas, and males and subordinate females adopt alternative foraging behaviors (Temeles 1986). Territory holders usually approach intruders at high speed before escorting them to the territory border. Escorting birds follow several meters below, and usually behind, the intruder, until the intruder flies out of the area. Intruders that land during such interactions are stooped on (Bildstein and Collopy 1985).

In se. U.S., winter territories of, on average, 65 ha defended from several hours to >15 d (Bildstein and Collopy 1985). In California, adult females defend areas of highly variable size (mean 33.6 ha, range 3.9–124.9), usually for ≤14 d; territory size inversely correlated with house mouse availability and with intruder pressure, particularly by adult female neighbors, although prey availability is the only significant predictor of territory size in high food years (Temeles 1987, 1989b). Females win virtually all aggressive interactions with males and about half with females; males rarely respond to approaches by conspecifics (Temeles 1986). Territorial adult females are most aggressive toward neighbors and least aggressive toward male floaters (Temeles 1989b, 1990a); aggressive intensity toward these classes varies following food consumption (Temeles 1989b). Neither the frequency nor duration of interactions between neighbors and owners decline significantly as season progresses. Floaters never observed to take over territories; on 2 occasions, however, neighbors expanded their territories (Temeles 1990a).

Individual distance. Often nests in loose assemblages, but internest distances and dispersion patterns highly variable among and within populations; both parameters influenced by polygyny and by the need to concentrate in patches of restricted nesting habitat or where prey are plentiful. There are, however, reports of concentrated nesting within areas of continuous habitat (e.g., Hecht 1951). Internest distances (population study area means) vary between 243 and 2,400 m (median 430 m, $n = 7$ sites); nests rarely closer than 100 m. Internest distances significantly shorter among harem members than among the population at large in Wisconsin and New Brunswick (Burke 1979, MacWhirter 1985, Saunders 1986). Polygynous females appear to place their nests closer to the harem's first-settling (primary) female than expected by chance (Simmons et al. 1986b). Distances are inversely proportional to annual nest densities and food abundance (MacWhirter 1985, Saunders 1986). In New Brunswick, wet areas have high concentrations of nests, dry areas fewer nests (Simmons 1983).

SEXUAL BEHAVIOR

Mating system and sex ratio. Generally monogamous, but also simultaneously polygynous, with

well-structured hierarchical harems of 2–5 females. No other raptor species exhibits either the degree, or regularity of occurrence, of polygyny (Simmons et al. 1986b). In New Brunswick, Wisconsin, and Washington populations, 11–14% of males polygynously mated; 20–29% of females in harems, others monogamous (Thompson-Hanson 1984, Hamerstrom et al. 1985, Simmons et al. 1986b, RBM). In New Brunswick, annual proportion of females in harems varies from 11 to 43% and, like the number of polygynous males, is positively associated with the abundance of microtine voles in spring (Hamerstrom 1979, Simmons et al. 1986a, b).

In New Brunswick, sex ratio among potential breeders about 1.2 females to 1.0 males ($n = 6$ yr; Simmons 1988b, RBM). Female-biased nestling ($n = 40$) and fledgling ($n = 35$) sex ratios reported in Missouri (Toland 1986b); similar trend in N. Dakota, but not statistically significant ($n = 64$; Sutherland 1987). Nestling ($n = 188$) and fledgling ($n = 225$) sex ratios not different from parity in New Brunswick (MacWhirter 1994). A female-biased adult sex-ratio is not the prime reason for polygyny in North America; rather, differences in male quality, as reflected by rates of courtship provisioning and display, appear to influence female mate choice (Simmons 1988b). During nest-building and courtship period, females occasionally abandon prospective partners, principally those with low courtship-provisioning rates, implying active mate choice by females. Some monogamous males also reject additional females (Simmons et al. 1987, Simmons 1988b).

In New Brunswick, old (≥ 3 yr) females somewhat more common in polygynous situations than monogamous ones; the opposite trend observed in Wisconsin. No yearling males polygynous (Hamerstrom et al. 1985, Simmons et al. 1986a).

In New Brunswick, evidence of assortative mating by age; 20% of 20 subadult females mated with subadult males, whereas <2% of 55 adult females did so (RBM). No strong evidence of assortative mating in Wisconsin (Hamerstrom et al. 1985).

Pair bond. Males advertise territory occupancy and court females by performing Sky-Dancing Display. Each aerial display comprises a sequence of as many as 74 deep, U-shaped undulations covering a distance of up to 1 km at a height of 10–300 m; most bouts about 25 Us at 20 m above ground (Simmons 1988a; see Breckenridge 1935 for full description). Females sky-dance, but less frequently than males (Simmons et al. 1987, RBM). Sometimes accompanied by chattering vocalizations at the zenith of undulations (Saunders 1913, RBM). Frequently ends with male disappearing into a potential nest site. Female attracted by display typically follows and displaces male from the site,

suggesting display plays a role in nest-site selection (Simmons 1991a). Adult males display more often and more intensely in food-rich than in food-poor years (Simmons 1988a); precipitation reduces frequency (Follen 1986, RBM). The most vigorously displaying males attract the largest harems (Simmons 1988a). Males will sky-dance over suitable nesting areas while on migration, so sky-dancing may not always reflect ownership of a breeding territory (Hamerstrom 1969).

Tentative pair bonds are evidenced by mutual male-female territorial soaring and food transfers (Simmons et al. 1987). Courtship feeding of females begins as much as 3 wk (but at least 1 wk) before laying (Simmons et al. 1987). Ground transfers occur commonly early in the breeding season when females are egg-laden (Simmons 1991b). Time between beginning of courtship-feeding and egg-laying is shorter in years of good food supply (Simmons et al. 1987). Polygynous males have significantly higher provisioning rates than monogamous males (Simmons 1988a). No overt mate-guarding by males.

Copulation mainly on the ground; also on small trees and fence posts (Simmons et al. 1987); usually before 1200 h (Martin 1987). Food pass often precedes copulation, but not a prerequisite. Balfour (1962–1963) describes copulation as follows. Once food is exchanged, "female will crouch over food and call with great urgency. As the male flies low toward her, she lowers her head and crouches with wings held out slightly from her sides. Just before he alights on her back, she raises her tail. The act is completed in a few seconds. Afterwards, both will preen. Coition continues to occur well into the egg-laying period, usually becoming less frequent as clutch nears completion"; apparently successful copulations (but not fertilizations) occur as late as the nestling period (RBM).

A small proportion (<25%) of pairs that begin nest-building do not stay to breed, although females rarely desert their mate once incubation has begun (Simmons et al. 1987). Desertion by females is associated with low food-provisioning rates (Bildstein 1979a). In Wisconsin, over 10-yr period, essentially no pair fidelity year to year; about 2% of females paired with a given male a second time (Hamerstrom 1969).

Extra-pair copulations. Known to occur (Hamerstrom 1969), but quantitative data lacking.

SOCIAL AND INTERSPECIFIC BEHAVIOR

Degree of sociality. See Spacing, above. Adults and fledglings roost individually on the ground. In Wisconsin, birds do not reuse roost sites on successive nights (Hamerstrom and De La Ronde Wilde 1973). Polygynous males roost, preen, and loaf more often in the vicinity of primary females than other harem

members (Simmons et al. 1986b). Juveniles apparently do not roost communally during early period of fall migration (Beske 1982).

From Bildstein 1988 and references therein, except where noted. In the nonbreeding season, between about late Oct and early Mar, Northern Harriers gather at communal roosts, sometimes with Short-eared Owls (*Asio flammeus*). Within the roost, individuals occupy small ($\leq 0.25 \text{ m}^2$) patches of open ground, e.g., in grassy or stubble fields, joined by short runways 2 m apart. Locations of communal roosts are often traditional (Bosakowski 1983, Christiansen and Reinert 1990); e.g., in s.-central Ohio, some sites have been occupied in most years for more than a decade (KLB). Average number of roost members about 20, although reported means vary widely (2–85). Single-bird roosts exist but are short-term ($< 4 \text{ d}$; Bildstein 1979b, Bosakowski 1983). Numbers of birds using individual communal roosts fluctuate throughout the winter, with reciprocal shifts in numbers of birds in different locations signaling movements of birds from one site to another (Bildstein 1976, Christiansen and Reinert 1990). In Ohio, as the season progressed, there was a general trend toward fewer roosts with more birds at each. Both intra- and interspecies interactions are common at roosts, especially as birds return each evening. Such interactions usually involve high-speed reciprocal chases and swooping.

Play. In the fledgling stage, juveniles chase and supplant one another, and occasionally pounce on and play with inanimate objects (Bildstein 1992, RBM). In winter, Bildstein (1980) observed Northern Harriers playing with inanimate objects, both before going to roost in evening and after roosting. Individuals picked up and manipulated vole-size corncobs and other crop residue; birds were more likely to initiate play when a nearby bird did so, and as many as 3 birds played with corncobs within 50 m of each other.

Nonpredatory interspecific interactions. Typically tries to elude mobbing passerines. Responses include rapid chattering calls, looking back over the wings at pursuing passerines, stalling and rolling, increasing flight elevation, and changing flight type (Bildstein 1982). Northern Harriers are mobbed more intensely when flying than when perched, and are much more likely to be mobbed while carrying prey than when not carrying prey.

When Northern Harrier is sympatric with Short-eared Owl in breeding season, territories frequently overlap (e.g., Linner 1980), with relatively few agonistic interactions (RBM).

In Ohio (Bildstein 1987), wintering Northern Harriers share habitat with other raptor species, but physical interactions (often in the form of midair talon-grappling) are uncommon. In 4 winters ($n =$

770 h), Northern Harriers without prey chased Red-tailed Hawks (*Buteo jamaicensis*) 7 times, Rough-legged Hawks 30 times, and conspecifics 32 times; over the same period, Northern Harriers with prey were pursued by Red-tailed Hawks 6 times, by Rough-legged Hawks 13 times, and by conspecifics 9 times; overall, 33% of all Northern Harriers seen with prey were chased by other raptors. Northern Harriers lost 5–10% of prey captures as a consequence of food-stealing by larger raptors, and may avoid hunting near larger Rough-legged Hawks, to which the harriers are subordinate (Bildstein and Collopy 1985, Bildstein 1987).

In California (Temeles 1990b), wintering territorial female Northern Harriers often evicted intruding raptors larger than themselves from their territories (particularly when the harriers were hunting) but never species smaller than themselves. Apparently, aggressive responses serve primarily to reduce stealing of Northern Harriers' prey by larger raptors. This lack of defense by Northern Harriers against smaller intruding raptor species apparently results from harrier's ability to steal prey from such intruders; females attempted piracy during 55% of prey-capture attempts by smaller species but 0% during 28 prey-capture attempts by larger species. Attempts to rob Black-shouldered Kites (*Elanus caeruleus*) often were unsuccessful (82%) and generally occurred when a harrier's rate of energy intake was less than that required for maintenance.

In British Columbia, 56% of 34 food-robbery attempts by Northern Harriers were directed toward Short-eared Owls rather than conspecifics (Temeles and Wellicome 1992). Aggressive interactions and food-stealing are more frequent in periods of severe weather (e.g., snow cover present) and where raptor densities are high (cf. Craighead and Craighead 1956, Bildstein 1987, Temeles and Wellicome 1992).

PREDATION

Kinds of predators and manner of predation. Terrestrial mammals appear to be important predators of eggs and nestlings, although species are usually unknown (Hamerstrom 1969, Powers et al. 1984, Simmons et al. 1986a). Coyote (*Canis latrans*), feral dog (*C. familiaris*), striped skunk (*Mephitis mephitis*), raccoon (*Procyon lotor*), and red fox (*Vulpes fulva*) probably most important; livestock and white-tailed deer (*Odocoileus virginianus*) trample eggs and nestlings (Hamerstrom 1969, Martin 1987). American crows (*Corvus brachyrhynchos*) and Northern Ravens (*C. corax*) known to destroy eggs; and raptors, particularly Great Horned Owls (*Bubo virginianus*), known to kill nestlings and fledglings (Simmons et al. 1986a, Toland 1986b, Sutherland 1987). Canid predators known to kill incubating females at nest (Saunders 1986, RBM).

In New Brunswick (Simmons et al. 1986a, b), 19% of 95 nests depredated; for unknown reason, predation on eggs and nestlings tended to decrease with increasing vole abundance. Polygynous females suffered higher rates of predation than either monogamous or primary females. The increased predation of later harem nests probably results from low male-provisioning rates, as later-settling females are forced to forage more often than earlier-settling females, thereby leaving their nests unattended.

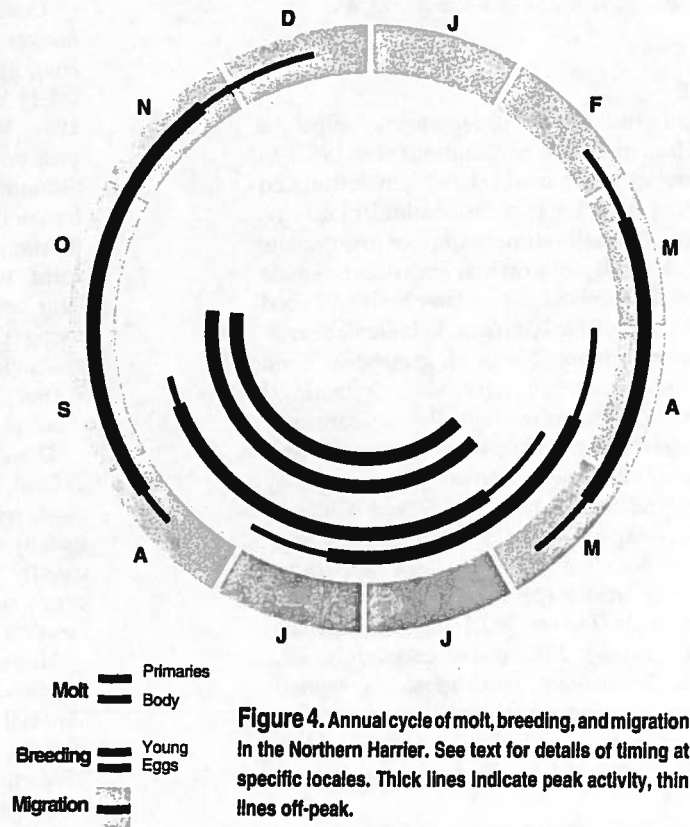
Response to predators. Generally, parents respond aggressively by uttering Distress Calls (see Sounds: vocalizations) and mobbing potential predators, human intruders, and some nonpredatory animals (e.g., deer). The defense response ranges from a silent retreat from the nest to striking the intruder with closed talons. On average, males and females contribute equally to defense (Simmons et al. 1987). In New Brunswick (RBM), males are more aggressive than females, whereas Martin (1987) observed the opposite pattern in Idaho. Both sexes dive closer and more persistently when mates are present than when alone (Simmons 1983). Harem members (or nonmembers) do not cooperate in offspring defense against simulated or real predators (Simmons 1988b, but see Powers et al. 1984). In Massachusetts, Northern Harriers nest only on islands free of mammalian predators (Veit and Petersen 1993), suggesting that predation may influence choice of nest site and thus distribution. See also Breeding: nest site, below.

BREEDING

PHENOLOGY

Pair formation. Probably occurs on breeding grounds (Hamerstrom 1986). Males arrive on breeding grounds in Mar in N. Dakota and central Wisconsin (Hammond and Henry 1949, F. Hamerstrom in Bildstein and Collopy 1990); in late Mar and early Apr in Manitoba and New Brunswick (Haugh 1972, RBM). Adult males generally arrive 5–10 d before females (Hamerstrom 1969, RBM). Aerial courtship/territorial displays, coincident with the arrival of adult females (RBM), occur late Mar and Apr in Wisconsin (Follen 1986); from Apr to mid-May (peaking in mid-Apr to early May) in New Brunswick and Massachusetts (Simmons et al. 1987, Christiansen and Reinert 1990, RBM); and in late Apr and early May in Montana (Saunders 1913). Courtship displays began as early as late Feb in Washington (Thompson-Hanson 1984).

Nest-building. Mar in Washington (Thompson-Hanson 1984); late Apr to early Jun in New Brunswick (Simmons et al. 1987); begins late Apr to early May in Minnesota and Missouri (Breckenridge 1935,



Toland 1986b). Nest completed within several days to 2 wk.

Only brood per season. See Figure 4. Most eggs laid mid-Apr to early May (extremes late Mar to mid-May) in Washington (Thompson-Hanson 1984); mid-May to early Jun (extremes mid-Apr to late Jun) in n. Great Plains (Kantrud and Higgins 1992), Wisconsin (Schmutz and Schmutz 1975), Massachusetts (Veit and Petersen 1993), and New Brunswick (Simmons et al. 1986a, RBM). In New Brunswick (Simmons et al. 1986a, b, RBM), timing of egg-laying significantly earlier in years of high, rather than low, vole abundance, but not significantly correlated with total precipitation or ambient temperature in spring. Older (≥ 3 yr) females precede younger ones by 6 d, on average. Primary female lays earlier than secondary females by 8 d, but range of settling dates highly variable within harems.

Nestlings usually hatch mid-May to early Jun (extremes late Apr to mid-Jun) in Washington (Thompson-Hanson 1984); mid-Jun to early Jul (extremes mid-May to late Jul) in n. Great Plains (Kantrud and Higgins 1992), Wisconsin (Schmutz and Schmutz 1975), and New Brunswick (Simmons et al. 1986a, RBM). Nestling period averages 6 wk. Fledgling period occurs late Jul to early Aug in New Brunswick (RBM), as juveniles remain in vicinity of

nest 2–4 wk (Bildstein 1992, MacWhirter 1994). Thus, breeding season is about 120–135 d (Fig. 4).

NEST SITE

Selection process. Male or female may select the nest site (Hamerstrom 1986, Simmons et al. 1987). In New Brunswick (Simmons et al. 1987), male initiated nest-building on 95% of 19 occasions; built platforms in presence of female, stimulating her to complete the nest. Male-built platform may act to locate female in a desired location; 8 females later built and used alternative nests within 20 m of male-built platforms.

Site characteristics. Nests on ground in open (treeless), vegetated habitats, including drained and non-drained wetlands as well as uplands. Extremely eclectic in choice of vegetative cover, even within a single area. In a continentwide sample analyzed by Apfelbaum and Seelbach (1983), 17% of 428 nests were in wet marsh meadows dominated by, e.g., willow, grasses, sedges (*Carex* spp.), and herbaceous shrubs; 18% in freshwater marshes dominated by tall grasses, reeds (*Phragmites*), bulrushes (*Scirpus*), and cattails (*Typha*); 26% in dry grasslands, e.g., brome grass (*Bromus*) and wheatgrass (*Agropyron*); 8% in cultivated fields, e.g., timothy grass (*Phleum*), alfalfa (*Medicago sativa*), and rangeland prairies. Nests rarely (<2%) reported from brackish or saltmarsh habitats.

Most nests built within patches of dense, often tall, vegetation (e.g., cattails, meadowsweet [*Spiraea*]) in undisturbed areas (e.g., Simmons and Smith 1985, Sutherland 1987, Kantrud and Higgins 1992). At most sites, even many of those in dry-land habitats, disproportionate number of nests located in wet areas, e.g., surrounding stock ponds or along creeks (Simmons and Smith 1985, Martin 1987, Grant et al. 1991). In Washington and New Brunswick, 79 and 27% of nests, respectively, were built in standing water on platforms raised above water level (Thompson-Hanson 1984, RBM). Wet sites are preferred, apparently because of reduced predation (see Demography and Populations: measures of breeding activity, below). A shift to suboptimal habitat (e.g., dry cropland) after the destruction of optimal nesting habitat may precipitate an increase in nest failures through predation and human disturbance.

Long-term shifts in nesting substrate occur in response to changes in vegetative cover resulting from herbicide use and changes in agricultural crops. For example, in Wisconsin over 19 yr, nest sites shifted from willow, young quaking aspen, sedges, and grasses to goldenrod (*Solidago*) and meadowsweet as the relative abundances of the former declined while those of the latter increased (Hamerstrom and Kopeny 1981).

NEST

Construction process; structure and composition matter. Both sexes carry nest material to the nest site, although most platforms are added to and lined solely by the female (Sealy 1967, Simmons et al. 1987). Male transfers material to female by an aerial pass or on the ground at nest site (Bildstein 1979a, Simmons et al. 1987). Most gathering of material by female (Toland 1986b, RBM). Nest built throughout the day; constructed in about 7–14 d of reeds, grasses, forbs, weeds, and water plants readily available near nest (RBM). Frequently, base of nests formed using thick-stalked plants (e.g., cattails, alder, willow), then completed with grasses, sedges, and rushes (e.g., *Spartina*, *Calamagrostis*, *Carex*, *Scirpus*; (Fleskes 1992, RBM). Also see Nest Site, above.

Dimensions. Data from Hecht 1951, Sealy 1967, Toland 1986b, Serrentino 1987, and RBM. Outside diameter usually 39–63 cm; height highly variable, usually 4–20 cm. Inside diameter 20–25 cm; depth usually 5–10 cm, rarely >20 cm. In general, nests over water are deeper, thicker, and bulkier than nests on dry ground.

Microclimate. No data.

Maintenance or reuse of nests; alternate nests. Material added to nest in incubation period and after hatching until nestlings 3–4 wk old (Sealy 1967, RBM); rates highly variable among females (RBM). Prolonged rainfall increases the rate of nest-material delivery (Follen 1986, RBM). Within populations, general nesting areas, but not identical nest sites, are used in subsequent breeding seasons (Breckenridge 1935, MacWhirter 1985).

For information on alternate nests, see Nest Site: selection process, above, and Eggs: egg-laying, below.

EGGS

Shape. Short subelliptical.

Size. From Bildstein 1988, except where noted. Length x breadth (mean, range [in mm]), volume (mean, range [in cm³]; volume 0.51 x l x b²). New Brunswick: length 45.98 (41.95–50.50) x breadth 35.58 (32.15–38.85), volume 29.78 (23.09–36.69), *n* = 125 eggs, 32 clutches (RBM). Alberta: length 45.6 (44.5–47.0) x breadth 36.2 (35.0–37.0), volume 30.48, *n* = 16 eggs (Sealy 1967). U.S.: length 46.6 (41.4–53.0) x breadth 36.4 (34.0–39.5), volume 31.49, *n* = 84 eggs. North America: length 46.32 (± 3.04 SD) x breadth 36.31 (± 1.54 SD), volume 31.14, *n* = 20 eggs; length 46.4 (41.4–53.0) x breadth 36.2 (34.0–39.5), volume 31.0, *n* = 96 eggs. Runt eggs occur occasionally. In New Brunswick (RBM), males and females emerged from eggs of similar volume; egg size increases with clutch size and with position in the laying sequence; at hatching, body mass and tarsus length, but not wing chord, positively correlated with egg size.

Mass. From Bildstein 1988. At Churchill, Manitoba, mean egg mass 30.1 g; in Alberta, mean 35.1 g (range 28.9–38.9, $n = 10$). Egg mass 6–7% of female body mass.

Color and surface texture. Smooth, with little gloss; eggs usually spotless, dull white with a pale blue hue when laid, but gradually fade to white over 2–4 d (Hamerstrom 1969).

Eggshell thickness (pre- and post-DDT). In 1980s in Oregon, average eggshell thickness 0.307 mm ($n = 3$; Henny et al. 1984). See Conservation and Management: effects of human activity, below.

Egg-laying. At 2-d, occasionally 3-d, intervals (Sealy 1967, Hamerstrom 1969), usually during early morning (Sealy 1967). Normally, 1 clutch/breeding season, but will lay replacement clutch in newly-finished nest (which may be based on male-built platform) if clutch disturbed during laying (Duebber and Lokemoen 1977, Simmons 1984). In New Brunswick (Simmons 1984), period between failure and renesting averaged 7.4 d. Distance between first nest and renest generally closer (<200 m) than the minimum distance recorded between concurrently occupied nests (260 m).

In New Brunswick (MacWhirter 1994), first-laid eggs in clutch were predominantly female (62%; $n = 50$), second- and third-laid eggs predominantly male (64%; $n = 85$). In years when vole numbers were high, however, first- and second-hatched eggs in large clutches were much more likely to be females than in years when vole numbers were low and clutches small. Offspring from the last 3 eggs in clutches were predominantly males (59%; $n = 112$), with a trend for the magnitude of the male bias to decline with laying sequence, such that regardless of clutch size, neither sex predominated in the last egg laid (53% male; $n = 34$).

INCUBATION

Onset of broodiness and incubation in relation to laying. In New Brunswick, most females begin at least partially incubating eggs on the day of, or the day following, laying of the first egg, which results in sequential hatching and a size hierarchy among broodmates (MacWhirter 1994). See Young Birds, below.

Incubation patch. One, in female only.

Incubation period. Typically 30–32 d, range 28–36 (Breckenridge 1935, Sealy 1967, Hamerstrom 1969).

Parental behavior. Female alone incubates, although male may shade or guard clutch for ≤ 5 min in female's absence (Breckenridge 1935, Hecht 1951, Simmons et al. 1987). Nest attendance constant except when female leaves for prey deliveries, collection of nest material, and short (≤ 30 min) "exercise" flights (RBM).

Hardiness of eggs against temperature stress; effect of egg neglect. No data.

HATCHING

From Sealy 1967, MacWhirter 1994, and RBM. Time from pipping of egg to emergence of nestling usually 24–48 h, occasionally <24 h. Eggs hatch in sequence in which they were laid; on average, at 2-d intervals, range 0–3 d. Duration of hatching interval increases with position in hatching order. No data on diel hatching pattern. No evidence that female responds vocally when offspring emit *peep* calls inside egg at time of hatching. Parents do not assist offspring in hatching. Eggshells are either eaten by the female or dropped ≥ 50 m from the nest.

YOUNG BIRDS

Condition at hatching. Covered with short, white down, very scanty on underparts, with only a slight tinge of buffy down on upperparts. Loes and space around eyes naked. Cere pale pinkish-tan; tarsi whitish yellow. Eyes open within hours of hatching; irises brown. Able to crawl to edge of nest to defecate, and to raise head and stretch neck to receive food; orient toward female in response to feeding Chuckle Call (see Sounds: vocalizations). Hatchlings utter faint Begging Call and Discomfort Chitter Call. Mean mass at hatching 23.8 ± 3.3 (SD) g, and sexes similar ($n = 23$; RBM). On average, oldest nestling in brood 4 d older and 2.5 times heavier than youngest sibling when the latter hatches (MacWhirter 1994). At hatching, culmen 6.1 ± 0.6 (SD) mm, tarsus 19.9 ± 0.8 (SD) mm, wing chord 18.8 ± 0.9 (SD) mm ($n = 23$; RBM). Linear measurements do not vary significantly with sex or position in hatching order (RBM).

Growth and development. From MacWhirter 1994, except where noted.

MASS INCREASE. Rates highest between 5 and 20 d for both males (19.5 g/d) and females (26.3 g/d). Females increase body mass significantly faster than males, although both reach near-asymptotic size at approximately the same age; sexes distinguishable via body mass at 17–20 d. Size hierarchy within brood established through asynchronous hatching usually persists throughout most of the nestling period, as males and females rarely gain a body-mass advantage over older same-sex siblings, and males never assume a higher size-rank than older female siblings. Females supercede the size-rank of at least 1 older male sibling only after 15–20 d of age. Females 32% heavier than males when they begin flying (520 vs. 394 g). Although Sealy (1967) noted a drop in body mass prior to fledging in Alberta, such a drop not evident in New Brunswick (RBM). See also Fledgling Stage, and Measurements, below.

GROWTH OF BODY PARTS. From MacWhirter 1994, except where noted. Culmen grows rapidly until

20 d; sexes distinguishable in this respect at 15–18 d; at fledging, 14% longer in female than in male (Saunders and Hansen 1989). Rates of tarsus growth highest in male between 5 and 16 d (3.6 mm/d), in female between 5 and 18 d (3.9 mm/d); tarsus grows significantly faster in females than in males; sexes distinguishable at 22–25 d. At first flight, tarsi 10% longer in females than in males. Sexes distinguishable based on tarsal thickness at 11–14 d (Hamerstrom 1968, RBM). Tail feathers emerge at 9–10 d. After 10 d, wing-chord length and tail length are linear functions of nestling age. Wing-feather growth rates slightly higher among females (10.0 mm/d) than males (9.2 mm/d), but tail-feather growth rates identical (7.4 mm/d). Within broods, a positive correlation between growth rates of females and males. Growth in females more variable and more strongly negatively associated with correlates of acute or chronic food shortages and increased mortality (including high precipitation, late hatch date, and late positions within the laying sequence) than is growth in males. Nestling growth not associated with brood size.

MOLT INTO JUVENAL PLUMAGE. Begins during second week. At 7 d, sheathed feathers appear at tips of wings; at 15–16 d, those feathers begin to emerge from sheaths, with sheathed feathers dense on back, shoulders, breast, and tail (Saunders 1913). See also Parental Care, and Appearance: molts and plumages.

CONTROL OF BODY TEMPERATURE. No data. Probably coincident with the cessation of diurnal brooding at 14 d (except when raining).

BEHAVIOR AND LOCOMOTION. By 10 d, nestling will turn over onto back and strike defensively with talons and bill or walk from nest when approached (Sealy 1967). After 15–20 d, spends much time in surrounding vegetation, returning to the nest when parents arrive. By 21 d, stands upright, walks well, and capable of feeding self (Simmons et al. 1987, RBM). Stretches and flaps wings vigorously by 21–25 d. First flights, which occur at 27–35 d, are brief vertical springs of 1–4 m. Within 1–2 d, flights extend horizontally from the nest for up to several dozen meters as young begin intercepting parents with prey (Bildstein 1992, MacWhirter 1994). See Fledgling Stage.

Although nestlings attempt to seize food from siblings, extensive observations ($n > 1,000$ h) do not indicate strong intersibling aggression, even under food-stressed conditions, and siblicide is very rare (RBM). Nestlings (and mothers) sometimes cannibalize siblings that have died (Breckenridge 1935, Lumsden 1981).

PARENTAL CARE

Brooding. From RBM. By female only, beginning immediately after hatching. Diurnal brooding ends

variably when oldest nestling is about 12–14 d, but female will brood older young in rain. Nocturnal brooding continues until 28–30 d, shortly before offspring begin flying. Female also stands with outspread wings to shade or shelter nestlings from rain or direct sunlight. Brooding decreases and shading increases with increasing ambient temperature; time spent brooding lowest, and that spent shading highest, in early afternoon.

Feeding. Male provides all food to female during incubation and virtually all food until nestlings 10–14 d old (Martin 1987, Simmons et al. 1987, Sutherland 1987). Polygynous females begin hunting and providing food to offspring earlier in the nestling period than do monogamous or primary females (Simmons 1983, RBM). During the nestling period, males ($n = 10$) provide about 67% of the food items delivered to monogamous and primary broods, and progressively smaller proportions to broods of later-settling harem females (Saunders 1986, RBM). Female's time spent foraging and contribution to food provided to nestlings are inversely proportional to her mate's provisioning rate (Simmons et al. 1987, E. J. Temeles in litt.). Approximately one-third of all nests are deserted by the male prior to the time nestlings begin flying (Simmons et al. 1987). Desertion is probably influenced by male physiological condition, and not linked to pursuit of additional mates. Over the entire period of parental care, monogamous males and females each provide about half of the food items delivered to offspring (RBM).

When female is near nest, male transfers prey to her by an aerial pass (see Fig. 5), and she generally delivers food to nestlings (MacWhirter 1985, Simmons et al. 1987). If female is absent, male will drop prey at the nest, but he does not feed nestlings; leaves within 15 s (Breckenridge 1935, Simmons et al. 1987). Female is responsible for apportioning food within the brood, at least prior to fledging, and does so even after offspring are capable of feeding themselves at 17–23 d (Barnard 1983, RBM). Female tears food into small pieces, and nestlings take food from her bill. Females do not favor the smaller nestlings in feeding (Breckenridge 1935, RBM). Older, larger siblings consume more food, particularly when nestlings are <2 wk of age and provisioning rates are relatively low (MacWhirter 1994). Older nestlings consume small (≤ 25 g) prey whole, especially when female is absent (see Fledgling Stage, below).

Young fed same food as adults eat (see Food Habits: diet, above). At some locations (Sutherland 1987), but not others (RBM), prey size increases with nestling age, probably due to increasing female participation in capturing prey and changing prey availabilities (Sutherland 1987).



Figure 5.
Aerial transfer
of prey (male
to female)
occurs
regularly
among
breeding
pairs of the
Northern
Harrier.
Drawing by
Tony
Henneberg.

Initial food delivery occurs within 2 h of sunrise, and deliveries continue steadily throughout daylight hours on most days (RBM, KLB). Food items virtually always delivered singly. Most items 20–80 g; large prey brought to nest in sections, usually of <200 g each (RBM). In North America, average feeding rate during nestling period 1.26 items/hour (range 1.03–1.79, $n = 5$ broods; Simmons et al. 1987). Feeding rates vary with number in brood, and may increase significantly with nestling age if food is abundant (Sutherland 1987, RBM). Average feeding rate in fledgling period 0.89 items/hour ($n = 22$ broods; RBM). Feeding rates are significantly reduced during moderate to heavy rains (Barnard 1983, MacWhirter 1985).

Nest sanitation. Nestlings defecate beyond edge of nest. Female removes uneaten food, skeletal remains, and pellets. Damaged eggs removed and may be eaten by female; unhatched eggs usually left in the nest, at least until late in the nestling period (RBM). Adult carrion beetles (*Nicrophorus*, *Silpha*) present in some nests (Hamerstrom 1986, RBM).

Parental carrying of young. Females retrieve displaced nestlings (<10 d) when young ≥ 0.5 m from nest. Carried in bill by the nape; movements slow and deliberate (Lumsden 1981, RBM).

COOPERATIVE BREEDING

Does not occur.

BROOD PARASITISM

An active Northern Harrier nest contained 5 Northern Harrier eggs and 2 Redhead (*Aythya americana*) eggs in Alberta (Fleskes 1992). Laine (1928) observed a female Northern Harrier on a nest of 12 prairie chicken (*Tympanuchus*) eggs. Clutches of 9–12 Northern Harrier eggs may represent the efforts of 2 females (Bildstein 1988).

FLEDGLING STAGE

Departure from the nest. From MacWhirter 1994, except where noted. Nestlings become ambulatory at about 2 wk of age, at which time they begin moving into the surrounding vegetation, creating narrow paths between the nest and ancillary resting and feeding platforms (Hecht 1951, RBM). Typically, use of nest for feeding, brooding, and roosting declines throughout latter half of nestling stage. Older juveniles (4–5 wk old) make brief flights near the nest, although the nest may be visited after flying begins; may also roost singly in vicinity of nest for 2–4 wk after flying. At 8 nests in Wisconsin, 7 males with siblings began flying at 29 ± 2.1 (SD) d of age; 14 females with siblings at 32 ± 3.8 (SD) d; a female with no siblings at 35 d. Males in all-male broods began flying 1.8 d earlier than those in mixed-sex broods; females in all-female broods began flying 1.4 d later than those in mixed-sex broods (Bildstein 1992). In New Brunswick, by contrast, the ages at which males and females began sustained flights were, on average, 33 d (range 29–37, $n = 18$) and 37 d (range 34–45, $n = 18$), respectively. Among males, but not females, individuals hatched late within large broods (≥ 4) begin flying at a younger age than those hatched early. Age at first flight is inversely correlated with growth in body mass and tail length. Food supplements advanced by 2 d the age at which females, but not males, began flying.

At fledging, females as heavy as adults, and males (16%) heavier than breeding adult males. Culmen $\geq 91\%$ that of adults. Median wing-chord length at time of first flight 78% (male) and 83% (female) of average wing-chord length among adults migrating in spring, and median tail length 75% (males) and 77% (females) of average tail length of adults.

Growth. No data. Extrapolation of linear growth-rates of wing and tail feathers at fledging suggest that juveniles attain adult size in these dimensions before independence. See Young Birds, above.

Association with parents or other young. From Beske 1982, Bildstein 1992, and RBM, except where noted. Parents roost away from the nest area and interact with offspring only to deliver food. Fledglings roost close to, but not with, siblings; do not follow parents on hunting flights. Siblings perch together within 50 m, occasionally fly in tandem,

and frequently chase and supplant one another, especially when parents return with prey and prey robbery is attempted. Interactions with unrelated fledglings are rare, even when they are <200 m apart for several weeks. Parents can discriminate their own offspring from foreign fledglings, as parents chase and strike intruding fledglings but not their own (Simmons et al. 1987). Brood-switching by fledglings rare (<2%, $n = 54$ birds).

In New Brunswick, family break-up quite synchronous (≤ 3 d) within broods, and does not appear to vary with brood size or offspring sex. Feeding rates decrease gradually, but offspring continue to receive food up to the point of break-up. Parents do not drive young from vicinity of nest. Among 20 broods, all siblings were present in the natal area on the last day parents were observed delivering food to fledglings. In Wisconsin, duration of family break-up is protracted, and highly variable among broods. Juveniles become independent of parents (usually mother) at a younger age in Wisconsin (6.5–8 wk) than in New Brunswick (7.5–9.5 wk). Siblings depart as individuals from the natal area, usually late in the day, and migrate alone. Parents may remain in the area after juveniles leave.

Ability to get around, feed, and care for self. See Young Birds, above. From Bildstein 1992 and RBM, except where noted. Although the center of activity may move several hundred meters from the nest, fledglings spend most of the day waiting on elevated perches for their parents to return with food; usually <20% of the day is spent flying. Most flights appear to be exercise flights in which the birds fly in wide circles before returning to their original perch site. Fledglings do not fly for >10 min at a time, even when soaring several days before departure from natal area.

Once capable of flying, males precede females in all measures of behavioral development, including flights/hour and duration of flights. In Wisconsin, 6 male fledglings took their first minute-long flight 9 d earlier (at age 35 vs. 44 d) than did 14 females, and perched at least 50 and 400 m from the nest 4–6 d earlier than did females. All males had departed the immediate vicinity of the nest (and parental care) by 47 d of age; 9 of 14 females did so 1–6 d later. By contrast, physical development and maturation of flight skills are slower, and independence from parents is achieved at an older age, in New Brunswick (males 59 d, females 63 d; $n = 36$ fledglings) than in Wisconsin.

Once all siblings are capable of flying, virtually all food items are exchanged by an aerial pass, and prey usually are relinquished to the first fledgling that reaches the parent. Ability to secure food from parents is strongly influenced by the sequence in which siblings begin flying (MacWhirter 1994).

Fledglings practice prey capture by pouncing on apparently inanimate objects, but spend little, if any, time hunting, and rarely capture live prey prior to independence (Linner 1980, Beske 1982, RBM).

IMMATURE STAGE

Few data. See Migration, above; also Food Habits: feeding, above; and Demography and Populations: measures of breeding activity, below.

DEMOGRAPHY AND POPULATIONS

MEASURES OF BREEDING ACTIVITY

Age at first breeding. In Wisconsin, 16% of 268 breeding females were yearlings, and in New Brunswick, 23% of 116 of females were subadults (≤ 2 yr; Hamerstrom et al. 1985, RBM). In both areas, the proportion of young females in the breeding population was independent of vole abundance (Hamerstrom et al. 1985, Simmons et al. 1986a). In Wisconsin and New Brunswick, 8% of 210 and 5% of 130 breeding males, respectively, were yearlings; the number of breeding yearling males increased with increasing vole abundance (Hamerstrom et al. 1985, Simmons et al. 1986a, RBM).

Clutch. Mean clutch size 4.4 ($n = 1,174$); no pronounced geographical trends (range 3.7–5.5, $n = 16$ studies; e.g., Hammond and Henry 1949, Apfelbaum and Seelbach 1983, Simmons et al. 1986a, F. Carpenter in Bildstein 1988, Kantrud and Higgins 1992). In New Brunswick, clutch size is positively correlated with spring vole abundance and pre-hatch food-provisioning rates of males (Simmons et al. 1986a), but is unrelated to small-mammal prey availability in female territory (Simmons 1988b). Adult females lay marginally larger clutches (mean 4.4, $n = 47$) than subadult females (4.2, $n = 17$; Simmons et al. 1986a). In New Brunswick and n. Great Plains of U.S. and Canada, clutch size declines progressively with season (Simmons et al. 1986b, Sutherland 1987, Kantrud and Higgins 1992). Seasonal declines may explain tendency of polygynous females to lay smaller clutches relative to primary and monogamous females (Simmons et al. 1986b).

Annual and lifetime reproductive success. Annual reproductive success (mean number of offspring fledged/pair) of all nests and of successful nests averaged 1.8 and 3.1, respectively (Appendix 2).

In New Brunswick, reproductive success most strongly predicted by male food-provisioning rate and laying date, and to a lesser extent by clutch size (Simmons et al. 1986a, Barnard et al. 1987). Reproductive success moderately, but not significantly, correlated with vole abundance in Aug (Simmons et al. 1986a, see also Burke 1979, Hamerstrom et al. 1985). Absence of strong correlation due to shift in

Table 1. Measures of Northern Harrier reproductive success in North America. Number of eggs or nestlings given in parentheses.

LOCATION	HATCHING SUCCESS ¹	NESTLING SUCCESS ²	FLEDGING SUCCESS ³	SOURCE
Alberta	57 (49)	75 (28)	43 (49)	Sealy 1967
Saskatchewan	68 (85)	83 (58)	56 (85)	Sealy 1967
North Dakota	59 (140) 58 (303)	77 (83) 20 (175)	46 (140) 12 (303)	Sutherland 1987 Hammond and Henry 1949
Missouri	70 (79)	60 (55)	42 (79)	Toland 1986a
Michigan	32 (56)	89 (18)	29 (56)	Craighead and Craighead 1956
New Brunswick	76 (417)	68 (319)	52 (417)	RBM

¹Percent eggs laid that hatched.
²Percent nestlings hatched that fledged.
³Percent eggs that yielded fledglings.

prey taken at or near time of Northern Harrier hatching, when increased availability of young passerines boosts prey base, especially when voles are scarce (Barnard et al. 1987). Nestling success (proportion of nestlings hatched that fledged) significantly higher, however, in the increase phase (81%) than the decrease phase (65%) of the vole cycle (Simmons et al. 1986a, RBM, see also Hamerstrom et al. 1985).

Although nestling success is negatively correlated with amount of rainfall, annual reproductive success is not strongly affected in New Brunswick (Simmons 1988b, RBM). Ground moisture and vegetation have a significant effect on nest success (proportion of clutches yielding ≥ 1 fledgling), whereas visibility plays no role. Wettest sites significantly more successful than dry sites because of reduced predation on the former (Simmons and Smith 1985; see also Thompson-Hanson 1984). Nests in forbs are significantly more successful than those in shrubs. Nest concealment may be an important factor in upland areas (see Sutherland 1987).

Among males in Wisconsin, annual success of all adult males 30% higher than that of subadult males (2.6 vs. 2.0; Hamerstrom et al. 1985). Among females in both Wisconsin and especially New Brunswick, reproductive success only marginally higher among adults (Hamerstrom et al. 1985, Simmons et al. 1986a). In New Brunswick, however, vole abundance differentially affected females of the 2 age-classes. During vole highs, subadult females were significantly more productive (3.4) than adult females

(2.2), whereas the converse was true in vole lows (1.2 vs. 2.2). Variance in reproductive success is higher among males: in New Brunswick, males reared 0–10 offspring/yr, females 0–5 offspring/yr (Simmons et al. 1986b). In Wisconsin, polygynous males reared up to 8 offspring/yr (Hamerstrom et al. 1985).

On average, polygynous males produced 70 and 62% more offspring than did monogamous males in Wisconsin and New Brunswick, respectively (Hamerstrom et al. 1985, Simmons 1988a). Conversely, female reproductive success tended to decline with increasing harem size (Burke 1979, Hamerstrom et al. 1985, Simmons 1988b). Specifically, the success of primary females, but not of other harem members, is as high as that of monogamous females; reduced success of polygynous females is best explained by low male-provisioning rates, rather than by laying date (MacWhirter 1985, Simmons et al. 1986b).

In general, most (56%, $n = 696$) offspring deaths and about 70% of nest failures occur before hatching (RBM; see Table 1 and Appendix 2). In New Brunswick and n. Great Plains, predation and nest abandonment are responsible for most egg loss, starvation for most nestling loss (Simmons et al. 1986a, Sutherland 1987, Kantrud and Higgins 1992). In New Brunswick, annual nestling mortality rates due to starvation varied between 10 and 54% of nestlings ($n = 10$ yr; MacWhirter 1994). Starvation was significantly higher in male-deserted than nondeserted nests, probably because most such females were unable to compensate for lost food

provisioning of the male (Simmons et al. 1987). In N. Dakota and New Brunswick, similar proportions (about 10%) of clutches were abandoned by both parents (Sutherland 1987, Simmons et al. 1986a). In New Brunswick, abandonment accounted for 29% of 31 nest failures (Simmons et al. 1986a).

No data on lifetime reproductive success.

LIFE SPAN AND SURVIVORSHIP

Among 114 banded birds, mean age at death 16.6 mo (Keran 1981). Longest lifespan reported: 16 yr 5 mo (Bildstein 1988). Greatest reported known age of (female) breeding bird in North America: 8 yr (RBM). Pre-1950s mortality rates estimated as 59% in first year and 30% among adults (Bildstein 1988).

DISEASE AND BODY PARASITES

From references in Serrentino 1992, except where noted. Cholera-induced mortality rare and localized. Single report of Northern Harrier suffering avian botulism (*Clostridium botulinum*) in s.-central Manitoba (Manuwal 1967). Adult carrion beetles observed feeding on young live nestlings. Parasitic biting lice (*Colpocephalum flavescens*, *Degeeriella fusca*, *Philopterus taurocephalus*) and hippoboscids louse flies (*Lynchia americana*, *Ornithomyia fringillina*, *Ornithoica vicina*) reported on Northern Harriers. Data suggest that the prevalence of insect-borne haematzoa (e.g., *Haemoproteus*, *Leucocytozoon*, *Plasmodium*) much lower than among other accipitridae and North American birds in general (Greiner et al. 1975, Peirce et al. 1990). Helminth species include 2 intestinal trematodes (*Neodiplostomum* sp. and *Strigea falconis*) and 3 nematodes (*Cardiofilaria inornata*, *Cyrrnae* sp., and *Tetrameres robusta*). No cestodes or acanthocephalans detected in sample, nor evidence of pathology in individuals examined ($n = 2$; Taft et al. 1993).

CAUSES OF MORTALITY

Few data. Mortality rates <5% among fledglings (Sutherland 1987, MacWhirter 1994). See also Behavior: predation, above.

RANGE

Natal philopatry. Virtually no fidelity by offspring to their natal area or contribution to the local breeding population (Hamerstrom 1969, RBM). In Wisconsin, 1% of 739 nestlings were recaptured in the study area, and only 0.5% were found breeding in a later year (Burke 1979). No data on distance from natal site to first breeding site.

Fidelity to breeding site and winter home range. From Hamerstrom 1969 and Burke 1979. In general, low fidelity to breeding site. Nomadic (see Population Status, below). In Wisconsin, few (30–36%, $n = 88$) banded breeding adults returned to their

nesting area in subsequent years. Of those males that did return, most returned once only. Among birds that returned to breed in the study area, males settled closer (mean = 546 m) than females (1,092 m) to previous nest sites. Young females (≤ 3 yr) move farther than old females from a previous nesting site; no age-class differences among males. Among males and females, successful breeders are more likely than failed breeders to return to the study area.

No data on fidelity to winter home range, although the occurrence of communal roosts at the same location in subsequent winters suggests there may be some.

Home range. In breeding season, averages vary considerably among sites, owing to differences in food supply and habitat (170–15,000 ha, median 260 ha, $n = 8$ studies; Smith and Murphy 1973, Rees 1976, Toland 1985a, Martin 1987, Serrentino 1987). Typically, females forage closer to the nest than males do (Hecht 1951, Barnard 1983), and their home ranges are usually smaller than those of males (Craighead and Craighead 1956, Thompson-Hanson 1984, Martin 1987). Males known to hunt ≥ 10 km from the nest (Barnard 1983, Thompson-Hanson 1984), with ranges overlapping those of other males. Both sexes reported to increase home range by factor of >2.5 as the nestling period progresses (E. J. Temeles in litt.).

In California, wintering males occupy significantly larger hunting ranges than females do (E. J. Temeles in litt., KLB), possibly because males use a nonterritorial strategy and use areas that have lower prey densities or areas with preferred prey that differ from those of territorial females (E. J. Temeles in litt.). See also Behavior: spacing, above.

POPULATION STATUS

Numbers. Species is nomadic; densities in breeding and nonbreeding seasons vary in response to local changes in prey availability (e.g., Craighead and Craighead 1956, Grant et al. 1991). In New Brunswick and Wisconsin, and probably elsewhere (e.g., Clark 1972), breeding numbers fluctuate annually in synchrony with the abundance of voles in spring (Hamerstrom et al. 1985, Simmons et al. 1986a). Short-term studies in w. U.S. suggest very low (< 0.1/10 km²) nest densities in dry shrub-steppe and cold desert habitats (Appendix 3), although small, dense populations have been reported in shrub-steppe habitat (e.g., Martin 1987). Dry grasslands of n. Great Plains and mid-w. U.S. appear to support intermediate densities of breeding birds (Appendix 3), although localized, high-density populations also reported there (Sutherland 1987). Wet grasslands and marshes appear to support the highest breeding densities (Appendix 3). Conse-

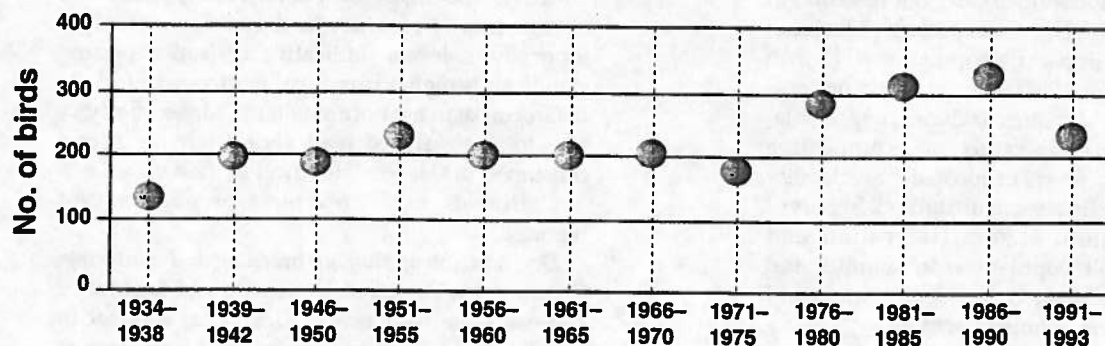


Figure 6. Fall counts of Northern Harriers migrating past Hawk Mountain Sanctuary, e. Pennsylvania, 1934-1993. Counts depict 5-yr averages, except for 1939-1942 and 1991-1993. Counts were not conducted in 1943, 1944, and 1945.

quently, although short-term studies suggest that the productivity of dry upland prairies may be high (>20 fledglings/10 km²; Toland 1986a, b, Sutherland 1987), long-term studies indicate that the productivity of predominantly wet marshlands in New Brunswick (6.6 fledglings/10 km²; RBM) is about 3 times higher than the dry, "non-marshy" grasslands of Wisconsin (1.9-2.2 fledglings/10 km²; Follen 1975, Hamerstrom et al. 1985). Regional variation in the relative importance of nesting habitat and prey availability as factors limiting nesting density has not been examined.

According to Root (1988), densest early-winter populations occur in s. Great Plains and Great Basin of U.S. Great Plains populations are especially high along the Pecos River in sw. Texas, in e. New Mexico, s. Colorado, w. Missouri, and throughout much of Oklahoma and Kansas. In the Great Basin, most abundant around Great Salt Lake and in Oregon. Also, high concentrations in grassland habitat of San Joaquin Valley, CA. Winter population densities of 1.3 and 4.6 birds/10 km² reported in Michigan and Ohio, respectively (Craighead and Craighead 1956, Bildstein 1987).

Breeding Bird Survey (BBS) data indicate that numbers are highest (1.1-1.9 birds/route) in the provinces and states of the n. Great Plains (Alberta, Saskatchewan, Manitoba, Montana, N. and S. Dakota; Robbins et al. 1986, Collins and Wendt 1989). Winter population in the Canadian provinces and contiguous states of U.S. estimated to be 111,500 birds, based on extrapolation of Christmas Bird Count (CBC) data (Johnsgard 1990). In Texas, California, and Arizona, estimated winter populations of 20,000, 13,200, and 9,900 birds, respectively. Presumably the summer population in North America exceeds 111,000 because an unknown component winters in Central America and Caribbean islands (Johnsgard 1990). Using primarily BBS data, Kirk et al. (1995) estimated that there are 20,000-50,000 breeding pairs in Canada.

Trends. Number of breeding Northern Harriers in North America has declined in twentieth century,

apparently owing mostly to loss of habitat through extensive draining of wetlands, monotypic farming, and the reforestation of farmlands (U.S. Fish and Wildlife Service 1987, Serrentino 1992). In the conterminous U.S., CBC data from 1952 to 1971 indicate a 40% decline in winter for that period, but with local increases, particularly in California, in the 1960s (Brown 1973). BBS and CBC data suggest that since the early 1960s the North American population has remained stable or declined slowly (Collins and Wendt 1989, Kirk et al. 1995), with significant regional declines in sw. and central U.S. (U.S. Fish and Wildlife Service 1987), and a statistically nonsignificant decline in ne. U.S. (Smith et al. 1993). In Canada, BBS data suggest long-term significant increases in western mountain provinces, with declines in the prairies, particularly during 1982-1991; elsewhere, numbers stable (Kirk et al. 1995).

Migration counts in Minnesota and several sites in w. U.S. suggest declines of about 3%/yr in these areas since late 1970s (Hoffman et al. 1992, Hussell and Brown 1992). Long- and short-term data from migration routes in Great Lakes region and e.-central U.S., however, reveal local increases or stability (Duncan 1986, Bednarz et al. 1990, Titus and Fuller 1990, Hussell and Brown 1992). Fall counts at Hawk Mtn., PA, from 1934 through 1991 (Fig. 6), for example, indicate nonsignificant increases from 1934 to 1942 (pre-DDT era), and from 1946 to 1972 (DDT era), and a nonsignificant decrease from 1973 to 1991 (post-DDT era; Bednarz et al. 1990, Hawk Mountain Sanctuary unpubl. data). Overall, numbers there increased slightly but significantly between 1934 and 1991. See also Hands et al. 1989, Martin 1989, Bildstein and Collopy 1990, and Serrentino 1992 for detailed regional accounts.

POPULATION REGULATION

Locally, nesting numbers and reproductive success are affected by prey availability, predation, nest-site quality, and weather (see Measures of Breeding Activity, and Population Status). The reason, or reasons, for the lack of large breeding

populations in the se. U.S. remain unknown. Loss of suitable nesting habitat (including reforestation of farmland in the East) has had, and probably continues to have, a negative impact on populations (U.S. Fish and Wildlife Service 1987). Factors affecting local winter-population densities include prey availability, snow cover, temperature, and competition with other raptors; effects of roost-site availability on population density remain unstudied. Impact of humans and natural factors (starvation and predation) on adult populations in summer and winter quarters not studied. See Conservation and Management: effects of human activity.

CONSERVATION AND MANAGEMENT

EFFECTS OF HUMAN ACTIVITY

Shooting and trapping. Earlier in twentieth century, when North American raptors were characterized as either "objectionable" or "beneficial" depending on their diet, Northern Harriers (because they feed largely on mice) were generally considered beneficial, and as such were rarely singled out as targets of predator control. Nevertheless, shooting pressure has been and remains a threat to certain North American populations, especially birds wintering at communal roosts in se. U.S. and Texas (KLB).

Pesticides and other contaminants/toxics. Across continent, eggshell thickness and mass were significantly lower between 1947 and 1969 than before 1947. Egg mass and thickness declined by about 19% in w. U.S. and by about 12% in e. and interior North America; attributed to organochloride pesticide contamination, particularly the metabolite of DDT, DDE (Anderson and Hickey 1972). Reproductive failure and population decline linked to use of organochloride pesticides in mid-twentieth century; population recovered relatively quickly following the regulation of DDT in early 1970s (Hamerstrom 1969, 1986). In Canada, 17% of eggs collected in late 1960s had critical levels of DDE, with lower levels of dieldrin, heptachlor epoxide (HE), and mercury; in 1980s, relatively low levels of organochlorines in tissues, yet levels high enough to cause eggshell thinning (Noble and Elliot 1990). No data on reproductive effects. In Oregon, at agricultural sites where HE once used as a wheat-seed treatment, all eggs contained pesticides (e.g., HE, DDE), but levels lower than those suspected of lowering reproductive success (Henny et al. 1984).

In n. Idaho, 5 yr after the closure of a 100-yr-old ore smelter, nestlings had blood lead concentrations no higher than a control area, in part because nestlings consume few bones, where lead occurs in prey

species. Lead poisoning may affect adult Northern Harriers, who digest most bone (Henny et al. 1994).

Ingestion of plastics, lead, etc. Few data. Protoporphyrin levels, indicative of lead exposure, significantly higher from nestlings from control site in Oregon than near ore smelter in Idaho, probably due to exposure to lead shot from waterfowl consumed in Oregon (Henny et al. 1994).

Collisions with structures or objects. Not reported.

Degradation of habitat: breeding and wintering. Continued widespread destruction of freshwater and estuarine wetlands in U.S. poses a threat to breeding and wintering populations. Conversion of native grassland prairies for monotypic farming has contributed to local population declines, and remains a major threat to populations (e.g., Duebbert and Lokemoen 1977, Toland 1985b). In upland areas, mechanized agriculture and early mowing have increased the threat of nest destruction. Overgrazing of pastures, and the advent of larger crop fields and fewer fencerows, together with the widespread use of insecticides and rodenticides, have reduced prey availability and thus the amount of appropriate habitat for the species (Duebbert and Lokemoen 1977, Hamerstrom 1986, KLB). In the Great Plains, Southwest, and U.S. Intermountain West, Northern Harriers reduce their use of livestock-grazed grasslands (Linner 1980, Bildstein 1987, Bock et al. 1993). In ne. U.S., loss of open habitat (through the destruction of wetlands and reforestation of agricultural lands) and restriction of nesting to predator-free offshore islands are the primary causes of the population decline (Serrentino 1992, Veit and Petersen 1993).

Nevertheless, Northern Harriers are food and habitat generalists, and the relative stability of the species in the second half of the twentieth century suggests that future changes in species status are likely to be indicative of widespread disfunction of both the upland and wetland habitats upon which this species depends.

Disturbance at nest and roost sites. In agricultural areas, nests are destroyed by livestock (trampling), haying, and other agricultural practices (Hamerstrom 1969, Henny et al. 1984). Haying activities near nests may cause parents to desert (Hamerstrom 1969, RBM).

Human/research impacts. In New England, Northern Harriers leave wintering areas with potentially suitable nesting habitat presumably in part because of heavy use of coastal areas by humans (Serrentino 1992). In Ohio, wintering birds avoid areas near active farms (Bildstein 1987). In New Brunswick, 45% of 20 nests discovered with ≤ 2 newly laid eggs were deserted, whereas none of 15 nests found with ≥ 3 fresh eggs were deserted (RBM).

Regardless of size, recently laid but complete clutches ($n = 35$) were not deserted following discovery (RBM). Of 9 nests destroyed by predators or deserted in response to human interference during egg-laying, 44% of pairs re-nested elsewhere within their territory (RBM). Parents desert nests when observation blinds are placed near nests (5–8 m) before hatching, but rarely after hatching (Simmons 1983, RBM). During the nestling period, 75% of 21 pairs "tolerated" a blind near their nest; remainder behaved erratically when blind was occupied (Saunders 1986, RBM). In Wisconsin, 40% of 15 nests failed during or after hatching due to trapping of breeding birds (Hamerstrom 1969).

MANAGEMENT

Although population trends vary regionally, overall the species appears to be declining globally (del Hoyo et al. 1995). In North America, Northern Harrier is not on the Federal Endangered or Threatened lists, but since 1972 it has been 1 of 6 species on the National Audubon Society's early-warning Blue List of declining species (U.S. Fish and Wildlife Service 1987). Listed as Endangered in Illinois, Iowa, Indiana, Missouri, New Jersey, Connecticut, and Rhode Island; as Threatened in Tennessee, New Hampshire, Massachusetts, and New York; and as Of Special Concern in Vermont, Michigan, and Wisconsin (Hands et al. 1989, Bildstein and Collopy 1990, Serrentino 1992). Of Management Concern in significant portions of the species' range in U.S., primarily because of its dependence on declining wetland and undisturbed grassland habitats (U.S. Fish and Wildlife Service 1987). Protected under Migratory Bird Treaty Act of 1972.

No conservation measures taken specifically for this species, but wetland preservation for waterfowl and habitat management for upland gamebirds are beneficial (Hamerstrom 1969, Duebbert and Lokemoen 1977). In n. Great Plains, management recommendations include the protection of undisturbed habitat in which annual vegetation and successional plants can grow and dead vegetation is not removed (Duebbert and Lokemoen 1977, Toland 1986b, Kantrud and Higgins 1992). In New England states in which the species is Threatened or Endangered, Serrentino (1987) recommended active maintenance of old fields and shrubby habitats through prescribed burning and grazing to prevent reforestation. Littlefield and Thompson (1987) advocated reducing or eliminating winter livestock-grazing from wetland and grassland ecosystems to improve winter habitat in n. Great Basin. In Iowa, advent of the Conservation Reserve Program has resulted in increased numbers of nesting Northern Harriers (Dinsmore 1988).

APPEARANCE

MOLTS AND PLUMAGES

The following description is for *C. c. hudsonius*. See Cramp and Simmons 1980 for more extensive information on *C. c. cyaneus*. Except as noted, descriptions are based on material in Bildstein 1988 and on examination of museum specimens and birds in the field by KLB.

Hatchlings. Whitish, sometimes faintly pinkish-buffy down, densest dorsally. Within 1 wk, replaced by a second, longer down, which is usually smoke gray and paler above than below.

Juvenal plumage. Juvenal feathers begin appearing during the second week and are essentially fully grown, except for remiges and especially rectrices, by 35–40 d (see Breeding: young birds, above).

Juvenal plumage is somewhat similar to adult female, but darker generally throughout (see Distinguishing Characteristics, above). Although considerable variation exists among individuals, there is no apparent difference between males and females in this plumage. Most of the head and dorsum are blackish brown with a few pinkish-tan streaks on the head; the perimeter of the facial ruff is highlighted light tan, as is the chin. Lower rump and uppertail-coverts are white, with some feathers showing a small and faint tawny central streak. Underparts, which vary among individuals, range from deep rufous-tawny to pale tan, with the latter occurring in late winter and beyond after fading has occurred. Feathers on upper breast have dark, heavy medial streaks, those elsewhere have finer shaft streaks, except along the flanks where streaks are wider. Streaks are more apparent in late winter after fading. Upper surface of wing is as dark as dorsum. Coverts with narrow buff margins; tips of secondaries and proximal primaries grade to whitish, more so on underside. Primaries are narrowly barred dark and white; greater-primary underwing-coverts mixed whitish, very dark or tan; remaining wing-lining buffy tan with dark medial marks. Under surface of secondaries noticeably darker overall than in female, Basic I, and Definitive plumages. Juvenal plumage is retained through the first winter and into spring and summer of the second calendar year. Tail is like that of adult female, but somewhat darker. Juvenal plumage is retained for 9–14 mo.

Basic I plumage. Flight and most body feathers acquired as a result of a protracted complete Prebasic molt beginning in late spring or later in second calendar year, and retained for about 1 yr. Individuals with 2-toned wings (gray outer secondaries and inner primaries, and brown remiges elsewhere) seen by late summer or early fall.

MALE. Quite variable. Differs from Definitive Basic plumage (see below) in that head is darker and browner, with the ends of feathers of the occipital spot having tawny margins; dorsum darker, with scattered tawny and tawny-margined feathers; underparts, especially upper breast, more heavily marked, many with tawny tinge, flanks barred brownish sepia. Smaller upper-coverts of wing tinged buffy brown to tawny. Undersurface of primaries with dark bars or irregular marks. Some underwing-coverts with darkish barring. Tail with tawny splotches on outer feathers. At least some males become progressively paler and less tawny over several molts.

FEMALE. Differs from Definitive Basic plumage (see below) in being darker with fewer conspicuous tawny streaks on head, less tawny overall on upperwing-coverts, and less gray on primaries. Secondaries and associated underwing-coverts form an especially dark patch on the underside of each wing.

Definitive Basic plumage. Definitive Prebasic molt complete. Definitive Basic plumage is acquired over a protracted period beginning in late spring and continuing through early fall (see Fig. 4). Primaries are molted first (inner to outer), then secondaries, then greater upper-coverts of remiges, and tail (inner to outer, except for central pair, which is delayed). Concurrently, new body feathers appear on head and foreparts, then elsewhere. In central Wisconsin, breeding females initiate primary-feather molt in early to mid-May, with males following 2 wk later. Males molt faster than females, with most having completed at least half of their primary molt by late Jun. No evidence that timing of molt is correlated with timing of nesting (Schmutz and Schmutz 1975).

MALE. Head and dorsum light to medium gray with considerable individual variation, some of which is due to age. Facial disk light to medium gray, without distinctively lighter facial ruff as in females. Supraorbital ridge, and sometimes cheek below eye, highlighted with light gray to whitish feathers. Younger males (<3–4 yr) darker dorsally and more often with feathers tinged with brown on nape, back, and scapulars. Gray of extreme upper breast grades to whitish white on lower breast, typically (but not always) with rufous or rusty markings, most of which are transverse, a few longitudinal. Markings are especially prominent on flank feathers. Upper wing matches gray of back, sometimes with lighter coverts. Secondaries have a blackish band distally, edged in white. Distal two-fifths of primaries black, remainder gray. Ventrally, inner webs of remiges white except for blackish tips. Underwing-lining whitish with transverse dark gray markings on greater primary under-coverts. Tail

darkish gray above and whitish below, with central feathers darker gray and barred. Bars on other rectrices darkest on outer web. Distal bars wider than more proximal bars. Feathers tipped in white. Uppertail-coverts form a distinctive white rump patch. Younger birds (<3–4 yr) sometimes with brownish markings distally on outer rectrices.

FEMALE. Head has a light, tan supraorbital ridge; auriculars are tan with dark brown streaks. Facial ruff is outlined with darkly streaked whitish feathers that highlight the facial disk. Supraorbital ridge and cheek below eye similarly highlighted in most individuals. Chin pale buff, crown and nape feathers dark brown with narrow tawny edges. Upperparts dark to blackish brown, with many feathers edged tawny. Uppertail-coverts and rump feathers white, sometimes with faint rusty marks. Dark feathering of dorsum grades to "dirty" white and tan ventrally. Feathers of breast, sides, and flanks often with dark shaft streaks. Upperwing-coverts match dorsum. Remiges mostly dark brown dorsally; ventrally, inner webs whitish, sometimes with faint rusty marks. Primaries with dark to blackish-brown tips and 4–6 dark brown bars medially. Secondaries whitish with 3 dark brown bars; distal one, the widest, has a tawny edge. Underwing-lining like breast and sides; axillars with tan or tawny edges and well-defined midportions. Central rectrices brown and barred gray-brown with tawny tips. Remaining rectrices tinged buff, with each succeeding pair (outward) darker, all tipped tawny, with 4–5 dark bars, except for outermost rectrices which have 6 narrower dark bars.

Aberrant plumages. Although both melanism and albinism have been reported from the Palearctic, neither is known from North America.

BARE PARTS

Bill. At hatching, bill blackish with white egg tooth, which is usually lost in several days; in fledglings and adults, bill dark, becoming bluish basally. Cere is muted flesh color at hatching, yellow by end of week 2; in adults, yellow, sometimes with a greenish tinge.

Iris. Brown at hatching, but with a grayish cast in males and a chocolate to medium-brownish cast in females; this difference reliably distinguishes the sexes at 11–14 d (Hamerstrom 1986, RBM). In males, iris smoke gray at fledging, usually changing to yellow over the course of the second calendar year. In adult males, iris and edge of eyelid are lemon to orange yellow. In females, iris remains brown with yellow flecks in the first year; by end of second calendar year, 50% yellow; by end of third year, mostly yellow (Hamerstrom 1968).

Legs and feet. Vary, possibly in relation to diet, from pale to vivid orange-yellow. Yellow by end of

third week after hatching. Females have thicker and proportionally shorter tarsi than males.

MEASUREMENTS

LINEAR

Bill length. Measured as exposed culmen (mean [in mm] \pm SD), adult male: 16.1 ($n = 48$), 16.4 \pm 0.7 ($n = 22$), 16.4 \pm 0.7 ($n = 10$); adult female: 18.5 ($n = 54$), 19.2 \pm 0.6 ($n = 15$), 19.3 \pm 0.4 ($n = 10$); subadult male: 16.5 \pm 0.8 ($n = 19$); subadult female: 18.8 \pm 0.6 ($n = 20$) (Friedmann 1950, Nieboer 1973, Temeles 1986).

Wing length. Unflattened wing chord (sample mean [in mm] \pm SD, or range), adult male: 340 (328–352, $n = 48$), 343 \pm 8 ($n = 81$), 346 \pm 9 ($n = 10$); adult female: 368 (335–405, $n = 54$), 382 \pm 9 ($n = 140$), 384 \pm 8 ($n = 10$); subadult male: 336 \pm 8 ($n = 27$); subadult female: 376 \pm 10 ($n = 47$) (Friedmann 1950, Temeles 1986, Bildstein 1988).

In Wisconsin, juveniles of each sex have significantly shorter wings than adults. Migrants have slightly longer wings than breeders, probably due to feather wear later in season (Bildstein and Hamerstrom 1980). For flattened wing-chord values, see Nieboer 1973 and Scharf and Hamerstrom 1975.

Tail length. Mean (in mm) \pm SD, adult male: 212 \pm 5 ($n = 23$), 209 \pm 8 ($n = 82$); adult female: 241 \pm 6 ($n = 16$), 235 \pm 7 ($n = 131$); subadult male 214 \pm 8 ($n = 19$), 206 \pm 7 ($n = 25$); subadult female: 241 \pm 8 ($n = 21$), 236 \pm 8 ($n = 48$) (Nieboer 1973, Bildstein and Hamerstrom 1980).

Tarsus length. Mean (in mm) \pm SD, adult male: 72.8 ($n = 48$), 73.6 \pm 2.4 ($n = 20$); adult female: 79.5 ($n = 54$), 81.6 \pm 2.0 ($n = 13$); subadult male: 73.5 \pm 3.1 ($n = 19$); subadult female: 81.6 \pm 2.4 ($n = 20$) (Friedmann 1950, Nieboer 1973).

WING AREA

For 5 males and 7 females, averaged 1,290 and 1,715 cm², respectively (Van Horn 1979). Estimated wing-loading for adult males and adult females in summer was 0.261 and 0.292 g/cm², respectively (Van Horn 1979, reanalyzed by RBM; Bildstein 1988).

MASS

From Bildstein 1988, except where noted. In Wisconsin, mean body mass among spring migrants, adult male: 370 g (range 297–469, $n = 29$); subadult male: 341 g (305–384, $n = 21$); adult female: 546 g (466–752, $n = 52$); subadult female: 511 g (443–594, $n = 25$). Among breeding birds, adult male: 336 g (308–387, $n = 57$); subadult male: 346 g (337–363, $n = 6$); adult female: 513 g (432–621, $n = 93$); subadult female: 500 g (435–654, $n = 24$).

Adults and juveniles of both sexes experience a seasonal decline in mass during spring migration

through Wisconsin; migrating adults heavier than migrating juveniles and breeding adults and juveniles. When timing of passage is controlled, however, adults not significantly heavier than juveniles; suggests that decline in mass reflects loss of migratory fat, or increased metabolic needs in the breeding season (Bildstein and Hamerstrom 1980). In New Jersey, body mass among fall migrants, adult male: 372 g (309–343, $n = 31$); subadult male: 341 (290–466, $n = 191$); adult female: 522 g (420–621, $n = 27$); subadult female: 502 g (470–650, $n = 121$).

OTHER

Saunders and Hansen (1989) provide statistical model for predicting age of nestlings using mass and morphometrics.

PRIORITIES FOR FUTURE RESEARCH

The importance of sky-dancing as a courtship and territorial display throughout the year should be explored further. The roles of adult sex-ratio and female choice as factors influencing polygyny in North America, vis-à-vis Europe, require further study.

Efforts should be made to detail the extent of the breeding range of this species, as well as to monitor populations at the perimeter of the range. Estimates of lifetime reproductive success and of age-specific survival are needed.

Much remains to be learned about the species outside the breeding season. Intensive monitoring of the species at communal roosts, as occurs in Europe, is needed. Such monitoring would provide considerable information regarding the distribution of the sexes and the stability of wintering populations. Communal roosts are also excellent locations for the collection of regurgitation pellets for studies of diet. Conservation needs include assessing the impact of predation on reproduction and monitoring habitat loss and the effects of environmental contaminants on populations.

ACKNOWLEDGMENTS

RBM's research was supported by the American Ornithologists' Union, Hawk Mountain Sanctuary Association, Zeiss Optical, Inc., Canadian Society of Ornithologists, Wilson Ornithological Society, Society of Sigma Xi, Faculty of Graduate Studies at The Ohio State University, and Mount Allison University. KLB's research was supported by the Ohio Biological Survey, American Philosophical

Society, Southern Regional Education Board, and National Science Foundation's Long-term Ecological Research Program. We thank Robert Simmons, Phoebe Barnard, Matthew Saunders, Gay Hansen, Ethan Temeles, and Hawk Mountain Sanctuary for use of their unpublished data. Sandy Gaunt, Borror Laboratory of Bioacoustics, kindly assisted in the preparation of sonograms. Referees Robert Simmons and Ethan Temeles, and editors Alan Poole and Keith Russell, provided many helpful comments. This is Hawk Mountain Sanctuary contribution number 35. Cover photo © B. K. Wheeler/VIREO.

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Appendix 1. Diet of breeding Northern Harriers from selected locations in North America. Tabular figures are percentages of prey items delivered to nests as assessed using direct observations or contents of nestlings' crops. Data from New Brunswick (Barnard et al. 1987), Manitoba (Hecht 1951), Wisconsin (Errington 1933), Iowa (Errington and Breckenridge 1936), and California (Selleck and Glading 1943).

	New Brunswick	Manitoba	Wisconsin	Iowa	California
<i>Microtus voles</i>	70.4	59.7	34.8	2.5	5.3
ground squirrels	0.0	5.5	35.7	38.2	0.0
muskrat	0.5	4.0	0.0	0.0	—
other rodents	0.6	4.0	1.4	0.5	1.4
Leporidae	0.0	2.5	9.2	7.3	11.4
shrews	2.5	0.0	0.8	0.0	0.0
quail	—	—	—	—	11.9
Ring-necked Pheasant	0.0	—	0.0	4.5	0.0
other Phasianidae	0.0	0.0	0.0	1.6	0.0
waterfowl	0.6	1.5	0.0	0.2	0.0
rails, coots	0.0	4.5	0.0	2.4	0.5
doves	0.0	0.0	0.0	2.0	3.2
woodpeckers	0.0	0.0	0.3	4.4	0.2
other nonpasserines	0.0	2.5	0.6	1.8	0.2
sparrows	1.9	2.5	0.8	2.4	17.6
finches	0.0	0.0	0.0	0.0	13.9
other Fringillidae	0.0	0.5	0.0	4.4	3.0
meadowlarks	—	0.0	3.1	5.1	3.2
Bobolink	13.4	0.0	0.0	0.2	—
Red-winged and Yellow-headed blackbirds	1.1	6.5	1.1	7.8	22.8
other Icterinae	0.3	0.5	0.3	3.6	0.2
other passerines	4.2	2.5	7.0	5.6	3.9
frogs	4.4	2.0	4.2	2.9	0.0
snakes	0.2	1.0	0.0	0.0	0.0
lizards	—	0.0	0.0	0.0	1.4
Number of prey individuals	642	201	359	550	438

Appendix 2. Measures of Northern Harrier reproductive success in North America. Hatching rate = % clutches with ≥ 1 egg hatched; nest success = % clutches with ≥ 1 young fledged. - = no data. ARS1 = mean number of fledglings/nest with eggs. ARS2 = mean number of fledglings/successful nest. Sample size (number of clutches or nests) given in parentheses.

Location	Hatching rate	Nest success	ARS1	ARS 2	Source
Alberta	-	-	1.9 (11)	-	Sealy 1967
Saskatchewan	-	-	2.3 (21)	-	Sealy 1967
Washington	-	43 (30)	1.5 (30)	3.5 (13)	Thompson-Hanson 1984
Northern Great Plains (U.S. and Canada)	61 (112)	-	-	-	Kantrud and Higgins 1992
N. Dakota	72 (60) 72 (29)	18 (60) 59 (29)	0.6 (60) 2.2 (29)	3.2 (11) 3.8	Hammond and Henry 1949 Sutherland 1987
N. Dakota and S. Dakota	65 (20)	-	-	-	Duebbert and Lokemoen 1977
Missouri	-	67 (15)	2.2 (15)	3.3	Toland 1986b
Minnesota	-	50 (10)	-	-	Breckenridge 1935
Wisconsin	74 (80)	73 (330)	2.2 (330)	3.0 (241)	Hamerstrom 1969, Hamerstrom et al. 1985
	-	75 (79)	2.8 (79)	3.7 (59)	Follen 1975
Michigan	-	38 (15)	1.3 (15)	3.2	Craighead and Craighead 1956
New York	-	44 (46)	1.0 (46)	2.3 (20)	M. England, cited in Serrentino 1987
New Hampshire	-	79 (15)	2.1 (15)	2.6 (11)	Serrentino 1987
New Brunswick	75 (64) 84 (90)	67 (95) 63 (38)	2.2 (94) 1.9 (36)	3.2 (64) 3.1 (22)	Simmons et al. 1986a, 1987 RBM

Appendix 3. Breeding population densities (nests/10 km²) of the Northern Harrier in selected areas of North America.

Location	Years (n)	Area (km ²)	Density (nests/10 km ²)	Habitat	Source
New Brunswick	10	55	3.1	wet marshlands, cultivated grasslands	MacWhirter 1994
New Hampshire	2	40	1.8	wet and dry abandoned fields, cultivated grasslands	Serrentino 1987
Manitoba	2	10	9.4	wet marshlands	Clark 1972
Minnesota	2	3	19.5	damp meadows, agricultural lands	Breckenridge 1935
Wisconsin	24	167	0.8	dry (drained) marshlands, cultivated upland grasslands	Hamerstrom et al. 1985
Wisconsin	11	92	0.8	dry and wet grasslands, agricultural lands	Follen 1975
Michigan	3	92	0.8	agricultural lands, grasslands	Craighead and Craighead 1956
North Dakota	2	11	13.0	dry upland prairie, agricultural lands	Sutherland 1987
Missouri	2	8	9.4	dry upland prairie	Toland 1986a
Utah	4	210	<0.1	"cold" desert shrubland	Smith and Murphy 1973
Idaho	2	12473	<0.02	"cold" desert shrubland	Howard et al. 1976

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The Birds of North America is supported by charitable and governmental organizations including: The Office of Migratory Bird Management (USFWS), National Fish and Wildlife Foundation, The McLean Contributionship, The Geraldine R. Dodge Foundation, The Richardson Foundation, and the American Birding Association. Benefactors of this program include Wallace C. Dayton and Joseph and Helen Taylor.

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MacWhirter, R. B., and K. L. Bildstein. 1996. Northern Harrier (*Circus cyaneus*). In *The Birds of North America*, No. 210 (A. Poole and F. Gill, eds.). The Academy of Natural Sciences, Philadelphia, PA, and The American Ornithologists' Union, Washington, D.C.



