

*Motacilla  
flava*FRENCH:  
*Bergeronnette printanière*RUSSIAN:  
*Zholtaya Tryasoguzka*ESKIMO:  
*Piorgak, Pshu.kuk, Psu.guk, Pispah*

# Yellow Wagtail

**D**uring the breeding season, the Yellow Wagtail is one of the most conspicuous passerines of the arctic tundra. Its bright yellow coloring, its wagging tail with flashing white outer feathers, its use of elevated perches for observation, pursuit-feeding, singing, and territorial defense, and its loud, sharp, persistent vocalizations when disturbed—all combine to attract the attention of nearly every traveler to northern and western Alaska.

The North American breeding form of this wagtail (*M. f. tschutschensis*) apparently differentiated in the area of the Bering Land Bridge during the Wisconsin glaciation, at which time the emergent land mass supported a tundra-steppe vegetation. Today, this Beringian subspecies breeds on both sides of the Bering Strait, the continental land connection having been broken some 10,000 years ago by rising sea levels at the end of the Pleistocene glaciations.

## The Birds of North America

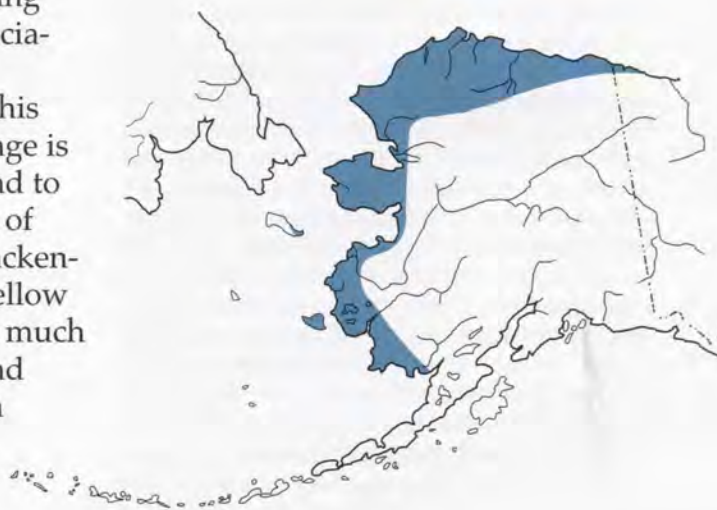
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In North America, this wagtail's breeding range is restricted to Alaska and to the Beaufort Sea coast of Canada east to the Mackenzie River delta. The Yellow Wagtail is common in much of its range in mainland western Alaska and in the western portions

of northern Alaska, but it decreases in abundance farther east. Concentrations of migrants on St. Lawrence Island and on the Seward Peninsula indicate the retention of ancestral migration routes that developed



before the most recent submergence of the Bering Land Bridge.



**Figure 1.** Distribution of the Yellow Wagtail in North America. This species also breeds in Europe and Asia.

Another Asian subspecies of Yellow Wagtail, *M. f. simillima*, is a regular spring-passage migrant in the western Aleutian Islands. Widely distributed and well-studied western Palearctic subspecies of the Yellow Wagtail are especially known for their association with large grazing mammals on wintering grounds, for the formation of huge communal roosts on migration, and for their considerable accumulation of fat during the fall premigratory period.

## DISTINGUISHING CHARACTERISTICS

Medium-sized (17 cm), slender, terrestrial passerine. Two subspecies occur in North America; for differences, see Systematics: Subspecies. In Definitive Alternate (breeding) plumage, underparts yellow, upperparts dark grayish olive, crown gray, white superciliary stripe, speckled or broken dark pectoral band, and outer tail-feathers white (see Systematics: subspecies, below, for differences between North American breeders and ne. Asian migrants). Adults sexually dimorphic in plumage (female similar to male but paler) and wing length (female smaller). In Definitive Basic (winter) plumage both sexes similar but duller overall; upperparts veiled olive. Immatures during first autumn vary; may be similar to adults or duller; underparts often have little yellow, especially in females.

Yellow Wagtail differs from other wagtails in Alaska: Has proportionately shorter tail, more like that of American Pipit (*Anthus rubescens*). Gray Wagtail (*Motacilla cinerea*), a rare visitor to w. Alaska, has much longer tail (>82 mm versus <77 mm in Yellow Wagtail), bright yellow green rump, and in adult males, black chin and throat. Yellow Wagtail easily distinguished in most plumages from White Wagtail (*M. alba*) and Black-backed Wagtail (*M. lugens*), which breed in w. Alaska, by yellow (not white) underparts. Immature Yellow Wagtails with whitish underparts are distinguished from immatures of these species by dark versus white forehead and ear-coverts, and darker gray versus medium gray upperparts. Citrine Wagtail (*M. citreola*), especially immatures, may be very similar to Yellow Wagtail, but note pale forehead, pale-centered ear-coverts, broader supercilium that usually extends around ear-coverts, and in all plumages, dark gray rump and blackish uppertail-coverts.

## DISTRIBUTION

### THE AMERICAS

**Breeding range.** Figure 1. Yellow Wagtail (*M. f. tschutschensis*) is a common breeder in mainland w.

Alaska (mostly confined to coastal uplands; Kessel and Gibson 1978); on e. St. Lawrence I. at Southeast Cape and Punuk I. (Thompson 1967, K. D. Schafer in litt.); and in nw. Alaska in Brooks Range and its northern foothills (Kessel and Gibson 1978). Progressively less numerous eastward in n. Alaska; rare east of 148°W (Byrd et al. 1978, Kessel and Gibson 1978); very rare along Beaufort Sea coast to Mackenzie River delta (Fraker and Fraker 1980, Salter et al. 1980). Casual breeder on w. St. Lawrence I. (Sealy et al. 1971). May breed on Nunivak I. (BK and DDG).

**Winter range.** No winter records in New World.

### OUTSIDE THE AMERICAS

**Breeding range.** *M. f. tschutschensis*: Ne: Asia; tundras and low mountains of Chukchi Peninsula (Zasytkin 1981), forest-tundra of Beringia south to Penzhina and Olyutorskiy Bays (Kistchinski 1988); Anadyr area, west to Kolyma River.

*M. f. simillima*: Kamchatka Peninsula, including northernmost parts of peninsula and n. Kuril Is., upper reaches of Kolyma River and west to Okhotsk (extreme ne. Asia; Dement'ev and Gladkov 1954); regular spring migrant and occasional breeder on Commander Is. (Johansen 1961, Artiukhin 1995). Southern part of Kolyma Mtns. occupied by intergrade populations (Kistchinski 1988).

**Winter range.** Entire winter range for *M. f. tschutschensis* is unknown. A few *tschutschensis* from Point Barrow, AK, and n. and ne. Siberia recorded in Taiwan and Indonesia (see below; Johnstone 1982). In e. Australia, a Yellow Wagtail seen in Derby, w. Australia, 7 Dec 1960 (Lindgren and Slater 1961, Hunt and Standring 1995). Three birds of *tschutschensis* subspecies collected in winter in Indonesia: 1 from Borneo, at Satang I., and 2 from 1 flock near Bogor, w. Java. However, main winter range is outside of w. Indonesia (Johnstone 1982). Presumably winters close to Equator in Sunda Isles and Moluccas (Johnstone 1982).

*M. f. simillima* is regular in w., e., and n. Australia, New Guinea (Gill 1976, McCrie 1987), and w. Indonesia (Johnstone 1982). Collected 11 Jun 1905 on Dawson River in Queensland, Australia (Crawford and Parker 1971); regular in winter to Kerala (India), Sri Lanka, and Andaman Is. (Ali and Ripley 1973), and se. China and Taiwan (Dement'ev and Gladkov 1954). Regular migrant and winterer on Malay Peninsula, south of Singapore (Medway and Wells 1976).

### HISTORICAL CHANGES

No satisfactory evidence of range expansion in North America during last century, although increased field study in recent years has revealed breeding or probable breeding of a few birds near

Beaufort Sea coast as far east in Canada as Mackenzie River delta (Fraker and Fraker 1980, Salter et al. 1980).

#### FOSSIL HISTORY

Tarsus and tibia of a fossil wagtail similar to Yellow Wagtail found in Miocene deposits in central France (Milne-Edwards 1871).

### SYSTEMATICS

Formerly placed in genus *Budytes*. Relationships among morphologically distinct groups within Yellow Wagtail uncertain; some regarded as separate species. North American populations and migrants usually classified with nominate *flava* complex (see Subspecies, below).

#### GEOGRAPHIC VARIATION

Complex, marked variation in coloration, mainly involving head pattern of Alternate-plumaged male. Color of head varies from white to gray to glossy black; white supercilium varies in extent and may be lacking entirely; color of throat varies from yellow to white. Slight variation in size (wing, bill, tarsus, and hindclaw). Vocalizations show broad patterns of geographic differentiation, including placement of syllables in Contact-Alarm Call, structure of Territorial Song, and song phenology (see Sounds: vocalizations, below; Czikeli and Knötzsch 1979). Grouping of populations based on these acoustic characters from data collected in European part of range apparently are more concordant with observed geographic variation than are results of differentiation based on morphology (Czikeli and Knötzsch 1979, Czikeli 1985).

#### SUBSPECIES

Subspecific taxonomy is complex and confusing. The situation is complicated by areas of racial hybridization and rather broad variability of individuals. No good phylogenetic studies on how to partition various forms. One possible arrangement presented by Cramp (1988) recognized 18 subspecies, subdivided into 2 complexes, each sometimes regarded as separate species: *lutea* complex contains 3 subspecies, *flava* complex contains 15. The *flava* complex is further subdivided into 3 groups: *flava*, *feldegg*, and *thunbergi*. The *thunbergi* group includes the 2 races that occur in North America (*tschutschensis*, *simillima*) and encompasses subspecies across n. Europe and Asia. For detailed discussion of geographic variation in Palearctic subspecies of Yellow Wagtail see Johansen 1944, Dement'ev and Gladkov 1954, Dittberner and Dittberner 1984, and Cramp 1988.

*M. f. tschutschensis* Gmelin, 1789. Breeds in ne. Siberia to w. Alaska (see Distribution, above). Characters as described in Appearance, below, and Distinguishing characteristics, above. Compared with *simillima* (see below), slightly smaller (see Appendix); duller above; back grayer; underparts not as intense or as pure yellow; tendency to show broken olive pectoral band. Includes "*alascensis*" of Ridgway.

*M. f. simillima* Hartert, 1905. Breeds in Kamchatka (possibly bred once on w. St. Lawrence I. (Phillips 1991; see also Distribution, above). Primarily spring migrant in w. Aleutian Is. Similar to *tschutschensis*, but slightly larger (especially wing; see Appendix), more intensely yellow ventrally, bright green dorsally; also has less tendency to develop the broken pectoral band that is characteristic of *tschutschensis*. Juveniles probably not identifiable to subspecies. Areas of gradation between *tschutschensis* and *simillima* and their taxonomic relationship with other Asian Yellow Wagtails described in Kistchinski 1980 and Balatsky 1992.

Remaining 16 subspecies in Palearctic: nominate *flava* (central Europe); *beema* (se. Russia from Volga River to Yenisey River); *leucocephala* (nw. Mongolia and n. China); *cinereocapilla* (Italy and nw. Yugoslavia); *iberiae* (Iberian Peninsula and sw. France to nw. Africa); *pygmaea* (Egypt); *thunbergi* (n. Europe and w. Siberia); *plexa* (n. Siberia); *angarensis* (central Siberia); *macronyx* (s. Ussuriland to extreme ne. China and adjacent Russia north of Vladivostok); *zaissanensis* (central Ussuriland in Zaysan area of Irtysh River); *feldegg* (Balkan Peninsula to central Asia); *melanogrisea* (e. Caspian Sea to Ili R., Kazakhstan); *lutea* (lower Volga River of Kazakhstan); *flavissima* (Britain); *taivana* (e. Siberia to shores of Sea of Okhotsk and on Sakhalin I).

Frequent hybridization and gradation among races and subspecies. Subspecies that form hybrids with nominate *flava* include *lutea*, *flavissima*, and *feldegg* (Antikainen and Sorvari 1985; see Panov 1989 for list of hybrid locations). In s. Ussuriland, out of 64 collected individuals, 1 was hybrid *flava* x *taivana*; in ne. Siberia, 11 of 65 (17%) were hybrids (Panov 1989). See Shirihai 1990 for morphological variation in hybrids with Citrine Wagtail. See Cramp 1988 for hybrids in w. Palearctic.

Examination of 17 protein loci in 3 subspecies of Yellow Wagtail complex showed the following results: mean heterozygosity is 0.116 (0.101 in *flava*, 0.063 in *cinereocapilla*, and 0.150 in *feldegg*), 41% of loci polymorphic, and Nei genetic distance among the subspecies 0.0034–0.0054; *cinereocapilla* appears to be intermediate between *flava* and *feldegg*; overall genetic differentiation is congruent with morphological and acoustical grouping (see Czikeli 1985 for more details).

## RELATED SPECIES

Closely related species are Cape Wagtail (*Motacilla capensis*), Madagascar Wagtail (*M. flaviventris*), and Citrine Wagtail, according to Sibley and Monroe (1990).

## MIGRATION

## NATURE OF MIGRATION IN THE SPECIES

Most subspecies, including North American populations, are completely migratory. Southern populations of *pygmaea* may be resident. Primarily diurnal migration; huge aggregations at stopover locations and use of massive communal roosts that facilitate banding have made this species one of the most studied migrants in Palearctic fauna. Species is notable for undertaking long, nonstop (estimated up to 60–70 h) movements over deserts and water areas (see Timing and routes of migration, below). Northernmost Eurasian subspecies winter farthest south; more southern subspecies migrate to northern parts of wintering ranges (Wood 1992 and references therein). See Bell 1996 for discussion of causes of leapfrog migration of Yellow Wagtail.

## TIMING AND ROUTES OF MIGRATION

**Spring.** In spring, *M. f. tschutschensis* usually arrives in w. Alaska in fourth week of May (earliest, 9 May 1947 at Mountain Village [H. C. Kyllingstad in litt.]; 12 May 1967 at Bethel and 17 May 1985 at Kotzebue [BK and DDG]). Migration peaks early Jun; continues to mid-Jun. Migrants reach n. Alaska during last few days of May (earliest: 27 May 1979 at Meade River and 28 May 1972 at Point Barrow; BK and DDG) and easternmost Brooks Range (including Yukon Territory) in early Jun. Numerous on Chukchi Peninsula by 6–7 Jun; arrives Providence Bay second half of May, Plover Bay first days of Jun (Dement'ev and Gladkov 1954).

Spring migrant *M. f. simillima* usually arrive in w. Aleutians in mid-May (7–10 d earlier than *tschutschensis* in n. Bering Sea and mainland w. Alaska); migration peaks during third week of May, with day counts in some years of 15–30 birds, and continues through first week of Jun (BK and DDG). This subspecies occurs on passage along southern coast of Sea of Japan in early May (Dement'ev and Gladkov 1954).

**Fall.** In fall, *tschutschensis* individuals return to Asia across s. Chukchi Sea and n. and central Bering Sea (Bent 1950, BK and DDG), then apparently down Asian coastline to wintering grounds somewhere in s. Asia and East Indies (Étchécopar and Hüe 1983, Anonymous 1987; see below). Migrants (unknown subspecies) also recorded crossing n. Sea of Japan (Kosigyn and Kuzin 1984). Seven

recoveries of Yellow Wagtails that had been banded on Taiwan 15 Apr–8 May (Ostapenko 1981) included 1 in Sakha (formerly Yakutia, ne. Asia) on 11 May; 2 breeding birds in Sakha in Jun; 1 breeding bird near Magadan (ne. Asia), n. Sea of Okhotsk, on 7 Jul; and 2 in central and s. Ussuriland (se. Asia) during fall migration on 25 Aug and 20 Sep, respectively. A bird banded in Taiwan that was erroneously reported (Ostapenko 1981) to have been recovered at mouth of Mackenzie River in n. Alaska was probably a female that had been banded 28 Apr 1966 on Taiwan (Yang River) and collected 26 Jun 1966 on its nest on Meade River, about 100 km south of Barrow, AK (Museum of Vertebrate Zoology no. 156836, P. DeBenedictis).

Fall migration of *tschutschensis* in n. Alaska lasts about 2 wk; starts by early Aug (Kessel and Cade 1958) and ends on e. North Slope of Alaska by mid-Aug and farther west by third week of Aug (BK and DDG). In w. Alaska, lasts about 5 wk; starts early Aug and peaks during last 3 wk of Aug. Last sightings: 10 Sep 1973 and 16 Sep 1977 on Seward Peninsula (Kessel 1989); exceptionally late 23 Sep and 4 Oct 1992 on Nunivak I. (B. J. McCaffery pers. comm.); 18 Oct 1970 in Bering Strait (Watson and Divoky 1972).

Yellow Wagtails (subspecies not known) are very rare fall migrants in w. Aleutian Is. from late Aug to mid-Sep (Gibson 1981; latest 23 Sep 1993 [BK and DDG] and 8 Oct 1880 [Turner 1886]—both at Attu I.), but occur only erratically in autumn in Pribilof Is., on Alaska Peninsula, and in e. and central Aleutian Is., where, if reflecting movement west and south from Alaska mainland, may represent only juveniles that were not successful in reaching Asia (e.g., 6 Aug 1990 at Adak I., 11 Aug 1975 at Unimak I., and 11 Aug 1981 at St. George I.).

Subspecies *tschutschensis* departs Gulf of Anadyr at end of Aug (Dement'ev and Gladkov 1954); last birds leave ne. Siberia 20–22 Aug, where latest record 7 Oct; *simillima* leaves Kamchatka in second half of Aug, and during migration, occurs on Kuril I. to mid-Sep (Kistchinski 1980).

South and east of Alaska breeding range, Yellow Wagtails are casual fall migrants in central and southern coastal Alaska from mid-Aug (earliest: one, 17 Aug 1987, Homer) to mid-Sep (latest: one, 28 Sep 1979, East Copper River delta; BK and DDG). In North America south of Alaska, Yellow Wagtails reported in autumn in British Columbia; casual or rare fall migrants in coastal California. These birds are probably *tschutschensis*, but no specimens document this phenomenon. In British Columbia, single birds reported at Burnaby Lake on 6 Oct 1985 (Kautesk and Jensen 1986) and at Sandspit on 1 Sep 1991 (Am. Birds 46: 139, 1992). In coastal California, 10 records by 1996 (Heindel and Patten 1996; first in

1978 [Morlan 1985])—all of single birds between 27 Aug (National Audubon Society Field Notes: 117, 1997) and 21 Sep (Heindel and Garrett 1995). Elsewhere, extralimital at sea between Chukchi Peninsula and Wrangel I. (1 caught on deck of icebreaker *North Pole*, 12 Aug 1946, at 70°08'N, 177°41'W; Portenko 1973), at Wrangel I. ("April" 1880, *Jeanette* expedition; Newcomb 1888), and in Baja California Norte (one, 22 Sep 1997, near San Quintín; S. N. G. Howell in litt. 1997).

*M. f. simillima* recorded on passage in Nov and May on Hokkaido, Honshu, and Iwo Is., Japan (Brazil 1991); and on Malay Peninsula (Medway and Wells 1976). Adults and immatures of *simillima* and *tshutschensis* recorded as summer visitors in n. Australia; male in breeding plumage recorded on Heron I., Queensland, 27 Jun 1979 (Moffat 1981) and 11 Jun 1905 (Crawford and Parker 1971). Most individuals recorded in w. Australia are *simillima* or *taivana* (Johnstone 1982). Birds wintering in Australia (mostly *simillima*) arrive Nov, stay until late Mar; groups of 3–5 birds recorded in Northern Territory 4 Feb and 15–21 Dec 1968 and 9 Dec 1969 (see Johnstone 1982 for complete Australian records and map of wintering locations).

#### MIGRATORY BEHAVIOR

Before onset of fall migration, Yellow Wagtails assemble into small groups of 8–20 individuals and "generally signalize their readiness to depart by assembling on the low banks, bordering the beach, and dart high into the air to return to the same, or similar, place after a few minutes time" (Turner 1886: 180). Mostly a diurnal migrant; 2 daily peaks of migration (07:00–09:00 and 18:00–19:00; Gwinner et al. 1992). Estimated speed of migration about 30 km/h (Wood 1982); measured speed of migration 48 km/h on average (Meinertzhagen 1955). Migrates in loose flocks or small groups 30–50 m above ground (Mal'chevski and Pukinski 1983). In European part of migratory route, often flies nonstop for 24 h, up to 70 h when crossing seas and deserts (Mal'chevski and Pukinski 1983). On stopovers, often waits to leave until wind conditions are favorable, especially before long-range nonstop flights (e.g., see Biebach et al. 1986). Forages on average 5.5 d in oases during desert crossing, accumulating 0.37 g/d (2.59% mass change/d; see Biebach et al. 1986 for estimates of flight energetics). During fall migration, roosts in huge aggregations (up to 60,000 birds; Dittberner and Jander 1985). See Sounds, vocalizations, below, for patterns of calling in migrating flocks. Male-biased sex ratio in northern parts of winter range, and female-biased sex ratio in southern parts of range, apparently because of dominance interactions between sexes (Wood 1978, 1992).

#### CONTROL AND PHYSIOLOGY

On wintering grounds, onset of northward migratory movements is likely under endogenous control (Curry-Lindahl 1958), since physiological changes (e.g., fattening and Prealternate molt) show little correlation with local environmental conditions (Wood 1978, 1982, 1992, Bell 1996), but correspond well with time when breeding grounds become available. Birds that depart for wintering grounds later accumulate significantly more fat (Cantos and Asensio 1989).

Body mass increases by 30–40% in fall premigratory period, almost entirely as result of deposition of fat (Wood 1982); about 12% of body weight may be lost during every night of nonstop flight, causing birds to forage intensively at stopovers (Cantos and Asensio 1989; see Migratory behavior, above). Some birds are partly dehydrated after long nonstop flights (Wood 1982, Cantos and Asensio 1989, which see for dynamics of water indexes and mass change during migrations). However, plasma corticosterone level of Yellow Wagtails captured during beginning of fall migration (4–13 ng/ml) is well below stress level (Gwinner et al. 1992). See Biebach et al. 1986 for estimates of flight energetics during migration.

#### HABITAT

##### BREEDING RANGE

Occurs in open shrubby areas, especially where shrubs form edge with ground cover of sedge, grass, or dwarf shrub. Favors moist areas with tussocks and vegetated hummocks, faces of solifluction terraces, cut banks along creeks, tops of river bluffs, roadsides, ditches and all-terrain vehicle ruts, and mining operations (BK and DDG). In coastal tundras, often occurs along rivers and creeks, where closely associated with willows (e.g., diamond-leaf willow [*Salix pulchra*]) in lowland tundra, and taller felt-leaf willow (*S. alaxensis*) on slopes along rivers; Kistchinski 1988, Kessel 1989). In ne. Siberia, along streams and open slopes to subalpine zone of mountains, but usually not >200 m above floodplains (Kistchinski 1980, 1988); nests near human settlements, but Asian races only rarely nest within such settlements (Dement'ev and Gladkov 1954, Portenko 1973). Builds nests in vegetation around huts and occasionally within abandoned huts (Portenko 1973). Elsewhere also nests in pastures, but avoids abandoned agricultural fields overgrown with tall grass (Mal'chevski and Pukinski 1983). For detailed description of vegetation composition and habitat structure within breeding territories of Yellow Wagtails, see Dittberner and Dittberner 1984 and Kouki et al. 1992.

## SPRING AND FALL MIGRATION

After breeding and before fall migration, occurs primarily in nesting habitats (see above); in late Jul and early Aug, most birds move to riparian areas with tall willow and alder (*Alnus*; Kistchinski 1980, Zasyupkin 1981). In Japan, transient *simillima* occurs on farmland, in dump grasslands, and along streams and seacoast (Brazil 1991). On Malay Peninsula, transients found from coast to at least 1,300 m above sea level, feeding on grasslands, airfields, gardens, and swamps; roost communally in reed beds, and occasionally on thatched roofs of huts in mangrove (Medway and Wells 1976).

## WINTER RANGE

In n. Australia, wintering *tschutschensis* recorded in open areas of short grass with clumps of pandanus (*Pandanus*) and small eucalyptus (*Eucalyptus*); *simillima* observed feeding near sewage ponds (Johnstone 1982). Elsewhere, in open areas with water, along banks of semipermanent streams, in areas adjacent to sugarcane (*Saccharum officinarum*) fields that are used as roosts; as well as in rice (*Oryza sativa*) fields, sparse grasslands, cassava (*Manihot*) plots, acacia (*Acacia*) steppe, and drying swamps; usually in association with wild and domestic grazing mammals (Moreau 1972, Wood 1978).

## FOOD HABITS

## FEEDING

**Main foods taken.** Terrestrial and aquatic invertebrates.

**Microhabitat for foraging.** During breeding season, feeds on river alluvia, muddy edges of ponds, marshes, wet meadows, agricultural fields, estuarine flats, tidal beaches, and fishery dumps (Kistchinski 1980, BK and DDG). During pre-migratory movements in ne. Siberia, forages in and under bushes, on sandy, muddy, or rocky shores (Kistchinski 1980). See Kouki et al. 1992 for quantitative description of foraging habitat.

**Food capture and consumption.** Forages on the ground (picking and run-picking; see below) and fly-catches. In contrast to other *Motacilla* species, often digs through debris in search of food. During pre-migratory movements in ne. Siberia, picks food items from ground and at water's edge; often flies low over water, snatching insects from surface (Kistchinski 1980). Fly-catching by juveniles at Umiat, AK, described by Baldwin (1955: 34): "Juveniles were active mosquito-hawkers and in chasing insects would approach man within a few feet. Juveniles seen stalking among herbs and overhanging arctic lupines (*Lupinus arcticus*) leaves, jumping up now and then for mosquitoes."

In *M. f. flava* in ne. Europe during summer, of 126 prey captures, 94.5% picked from ground, 5.5% captured by fly-catching; intensity of feeding 11.2 pecks/min  $\pm$  1.96 SE (Rezanov 1981). Frequency of feeding techniques in *M. f. flavissima* flocks near Oxford, England: picking, 99.6–99.7%; run-picking 0–0.1%; fly-catching, 0.1–0.3% ( $n = 5,880$  capture attempts); feeding rate 29.1 items/min  $\pm$  1.5 SD ( $n = 142$  individuals) to 35.8 items/min  $\pm$  1.2 SD ( $n = 63$ ). Frequency of feeding techniques of single Yellow Wagtails: picking, 83.8%; run-picking, 8.7%; fly-catching, 7.5% ( $n = 173$  feeding attempts); average feeding rate 8.7 items/min  $\pm$  1.1 SD ( $n = 11$ ; Davies 1977). Fly-catching rate 1.3 flights/30 s  $\pm$  0.9 SD; number of captured prey per flight 1.0  $\pm$  0.5 SD (range 0–4); 97% of flights successful; average flight time 4.0 s/captured prey  $\pm$  1.8 SD ( $n = 25$ ; Cuadrado 1994). Foraging success decreases as season progresses on wintering grounds; average number of paces between successful prey captures increases from 6.5 in late Nov, to 14.8 in Feb, to 22.6 in late Mar (Wood 1978).

During migration and on breeding and wintering grounds, Yellow Wagtail is one of the most regular commensal followers of large grazing mammals (Rezanov 1981). Wagtails initially position themselves near animal's muzzle or feet; 3–5 birds typically associate with a grazing animal, but the birds move constantly and change position between the animal's hind and front feet, or between front feet and muzzle; peck prey off vegetation with upward jumps, forward darting movements, or aerial chases (Källander 1992). Birds perch on back of sheep (*Ovis*) for average 4.8 s ( $n = 118$ ) before darting down to pick insects disturbed by moving sheep; also pick insects directly from animals and fly-catch while perching on sheep (Rezanov 1981). During fall migration of Yellow Wagtails in Sweden, 78.9% pastures with cattle (*Bos*) or horses (*Equus*) had foraging wagtails; no wagtails were found on pastures that lacked grazing animals (Källander 1992); wagtails actively preferred grazing cattle to resting ones (Rezanov 1981); cattle that stopped grazing were abandoned within 17.8 s  $\pm$  10.9 SE, and wagtails often shifted between animals grazing close to each other (Källander 1992). Foraging success was higher for wagtails that associated with grazing animals (0.424 peck/s  $\pm$  0.09 SE) compared to those foraging alone (0.275 peck/s  $\pm$  0.124 SE); wagtails moved more slowly when associated with cattle (6.49 cm/s  $\pm$  1.76 SE) than when foraging alone (11.38 cm/s  $\pm$  4.11 SE; Källander 1992).

Swallows small prey whole immediately after capturing it; handles some large tipulids crane flies (Tipulidae) 17.2 s  $\pm$  4.9 SE; usually beats large prey against ground or shakes it vigorously before swallowing it (Rezanov 1981, Källander 1992).

## DIET

**Major food items.** Diet of *tschutschensis* during premigratory movements in ne. Siberia consists mostly of imagoes of flies (Diptera) and caddis flies (Trichoptera; Kistchinski 1980); in breeding season at Chukchi Peninsula, mostly bees and wasps (Hymenoptera) and snout beetles (Curculionidae), also flies, ground beetles (Carabidae), leaf beetles (Chrysomelidae), butterflies and moths (Lepidoptera), and rove beetles (Staphylinidae); and small sand particles (Portenko 1973). Elsewhere, Yellow Wagtails consume mayflies (Ephemeroptera), various dragonflies and damselflies (Odonata), stone flies (Plecoptera), various grasshoppers (Orthoptera), earwigs (Dermaptera), termites (Isoptera), bugs (Hemiptera), various caterpillars, larval and adult caddis flies, flies, bees and wasps, larval and adult beetles (Coleoptera), spiders (Araneae), and various mollusks (Mollusca; Smith 1950, Ptushenko and Inozemtsev 1968, Dittberner and Dittberner 1984). On wintering grounds, beetles, bugs, bees and wasps, and grasshoppers (Wood 1978, Cramp 1988).

**Quantitative analysis.** Stomach content of 7 *tschutschensis*, respectively, collected during breeding season in extreme e. Asia: (1) 1 leaf beetle; (2) 1 snout beetle, 13 hymenopterans; (3) 31 hymenopterans, 1 adult *Tipula* crane fly, 150 *Tipula* eggs, 1 fly; (4) 2 ground beetles, 20 hymenopterans; (5) 3 ground beetles, 1 caterpillar; (6) 2 snout beetles, 1 hymenopteran, small grains of sand; (7) 1 snout beetle, 1 rove beetle, 1 beetle (species unknown), 4 hymenopterans, 15–20 unknown insect larvae (Portenko 1973). Frequency of prey eaten by flocks of *flavissima* over flooded meadows in Apr ( $n = 1,335$  prey items) and May ( $n = 2,862$ ), respectively: 85.9, 34.8% midges (Chironomidae); 0, 44.1% pomace flies (Drosophilidae); 4.8, 2.0% anthomyiid flies (Scatophagidae); 3.5, 5.2% small dung flies (Sphaeroceridae); 0, 0.1% black scavenger flies (Sepsidae); 1.4, 0% frit flies (Chloropidae); 0, 3.4% ichneumonid flies (Ichneumonidae); 0, 4.3% aphids (Aphididae); 1.2, 1.4% beetles; 3.2, 4.5% others (England; Davies 1977). Prey eaten by single Yellow Wagtails on dung pats: 35.1% anthomyiid flies; 42.6% small dung flies; 6.4% beetles (Davies 1977). In Apr–May, 168 prey items eaten by 10 Yellow wagtails were 83% psyllids (Psyllidae), 7% leaf beetles, 2.3% flies, 2.3% cynipids (Cynipidae), 1.8% butterflies and moths, 2.6% others (Ptushenko and Inozemtsev 1968). In central Asia, of 56 stomachs, 41% contained snout beetles, 15% leaf beetles, 11% metallic wood-boring beetles (Buprestidae), 4% click beetles (Elateridae), 4% rove beetles, 11% ground beetles, 16% spiders, 2% millipedes and centipedes (Myriapoda), 4% dragonflies and damselflies, 11% grasshoppers, 14% aphids, 21% other leafhoppers

(Homoptera), 23% bees and wasps, 25% flies, 32% butterflies and moths, and others (Popov 1978).

## FOOD SELECTION AND STORAGE

See Davies 1977 for prey selection in breeding *flavissima* in England.

## NUTRITION AND ENERGETICS

Average energy intake of *flavissima* when foraging around a flooded meadow: feeding rate 29.1 items/min, energy intake 46.6 cal/min or 1.6 cal/item. When foraging on dung pats: average feeding rate 8.7 items/min, energy intake 67.9 cal/min or 7.8 cal/item (Davies 1977). On wintering grounds late in season, spends up to 75% of daylight foraging (Cramp 1988). See Biebach et al. 1986 for estimates of energy demands during migration. See Wood 1978 for weight dynamics of wintering *flava*.

## METABOLISM AND TEMPERATURE REGULATION

No information.

## DRINKING, PELLET-CASTING, AND DEFECACTION

Drinks by sipping and dip-and-tilt action (Cramp 1988).

## SOUNDS

## VOCALIZATIONS

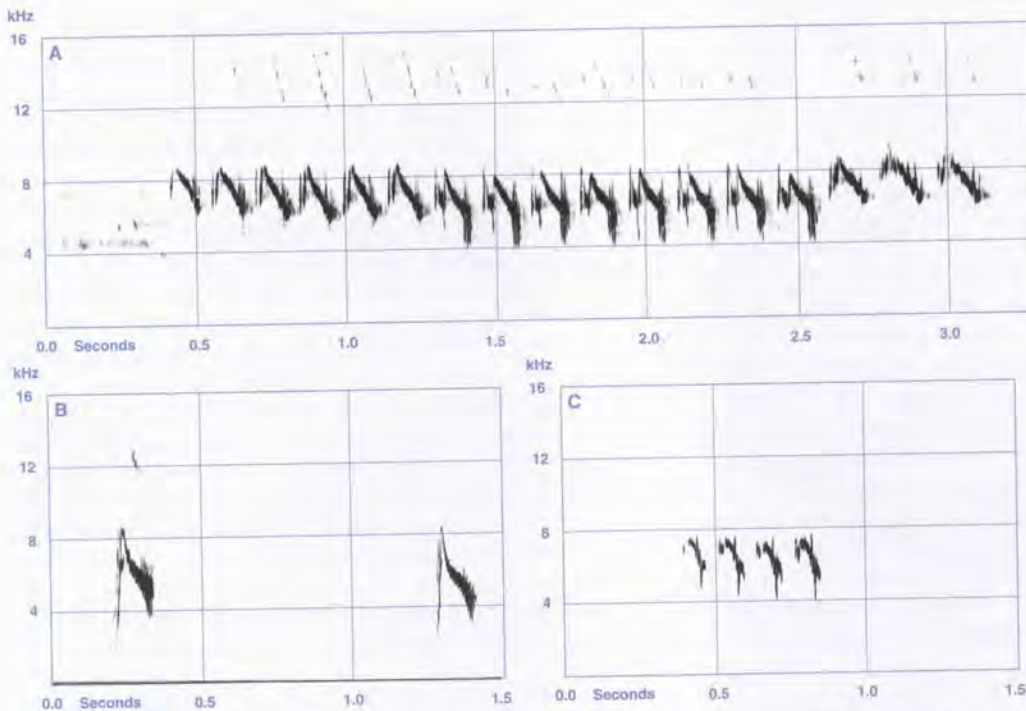
**Development.** No information.

**Vocal array.** Classification below follows that of Dittberner and Dittberner (1984) for *M. flava*.

**COURTSHIP SONG.** Described as high *tzee-zee-zee*, or a *ter-zwee-ter-zee-zwee-zwee*. Given in Song Flight (see Behavior: sexual behavior, below), or from perches during breeding season. Song perches 30 cm above ground, on tops of tussocks; some on tops of bushes about 180 cm above ground. The version given from perches is more melodious and a quieter "warbler like song," usually sung on warmer days (Walkinshaw 1948).

**TERRITORIAL SONG.** See Figure 2A. Rapid sequence of sounds similar to Contact-Alarm Call (see below). In *flavissima*, described as repeated high-pitched *tsee-wee-sirr tsee-wee-sirr*, with Contact Call *tsweep* interspersed (Smith 1950). Given from ground or song perches along territory perimeter (e.g., Nelson 1887, Walkinshaw 1948, Baldwin 1955). For other types of song—e.g., threat song directed at predators—see Dittberner and Dittberner 1984 and Cramp 1988.

**CONTACT-ALARM CALL.** See Figure 2B and C. Described as a frequent, faint *pe-weet* (Grinnell 1900). Given while perched or by pairs in flight; during incubation changeovers and while in



**Figure 2.** Vocalizations of the Yellow Wagtail. A. Territorial Song (recorded 17 Jun 1976 on Inglutalik River [16.8 km southeast of Koyuk, AK] by L. J. Peyton). B and C. Two variations of Contact-Alarm Call: *tsouweep* or *tsweep* (B); *tsip* or *tsit* (C). (Both B and C recorded 22 Jun 1968 in Nome, AK, by William W. H. Gunn.) Sonograms prepared by staff of Borror Laboratory of Bioacoustics, Ohio State University, using a Kay Elemetrics DSP 5500 Sona-Graph (with effective frequency resolution of 300 Hz and a 200 point FFT transform size).

foraging or migrating flocks. High-intensity Contact-Alarm Calls are given when predators approach nest. Contact Calls described as *tsit*, that in alarm situations changes to *tsvit* in males and *drzhzhi* or *dzhrrt* in females (Portenko 1973). Both sexes give "a sparrow-like" *kee* or *zeep* while hovering above intruders (Walkinshaw 1948). This call described by Nelson (1887) as the sharp *ple-ple-ple* given while birds circle over an intruder.

**OTHER CALLS.** The following calls are described for different races and subspecies of Yellow Wagtail (after Smith 1950, Dittberner and Dittberner 1984): (1) Enticement Call: *psiehp*. Given by adults to nestlings during fledging (apparently "luring" them to leave nest). (2) Feeding Call: *syew... syew... syew*. Given to nestlings (especially to nonbegging nestlings) by adults before they feed nestlings; (3) Excitement Call: *durr... quurrr... djurrr* (*M. f. flava*) and *sreeze*. Given by males before copulation in Advertising Display (see Behavior: sexual behavior, below). (4) Distraction Call: *krrr... krrr... krrr* or *chra... chra... chra*. Given during predator distraction flights or Disablement Displays near nest (see Behavior: predation, below). See Dittberner and Dittberner 1984 and Cramp 1988 for other calls.

**NESTLING AND FLEDGLING CALLS.** High-pitched, quiet variation of adult Contact-Alarm Call; described as *sisisisi* or *psieh*. Nestlings 9 d or older give *srieh... srieh... srieh* calls (closely resembling Contact-Alarm Call of adults) when soliciting food, and periodically give *psiehp* call (resembling adult Enticement Call), which after leaving nest, they use to indicate their location (Dittberner and Dittberner 1984). Nestling Distress Call, a loud *tshirrrp*, is given by nestlings older than 8–9 d when they are handled; causes immediate abandonment of nest by other nestlings (Dittberner and Dittberner 1984).

Calls differ markedly among subspecies and races, show extensive geographic variation, and frequently are used to examine phylogenetic relationships among Yellow Wagtail subspecies (see Systematics: subspecies, and Systematics: related species, above; Czikeli and Knöttsch 1979, Czikeli 1985).

**Phenology.** Intensive singing on 2 Jun near Bethel, w. Alaska (Walkinshaw 1948). Late song of male on 16 Jul (Portenko 1973) was probably related to reneating. In migrating flocks, proportion of birds calling decreases with size of flock, from 70–100% in flocks of 1–3 birds, to 50% in groups of 4, to 34% in groups of 6–10, to 20% in groups of 11–20



(Dierschke 1994). For quantitative description of habitat used for singing, see Kouki et al. 1992.

**Daily pattern.** Average rate of singing is 7 songs/min, mostly in morning and afternoon; sings periodically throughout day, but not continuously (Walkinshaw 1948).

#### NONVOCAL SOUNDS

Bill-snapping frequently recorded during threat displays (see Behavior: agonistic behavior, below) or when bird is reacting to predators (e.g., Dittberner and Dittberner 1984).

## BEHAVIOR

### LOCOMOTION

**Walking, hopping, climbing, etc.** Walks, runs, and hops on ground. Moves head back and forth when walking. Wags tail when walking, especially at end of runs and when disturbed by intruders on territory. Tail aids considerably when negotiating sharp turns in fly-catching (Davies 1977).

**Flight.** Strongly undulating flight.

**Swimming and diving.** Not known.

### SELF-MAINTENANCE

**Preening, head-scratching, stretching, bathing, anting, etc.** Often preens on pre-roost gatherings. Scratches head by bringing foot over wing; walks in shallow standing water and bathes.

**Sleeping, roosting, sunbathing.** Forms huge communal roosts in nonbreeding season. Number of individuals at 1 premigratory reed bed roost site of *flavissima* varied from 200 to 6,500 birds and peaked late Aug; roost sites at reed beds of large lakes along Black Sea coast accumulate 20,000–60,000 Yellow Wagtails during fall migrations (Dittberner and Jander 1985, which see for detailed description of roosting habitats). On wintering grounds, attendance at roost site is apparently influenced by nearby food availability; declines from 16,000 in Nov to 2,000–3,000 in Mar (Wood 1978). During breeding season, may roost solitarily on breeding territories or communally. Female sleeps on or near nest throughout nesting season (Dittberner and Dittberner 1984, AVB). Roosting behavior well studied; here described briefly for *M. f. flava* (after Dittberner and Dittberner 1984, Dittberner and Jander 1985, Cramp 1988): Birds start to gather near roosting areas about 1–2 h before sunset; small arriving flocks often circle roost site while calling before landing. Before entering roost site, birds gather at pre-roost sites, commonly walk or preen, and then enter roost all together before or shortly after dark. In morning, birds depart in waves.

Yellow Wagtail “exposes itself to the sun on the ground without adopting any special posture” (K. E. L. Simmons in litt.).

**Daily time budget.** See Dittberner and Dittberner 1984 for detail of daily budget of Yellow Wagtail during breeding season. See Breeding: nest, below, for daily budget during that period. On wintering grounds, may spend up to 75% of daylight foraging (Wood 1978).

### AGONISTIC BEHAVIOR

**Physical interactions.** Highly aggressive toward intruders on foraging (migration and wintering) territories and breeding territories. Intense fighting and threat displays (see below) common along breeding-territory boundaries, especially after females' arrival in spring (Walkinshaw 1948, Smith 1950, Brosset 1971, Portenko 1973, Dittberner and Dittberner 1984).

**Communicative interactions.** **THREAT DISPLAYS.** In Upright Threat Posture, “the head is thrown well back, with the nape tucked almost between the scapular feathers; the breast is thrown forward and the feathers greatly puffed out; the wing tips are depressed almost to the ground, whilst the bird sits back on its long tail” (Smith 1950: 35–36). One of the contenders then crouches forward with still-erected breast-feathers and half-open beak, emitting low hissing sound (possibly intense Contact-Alarm Call; see Sounds: vocalizations, above). Rival responds by swaying from side to side while maintaining Upright Threat Posture. In the prolonged fierce fights that usually follow, birds peck and claw each other intensely, while rolling over each other on the ground and in aerial fights (Walkinshaw 1948, Smith 1950, Portenko 1973, Dittberner and Dittberner 1984). See Cramp 1988 for description of the Forward Threat Posture (seen on winter feeding territories).

### SPACING

**Territoriality.** Territorial during breeding season; depending on food availability and distribution, some birds, mostly males, maintain winter territories. Most birds forage in small flocks on wintering grounds and during first 2 wk after spring arrival. Highly gregarious on roost sites and on migratory stopovers.

**NATURE AND EXTENT OF TERRITORY.** Territory serves for feeding and nesting. Frequently forages outside of territory. Defended territory 67–100 m in diameter at Umiat, AK (Baldwin 1955). Breeding territories often clumped within homogeneous habitat (see below); on 20 km<sup>2</sup> of homogeneous marsh habitat in ne. Russia, and 7 nest aggregations of 3–6 pairs each, only 2 pairs nested >500 m from nearest neighbors. Average distance between nests 75–

100 m (minimum 11; Mal'chevski and Pukinski 1983). In clumped nesting settlements, territory size 400–500 m<sup>2</sup>, in solitary nesting pairs, 1,200–2,000 m<sup>2</sup> (Ptushenko and Inozemtsev 1968). Elsewhere in clumped settlements, distances among nests 30–60 m (minimum 20); if first nest is destroyed, re-nests within previous breeding territory, 17–100 m from first nest site (Dittberner and Dittberner 1984). Distance between nesting pairs in linear stretches of habitat in w. Alaska has varied from 1.6 pairs/km in north to 7 pairs/km farther south at lower edges of brush zone adjacent to tundra and marsh in Askinuk Mtns. (Kessel et al. 1964, BK and DDG; see also Demography and populations: population status, below).

**MANNER OF ESTABLISHING AND MAINTAINING TERRITORY.** Maintains territory by periodic aerial displays along perimeter or by calling from song perches (Walkinshaw 1948, Baldwin 1955). Unpaired males constantly invade territories of paired males, provoking fierce fighting (see Agonistic behavior, above). Most fights are between males, although during nest-building, females may fight with intruding females (Dittberner and Dittberner 1984).

Breeding territories in clumped settlements (see above) form around territory of a single, brightly colored, apparently older male that arrives earliest. Within 10–12 d his territory is surrounded by territories of other males (Mal'chevski and Pukinski 1983). Interestingly, the males in such settlements show no initial aggression to each other, often feed together near same puddle, and use same bush to display to transient females (Mal'chevski and Pukinski 1983, G. N. Simkin pers. comm., AVB), while males nesting solitarily are very aggressive to conspecific males (Ptushenko and Inozemtsev 1968).

**INTERSPECIFIC TERRITORIALITY.** Highly aggressive toward passerines (e.g., Linnet [*Carduelis cannabina*], Red-throated Pipit [*Anthus cervinus*]) that intrude on breeding territories, especially early in nesting cycle (Portenko 1973, Dittberner and Dittberner 1984, Cramp 1988).

**WINTER TERRITORIALITY.** Some wintering males occupy feeding territories along banks of streams; other birds do not maintain such territories, and forage in small flocks of 3–6 individuals (Wood 1978). Winter territories along stream banks range from 60 to 130 m (mean 82.5,  $n = 6$ ), about 600 m<sup>2</sup> (Brosset 1971); average area 0.25 ha (range 0.15–0.36; Wood 1978).

**DOMINANCE HIERARCHIES.** No data for Alaska wagtails (*tschutschensis* or *simillima*). See Dittberner and Dittberner 1984 for other subspecies.

**Individual distance.** Variable. When individuals forage solitarily, maintain distance of 500–1,200 m; <1 m when in flocks or on roosts (Davies 1977, Dittberner and Dittberner 1984).

#### SEXUAL BEHAVIOR

**Mating system and sex ratio.** Socially monogamous, but extra-pair copulations are common in e. Palearctic races (Dittberner and Dittberner 1984).

**Pair bond.** No detailed information on timing of pair formation. Pairs observed in migrating flocks may have formed on wintering grounds, in previous year, or during migration. Most birds apparently pair soon after arrival on breeding areas. Pairs usually remain together throughout breeding season (Dittberner and Dittberner 1984).

**Courtship displays.** Classification follows that of Cramp (1988) for *M. flava*. Upon first arrival of female on territory of singing male, pair exchange Contact-Alarm Calls (see Sounds: vocalizations, above), then male gives Advertising Display (see below); if female remains on territory, male performs frequent Advertising Displays alternating with Song Flight (see below) or Courtship Song (see Sounds: vocalizations, above) and flight chases; copulation follows either one of these male displays when female adopts Soliciting Posture (see below; Smith 1950, Dittberner and Dittberner 1984).

**SONG FLIGHT.** In this display, "the male starts up from a bank or clump of bushes, and, rising for 20 or 30 yards at a sharp angle, suddenly stiffens and decurves his wings, at the same time slowly spreading and elevating his tail nearly perpendicularly to his body, and in this curious position he floats slowly down until within a foot or two of the ground, uttering a low, clear, and rapid medley of jangling notes which can only be compared to the sound made by lightly rattling together the links of a small steel chain [see Sounds: vocalizations, above]. As he approaches the ground in his descent he suddenly glides away to a neighboring bush or knoll, whence he repeats the maneuver" (Nelson 1887: 206). In another account, males rose to 8–12 m above ground in Song Flights; a male once gave an aerial display 60 cm above ground on a cold and windy day (Walkinshaw 1948). Copulation on ground follows Flight Song (Baldwin 1955). Males also sing Courtship Song (see Sounds: vocalizations, above) while perched (Dittberner and Dittberner 1984).

**ADVERTISING DISPLAY.** Male runs toward female; when about 50 cm away, "puffs out his breast feathers, depresses and half-opens his wings, raises his nape and mantle feathers and fans and drags his tail.... In this attitude he runs or pirouettes round the female, at the same time calling with musical 'sreeze' note" (see Sounds: vocalizations, above; Smith 1950: 44). At higher intensity, male may hover above female during this display.

**SOLICITING POSTURE.** Female may adopt this posture after either Song Flight or Advertising Display. Female "crouches flat on the ground, puffs out her

feathers, half-opens and depresses her wings and elevates her tail until it is vertical.... begins to twirl round and round on the ground, keeping to the same spot" (Smith 1950: 47). Copulation follows. Copulations observed 3–4 d before and during nest-building, and regularly before a second clutch (Dittberner and Dittberner 1984). Courtship-feeding absent in *flavissima* (Smith 1950); no data for other subspecies.

Yellow Wagtails show significant color discrimination in red, orange, and yellow families in Munsell system; the best discrimination occurred in spectral region corresponding to the species' sexually dimorphic plumage (Peiponen 1992).

**Extra-pair copulations.** No quantitative data for extra-pair fertilizations, but extra-pair copulations between resident female and trespassing or neighboring male Yellow Wagtails are frequent (Dittberner and Dittberner 1984, G. N. Simkin pers. comm.).

#### SOCIAL AND INTERSPECIFIC BEHAVIOR

**Degree of sociality.** Solitary and territorial during breeding season; migrates in small flocks. Mostly gregarious in winter; some birds territorial, depending on food availability. In nonbreeding season, forms large communal roosts; highly gregarious on migratory stopovers and roosts (see Self-maintenance, above). Within homogeneous breeding habitat, nests within visual or acoustic contact with other pairs, often semicolonially in nesting groups (Ptushenko and Inozemtsev 1968, Mal'chevski and Pukinski 1983). Neighboring 2–3 pairs cooperatively attack approaching predators (see Predation, below).

**Play.** No information.

**Nonpredatory interspecific interactions.** See Dittberner and Dittberner 1984 and Cramp 1988 for behavior at mixed-species roosts.

#### PREDATION

**Kinds of predators.** Eurasian Sparrowhawk (*Accipiter nisus*) and Eurasian Hobby (*Falco subbuteo*) successfully attack Yellow Wagtails (Cramp 1988). See Demography and populations: measures of breeding activity, below, for data on nest predation.

**Response to predators.** Several neighboring pairs often join together to chase avian predators from nesting territories, often provoking territorial fights among Yellow Wagtail males (G. N. Simkin pers. comm.). Wagtails sometimes are joined by other species (such as Pechora Pipit [*Anthus gustavi*]) when chasing or scolding predators (Portenko 1973). Both sexes, most often females, may perform Disablement Display: Drops wings and fans tail when trying to lure predator away from nestlings (Dittberner and Dittberner 1984). Reaction to

appearance of human on territory: "The male flew to meet us, coming to a spot about 8 to 15 meters overhead where he continued to scold while we were in the close proximity of the nest area.... males also scolded Sandhill Cranes [*Grus canadensis*] when they appeared in the vicinity of the nests, but they paid little attention to other birds" (Walkinshaw 1948: 50). See Portenko 1973 for evasive strategies of juvenile Yellow Wagtails. See Dittberner and Dittberner 1984 for more details.

## BREEDING

#### PHENOLOGY

**Testicular/ovarian cycle.** Largest testis of adult *tschutschensis* collected at Umiat, AK (69°23'N, 152°08'W) 5 Jun—8.5 × 6 mm ( $n = 2$ ; University of Alaska Museum); 15–25 Jun—4.5–10 mm (mean 7.41 ± 1.58 SD,  $n = 11$ ); 30 Jun–14 Jul—0.5–3.00 mm (mean 2.07 ± 0.84 SD,  $n = 7$ ); 13 Aug—1.5 mm ( $n = 1$ ). Largest oocyte: 15–25 Jun—1.5–2.5 mm (mean 1.93 ± 0.45 SD,  $n = 7$ ); 30 Jun–14 Jul—0.5–1.0 mm (mean 0.75 ± 0.29 SD,  $n = 4$ ); 25–28 Jul—0.2–0.3 mm ( $n = 2$ ); male cloacal protuberance 7 × 5 mm (Jun; Baldwin 1955). Testes of *tschutschensis* collected at Igiak Bay, AK (61°42'N, 65°45'W), 16 Jun 1963: left—7.9 × 4.8–5.8 mm (mean 7.65 × 5.4), right—6.8 × 4.6 mm (mean 7.1 × 5.3,  $n = 4$ ); on 20 Jun: left—9 × 6 mm (University of Alaska Museum). Diameter of largest ovarian follicle of females collected at same location: 9 Jun, 5 mm; 16 Jun, 8 mm; 20 Jun, 2.5 mm (University of Alaska Museum). From *tschutschensis* at Ogorok Creek, AK (68°08'N, 165°45'W), on 12 Jun: largest follicle 3 mm, oviduct diameter 2 mm; on Seward Peninsula on 30 Jun, left testis—5.5 × 4.3 mm, right—5.0 × 3.8 mm; at Ikpikuk River (69°28'N, 154°40'W) on 2 Jul, testes 3 mm, largest follicle 5 mm (University of Alaska Museum). Testes (in mm) of *tschutschensis* collected on Wrangel I. on 31 May: left—7 × 5, right—6 × 5; elsewhere on Chukchi Peninsula (extreme e. Asia) on 5 Jun, left—10 × 8, right—9 × 6; on 14 Jul, left—8 × 4, right—7 × 3; on 8 and 9 Jul, 2 birds, both with same measurements: left—5 × 3, right—4 × 2; on 10 Jul, 2 birds: left—6 × 4, right—3 × 3, left and right—3 × 3; on 11 Jul, 2 birds: left—4 × 3, right—3 × 2, and left—3 × 2, right—2 × 2, respectively; on 26 Aug, left and right—1.5 × 1 (juvenile; Portenko 1973).

**Pair formation.** In Alaska, numerous courtship displays (see Behavior: sexual behavior, above) 9–16 Jun 1952 at Etivluk River (Kessel and Cade 1958), and 11–14 Jun 1953 at Umiat (Baldwin 1955). In *tschutschensis* on Chukchi Peninsula, on patches of snow-free tundra on 13 Jun 1956, intensive courtship and fights among males on 15 Jun; paired birds seen 18 Jun; most pairs formed by 22 Jun (Portenko

1973). In *flava*, brightly colored individuals, most likely old males, arrive on breeding grounds first, followed in 4–6 d by young males and females (Smith 1950, Mal'chevski and Pukinski 1983). If cold weather returns, already-territorial individuals that arrived early may form groups of up to 40–50 individuals and undertake short local movements (Mal'chevski and Pukinski 1983).

**Nest-building.** Start of building often influenced by spring flood regime or snow cover and can be delayed for up to 2–3 wk after arrival (Kistchinski 1980); delayed emergence of young grass could postpone nest-building (G. N. Simkin pers. comm.; see Fig. 3).

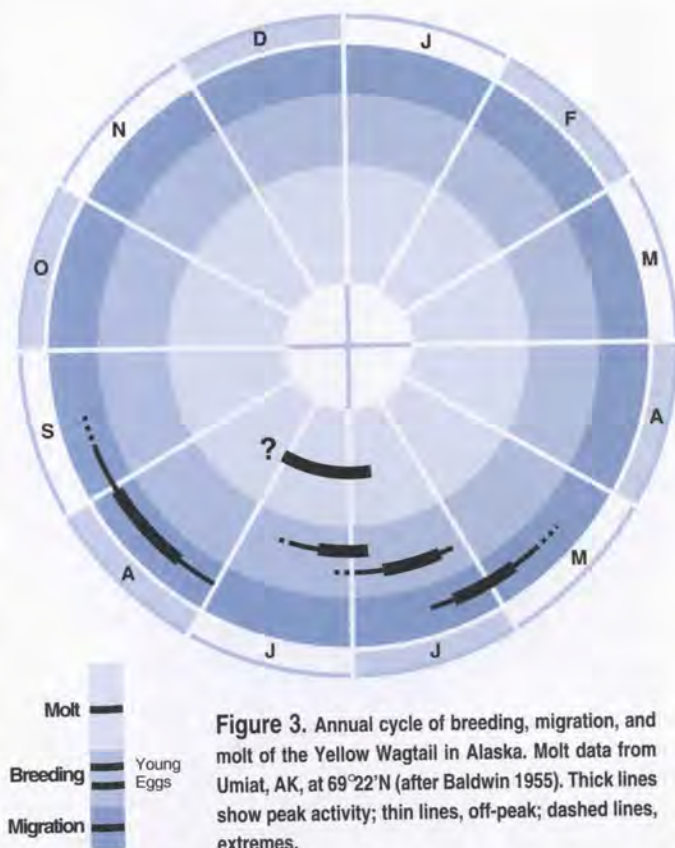
**First/only brood per season.** Egg-laying starts during first week of Jun in w. Alaska and a few days later in n. Alaska; peaks during second week of Jun; a few late nests still have eggs in early Jul (BK and DDG). In Alaska, hatching begins last week of Jun; late hatches: near Wales, clutch hatched on 7 Jul 1922 (Bailey 1943), and on Colville River delta, recent hatchlings on 4 Jul 1908 (Anderson 1913). Young begin to leave nest during first few days of Jul. Fledged broods common by mid-Jul; post-breeding flocks of mostly juvenile birds common by late Jul (BK and DDG).

In ne. Siberia, egg-laying starts 1–2 wk after arrival on breeding grounds. Full clutches on 13, 25, and 27 Jun. On 10 Jul 1976, 3 nests with 7-, 8-, and 10-d-old nestlings, respectively (Kistchinski 1980). In Anadyr area (ne. Asia), hatching first week of Jul, peaks 9–14 Jul; first fledglings 11 Jul; flocks of juveniles, some with females, numerous by mid-Aug; latest clutch (possibly repeat clutch) 10 Jul 1931 (Dement'ev and Gladkov 1954). On Commander Is. (*simillima*), hatching 10–13 Jul (Artukhin 1995). Flocks of juveniles common in ne. Siberia after 20 Jul; some families stay together until 10–12 Aug (Kistchinski 1980). At Lawrence Bay, Chukchi Peninsula, nest with 6 slightly incubated eggs on 21 Jun; nest with 6 nestlings on Jun 22; nest with 6 eggs at advanced incubation stage and nest with nestlings on 5 Jul. At Providence Bay, a pair finished nest on 12 Jun (Portenko 1973). See Ryzhanovskii 1987 for overlap between breeding stages and basic molt in northern populations of Yellow Wagtails.

**Second/later brood per season.** One brood / yr in Alaska.

#### NEST SITE

**Selection process.** No data from Alaska. Elsewhere, female (usually accompanied by male) prospect for potential nest sites within a territory and may initiate several nests during 1–2 d before start of nest-building at chosen site (Ptushenko and Inozemtsev 1968). In *flavissima*, while scraping initial depression in ground, female may adopt Soliciting



**Figure 3.** Annual cycle of breeding, migration, and molt of the Yellow Wagtail in Alaska. Molt data from Umiat, AK, at 69°22'N (after Baldwin 1955). Thick lines show peak activity; thin lines, off-peak; dashed lines, extremes.

Posture (see Behavior: sexual behavior, above) toward accompanying male (Smith 1950).

**Site characteristics.** Nests on the ground, in moss, sedge, or ground cavity (often excavated by female; Ptushenko and Inozemtsev 1968), among dwarf shrub roots, under edge of sedge tussock or frost hummock (Gabrielson and Lincoln 1959, BK and DDG). May be sheltered by low-growing dwarf shrubs, by lower branches of shrubs, or by drooping sedge leaves; nests often placed under mats of overhanging vegetation in dirt banks (Gabrielson and Lincoln 1959, BK and DDG).

#### NEST

**Construction process.** No data for Alaska subspecies (*tschutschensis*). In other races of Yellow Wagtail, nest built by female only; usually takes 5–7 d. Male closely guards female and accompanies her on flights to gather nest material (Ptushenko and Inozemtsev 1968, Mal'chevski and Pukinski 1983). Female may gather material up to 1 km away for nest site (Smith 1950), but most often within 150 m of nest site (Dittberner and Dittberner 1984). In 1 pair of *flava*, female brought material to nest from 06:14 to 20:02 (91 total trips); daily frequency of building as follows: 06:00–0900—30 trips, 09:00–12:00—47 trips, 12:00–15:00—7 trips, 15:00–21:00—

7 trips. Daily time budget of female during nest-building as follows ( $n = 15.5$  h of observation): searching for nesting material, 2.7 h; building nest, 1.2 h; guarding nest and maintaining presence near nest, 0.9 h; maintaining pair bond, foraging, and other activities, 10.7 h (Dittberner and Dittberner 1984).

**Structure and composition matter.** Outer layers built mostly of grasses, with bark shreds, dead leaves, lichens, and moss. Lined with fine grasses, and mostly ptarmigan (*Lagopus* spp.) feathers (including large contour feathers) or mammal hair (mostly caribou [*Rangifer tarandus*] and arctic fox [*Alopex lagopus*]; Gabrielson and Lincoln 1959, Kistchinski 1980, BK and DDG).

**Dimensions.** Overall dimensions of *tschutschensis* nests: outside diameter 10.16–11.43 cm, inside diameter 5.08–5.84 cm, height 6.35–7.62 cm, inside depth 4.32–4.57 cm ( $n = 3$ ; Bent 1950). Inside diameter 4.7–6.0 cm, inside depth 3.7–4.9 cm ( $n = 2$ ; Walkinshaw 1948).

**Microclimate.** No data.

**Maintenance or reuse of nests, alternate nests.** If nest depredated, builds new nest within territory. May initiate several half-finished nest sites before selecting final site (Ptushenko and Inozemtsev 1968).

**Nonbreeding nests.** None known.

## EGGS

**Shape.** Subelliptical.

**Size.** In 3 clutches of *tschutschensis* in Bethel, AK, length  $\times$  breadth (mm), respectively: 19.6–20.0  $\times$  14.5–15.0 (mean 19.8  $\times$  14.7,  $n = 6$  eggs); 18.5–19.6  $\times$  14.0–14.5 (mean 19.1  $\times$  14.3,  $n = 5$ ); 18.5–19.0  $\times$  15 (mean 18.8  $\times$  15,  $n = 6$ ; L. H. Walkinshaw unpubl., University of Alaska, Rasmuson Library Archives). Elsewhere in *tschutschensis*, length  $\times$  breadth (mm): 18.0–20.9  $\times$  13.2–15.6 (mean 19.1  $\times$  14.4,  $n = 50$  eggs; Bent 1950). Two eggs from Chukchi Peninsula 18.9  $\times$  15.3 mm and 18.5  $\times$  14.9 mm, respectively (Portenko 1973).

**Mass.** Average 2.03 g ( $n = 17$  eggs from 3 clutches; L. H. Walkinshaw unpubl., University of Alaska, Rasmuson Library Archives).

**Color.** Ground color varies from pale greenish clay to clay white or deep olive buff to dark olive buff, covered with profuse mottling of slaty to reddish brown that sometimes covers ground color; in some clutches, spots are large and less numerous (Bent 1950, Gabrielson and Lincoln 1959, L. H. Walkinshaw unpubl., University of Alaska, Rasmuson Library Archives).

**Surface texture.** No data.

**Eggshell thickness.** No data.

**Clutch size.** Usually 5 eggs. In 43 Alaska nests, range 4–7 eggs (average  $5.2 \pm 0.7$  SD); two 3-egg

clutches (8 Jun 1975 and 22–24 Jun 1983), not included in calculations, were probably incomplete (BK and DDG). Of 116 clutches of *flavissima*, 8 had 3 eggs, 12 had 4 eggs, 49 had 5 eggs, 45 had 6 eggs, 2 had 7 eggs (mean  $5.18 \pm 0.08$  SE; Mason and Lyczynski 1980). In e. Russia, of 24 clutches of *flava*, 8 nests had 4 eggs, 13 had 5 eggs, 3 had 6 eggs; of 43 clutches in ne. Russia, 8 nests had 4 eggs, 14 had 5 eggs, 21 had 6 eggs (Mal'chevski and Pukinski 1983). Mean 5.5 eggs in sw. Norway (Paulsen 1993). Clutch size declines strongly as season progresses (Mason and Lyczynski 1980, Paulsen 1993).

**Egg-laying.** Eggs laid daily during early morning; of 22 eggs, 16 were laid before 08:00 and 6 between 08:00 and 11:00 (Smith 1950).

## INCUBATION

**Onset of broodiness and incubation in relation to laying.** No data for Alaska subspecies. In other subspecies, full incubation starts after last egg is laid or, rarely, the day before.

**Incubation patch.** Female has single abdominal brood patch. When male incubates, he raises abdominal feathers for better contact with eggs (e.g., Smith 1950).

**Incubation period.** For *flavissima*, lasts 12–13 d (Smith 1950); mean 12.4 d (range 11–13,  $n = 18$  nests; Mason and Lyczynski 1980)

**Parental behavior.** Male participation in incubation varies among subspecies. In *tschutschensis*, both parents incubate during day (e.g., Bee 1958); only female at night. In *flavissima*, incubation rhythms during first week: On average, male incubates 16.6% of time, female 67%, nest unattended 16.6% of time ( $n = 4$  nests in 3 different years, 8 h of observation; Smith 1950). Second week of incubation: On average male 19.8%, female 69.8%, nest unattended 10.4%; bouts on nest lasted 1–2 h, but no detailed observations (Smith 1950). In *flava*, male incubates for about 25% of daylight time, females 75% of daytime and all night (Kukish 1976). Male closely watches predators and intruders around nest; when predator in sight, male gives Contact-Alarm Call (see Sounds: vocalizations, above), and female leaves nest and runs through grass for 10–20 m before flying up and joining male (Ptushenko and Inozemtsev 1968).

Method of changeover (after Smith 1950): Returning bird flies into territory and perches, then flies to ground, 50–60 m away from nest, and starts giving Contact Call (see Sounds: vocalizations, above). Incubating bird walks away from nest for some distance, then flies overhead while giving Contact Call, then flies away. Relief bird slowly walks toward nest while foraging; calls continuously, but stops just before entering nest. Frequency of incubation changeovers: 3–8 times (mean

5) during 8 h (Smith 1950). In *flavissima*, no mate-feeding recorded during incubation (Smith 1950). In *flava*, male occasionally feeds incubating female on nest (Ptushenko and Inozemtsev 1968).

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

#### HATCHING

In *flavissima*, entire clutch hatches within 6–12 h; incubating bird first places eggshells just outside nest, then collects them and drops them in flight about 30 m away (Smith 1950). In *flava*, entire clutch hatches within 26–47 h ( $n = 3$  nests); hatching synchrony varies from 1 to 3 nestlings hatched/24 h (Dittberner and Dittberner 1984).

#### YOUNG BIRDS

**Conditions at hatching.** Altricial and nidicolous. Hatchlings have yellowish reddish skin color and average 1.5 g (Dittberner and Dittberner 1984).

**Growth and development.** The following is based on Dittberner and Dittberner 1984 for *M. f. flava* in central Europe. Summary of nestling growth as follows: mass (g) 2.0 on day 1 after hatching; 2.9 on day 2; 4.0 on day 3; 6.0 on day 4; 10.6 on day 5; 13.2 on day 6; 15.0 on days 7 and 8; 15.2 on day 9; 15.4 on day 10; 16 on day 11; 16.2 on day 12; 16.4 on day 13 (day of nest departure); 16.9 on day 14, and 17.0 on day 15. Wing length (mm): 7 on day 1; 9 on day 2; 10 on day 3; 11.5 on day 4; 20 on day 5; 25 on day 6; 31 on day 7; 38 on day 8; 42 on day 9; 45 on day 10; 47 on day 11; 50 on day 12; 53 on day 13. Tail length (mm): 2.5 on day 4; 5.1 on day 5; 9 on days 6 and 7; 14.5 on day 8; 15.1 on day 9; 15.3 on day 10; 20 on day 11; 22 on day 12; 24 on day 13. Beak from nares (mm): 1.9 on day 1; 2.8 on day 2; 3.9 on day 4; 4.9 on day 6; 5.8 on day 10; 6.0 on day 11; 6.3 on day 12. See Dittberner and Dittberner 1984 for growth curves of contour feathers, claw and digits, and overall body length.

Additional details of *flava* development (after Dittberner and Dittberner 1984, which see for detailed account): Ear passages open on day 3; eyes start to open on days 4–5, open completely on day 6; ensheathed contour feathers appear on day 2, start to open on day 5; ensheathed primaries 4 mm long on day 4, start to open on day 6; iris dark brownish on day 8. On day 11, nestlings can fly up to 30 cm high and 1 m long and can walk away from nest and come back (Smith 1950, Dittberner and Dittberner 1984).

#### PARENTAL CARE

**Brooding.** Only female broods, until nestlings are 5–6 d old; broods most often in early mornings and late afternoons (G. N. Simkin pers. comm., AVB)

**Feeding.** No data for Alaska subspecies. Elsewhere, both parents feed nestlings. In s. Europe and central Asia, mostly small aphids and psyllids in diet of nestlings during first 3 d; later bigger prey (grasshoppers, butterflies and moths), with hard parts removed (Popov 1978). In *flava*, nestlings are fed mostly aphids and various flies; also blow flies (Calliphoridae), crane flies (Tipulidae), syrphid flies (Syrphidae), thick-headed flies (Conopidae), robber flies (Asilidae: *Dioctria*); grasshoppers, various beetles (e.g., snout beetles), caterpillars and imagoes of butterflies and moths, mayflies, dragonflies and damselflies, and small mollusks (Smith 1950, Mal'chevski and Pukinski 1983). Removes wings from dragonflies (*Aeshna* spp.), but leaves them on damselflies (*Enallagma*, *Pyrrosoma*, and *Ischnura* spp.; Smith 1950, Popov 1978).

Frequency of food deliveries (times/h) increases with age, from 7.3 for 3-d-old nestlings, to 15 for 5-d-old, 19 for 6-d-old, 29 for 7-d-old, 37 for 8-d-old, 34 for 9- and 10-d-olds, and 21 for 11-d-old (Euporean subspecies; data from Ptushenko and Inozemtsev 1968, Cramp 1988). Food deliveries more frequent in early morning and late afternoon; up to 200 food deliveries/d for 7- to 9-d-old nestlings (Mal'chevski and Pukinski 1983). In 9-d-old nestlings, 43% of daily food deliveries by male, 57% by female; frequency of deliveries by male and by female during day as follows: 03:00–09:00—male 20, female 36; 09:00–15:00—male 19, female 29; 15:00–21:00—male 28, female 29 (Dittberner and Dittberner 1984).

**Nest sanitation.** No data for Alaska subspecies. Following based on Smith 1950 for *flavissima*. When nestlings are <4 d old, parents either eat fecal sacs or carry them away and drop them in the air. Adults often stimulate nestling to defecate by touching cloacal region on nestling with beak. Adults then take fecal sac, run for some distance, then fly away. At ≥6 d old, nestlings defecate on rim of nest. At this age, adults pick up fecal sacs from rim of nest instead of directly from nestlings. In 9-d-old nestlings of *flava*, male performs 49% of fecal sac removal, female 51%; frequency of removal of fecal sacs by male and by female during day as follows: 03:00–09:00—male 8 times, female 5 times; 09:00–15:00—male 7 times, female 12 times; 15:00–21:00—male 12 times, female 11 times (Dittberner and Dittberner 1984).

#### COOPERATIVE BREEDING

Not known.

#### BROOD PARASITISM

None in Alaska. Elsewhere, Yellow Wagtail, including e. Siberian subspecies of *tshutschensis* and *simillima*, is rare host of Common Cuckoo

(*Cuculus canorus*). Despite being numerous in many habitats occupied by Common Cuckoo, Yellow Wagtail is only rarely parasitized (Mal'chevski 1987). Only 15 cases of known parasitism by Common Cuckoo in Soviet Union, compared to 97 parasitized nests of 294 nests for sympatric White Wagtail (Mal'chevski 1987, Badyaev et al. 1996). Of 233 cuckoo eggs found in nests of 4 Motacillidae species, only 18 were from Yellow Wagtail (Smith 1950). Parents intensively attack female cuckoo near nest; 2–3 neighboring pairs may join the aerial chase (AVB). Successful fledging of cuckoos from Yellow Wagtail nests reported in n.-central and e. Europe, central Asia, and w. Siberia (Mal'chevski 1987). Demographic consequences of parasitism in Old World are negligible because of low frequency of parasitism on Yellow Wagtails; none in Alaska.

#### FLEDGLING STAGE

**Departure from nest.** Nestlings normally leave nest when 12–13 d old ( $n = 2$  nests; Baldwin 1955). In *flavissima*, nestlings leave nests when 11.7 d old on average (range 10–16,  $n = 19$  nests; Mason and Lyczynski 1980); or 12–13 d old ( $n = 14$ ; Smith 1950). In *flava*, leave nest at 9–12 d old; still incapable of flight (Mal'chevski and Pukinski 1983). Nestlings depart nest soon after sunrise (Smith 1950).

**Growth.** See Dittberner and Dittberner 1984 for details of growth and development.

**Association with parents or other young.** Families of *flava* leave nesting territories within 2 wk of nest departure; broods disassemble within 2 wk, and young birds often feed with other species, such as White Wagtail (Mal'chevski and Pukinski 1983).

**Ability to get around, feed, and care for self.** Fledglings usually do not fly until sixteenth day (Smith 1950); begin to feed themselves when 17–18 d old (Dittberner and Dittberner 1984).

#### IMMATURE STAGE

No information for Alaska subspecies.

### DEMOGRAPHY AND POPULATIONS

#### MEASURES OF BREEDING ACTIVITY

**Age at first breeding; intervals between breeding.** Age at first breeding 1 yr (Cramp 1988). Breeds annually.

**Clutch.** In *tschutschensis*, mean 5.2 eggs  $\pm$  0.7 SD (range 4–7,  $n = 43$  nests; BK and DDG). In *flavissima*, mean 5.18 eggs  $\pm$  0.08 SE (range 3–7,  $n = 116$  nests; Mason and Lyczynski 1980). In *flava*, mean 5.12 eggs  $\pm$  0.77 SD (range 4–6,  $n = 67$ ; calculated from Mal'chevski and Pukinski 1983). See Breeding: eggs, above, for details. In w. Palearctic Yellow Wagtails,

clutch size decreases as season progresses, and increases with latitude of breeding (Mason and Lyczynski 1980, Paulsen 1993).

**Annual and lifetime reproductive success.** No data for Alaska subspecies. For *flavissima* in England ( $n = 157$  nests, 808 eggs): average 2.64 young fledged/nest; 67.6% of laid eggs hatch; 75.8% of nestling fledge; young fledged from eggs laid, 51.3%. Clutches of 3 eggs produced, on average, 0.88 fledgling; of 4 eggs, 2.50 fledglings; of 5 eggs, 3.04 fledglings; and of 6 eggs, 2.98 fledglings. Causes of nest failure: predation 29.2%, desertion 30.8%, weather 13.8%, agricultural activities 15.4%, infertility (all eggs) 1.5%, trampling by cattle 7.7%, other 1.5% ( $n = 65$  nests; Mason and Lyczynski 1980). In another English population ( $n = 19$  nests, 99 eggs): average 3.47 young fledged/nest; hatching success 75.8%; fledging success 88.0%; young fledged from eggs laid, 66.6% (Smith 1950). In sw. Norway, average 4.62 young fledged/nest; hatching success 76%; fledging success 97.4%; young fledged from eggs laid, 76% ( $n = 23$ ); 42% of nests lost to agricultural activities; nesting success higher outside of cultivated grasslands (Paulsen 1993). Average ratio of juveniles to adults in premigratory gatherings in s. Europe 2.19 ( $n = 6$  yr, 2,864 birds; Spina and Massi 1992).

**Number of broods normally reared per season.** One brood/yr in Alaska (AVB, BK and DDG).

#### LIFE SPAN AND SURVIVORSHIP

Oldest known *flava* 8 yr 5 mo (Cramp 1988). On basis of extensive banding on wintering grounds in Taiwan, McClure (1974) reported band recoveries of birds harvested for food as follows: 21% harvested within 2 mo on wintering grounds, 44% harvested by 6 mo (did not breed), 35% harvested the following year (after 1 breeding season). Of 1,758 birds banded on wintering grounds, only 4 recaptured: 1 during same winter, 2 after 1 breeding season, and 1 after 2 breeding seasons. Of 3,938 banded at different location in Taiwan, 13 recaptured within same winter and 9 the following winter. Of 33,700 banded in Taiwan in 1967, 3.2% were recaptured in 1968. In addition to mortality, extremely low resighting rates may be due to low winter-area fidelity (McClure 1974).

Annual mortality (actual mortality + dispersal) estimated by recaptures at w. African roost sites was 63.5–68% (Wood 1978). See also Range, below, for additional recapture data. For survival and population estimates using roost arrival data and capture-recapture models, see Buckland 1980.

#### DISEASE AND BODY PARASITES

Of 338 Yellow Wagtails examined in Thailand and Taiwan, 15 (4.4%) had *Haemoproteus* spp. (a

blood parasite), found in Feb–Apr and Sep–Dec; 1 of 75 birds in lowland Thailand (where some Alaska Yellow Wagtails winter) had *Haemoproteus* spp. (McClure et al. 1978). *Haemoproteus motasillae* found in Yellow Wagtails collected in Uganda, but this parasite not reported in New World populations (Bennett and Peirce 1990). Of 129 Yellow Wagtails examined in w. Europe, 13 were infested with *Leucocytozoon* spp., 4 with *Trypanosoma* spp., 2 with *Haemoproteus* spp., and 2 with *Plasmodium* spp.—all blood parasites (Peirce 1981). Yellow Wagtail is a host for feather mites *Analges pachycnemis* (occurs in contour and down feathers) and *Pteronyssoides motacillae* (occurs on ventral side of large primaries and primary-coverts; Mironov 1985; see also Kurbanova 1973 and Fedorenko et al. 1981). Tapeworm *Anonchotaenia globata* found in small intestine of 1 in 20 (5%) Yellow Wagtails (Petrova 1978). For details of transmission of Newcastle disease virus by Yellow Wagtails, see Mousa et al. 1988.

#### CAUSES OF MORTALITY

No data on mortality during nesting season. Inclement weather—especially unfavorable wind direction during long-range, nonstop migratory movements—may significantly increase mortality during sea and desert crossings (Wood 1982 and 1992 and references therein). Seasonal decrease in food availability on wintering grounds potentially causes increase in mortality late in winter (Wood 1978). Intensive commercial trapping of Yellow Wagtails for food in Taiwan contributes to high mortality on Asian wintering grounds (McClure 1974). Yellow Wagtails often share wintering roost sites with avian species that are controlled by avicides in Sahel Delta, w. Africa; as a result, many wagtails die of exposure to such chemicals (Mullié et al. 1991; see Conservation and management: effects of human activity, below).

#### RANGE

**Initial dispersal from natal site.** Most young *flava* left vicinity of breeding site within 1 mo after leaving nests; no recaptures in the following year (Mal'chevski and Pukinski 1983). For other data on natal dispersal in w. Palearctic populations, see Cramp 1988.

**Fidelity to breeding site and winter home range.** Male-biased fidelity to previous year's breeding site (Dittberner and Dittberner 1984). In 1 w. German population, return rate of adults 31–80% (Cramp 1988). Marked fidelity (up to 4 yr) to summer communal roost sites (Dittberner and Dittberner 1984). High fidelity also to wintering areas: Of 10,000 banded in n. Nigeria, 248 retrapped in first winter, 97 in second, 23 in third, 6 in fourth, 2 in

fifth, and 1 in seventh (Moreau 1969). Of 10,000 banded in s. Nigeria, 150 recaptured; of 6,612 banded in e. Africa, 152 recaptured on same wintering grounds (Simms 1992). However, little fidelity to wintering roosts of previous year after disturbance. Frequent disturbance by trappers and agricultural operations on wintering grounds in Taiwan disturbs traditional roosts in sugarcane fields, leading to decreased winter-roost fidelity; average distance of recoveries from previous winter roost site was about 34 km in year after disturbance (McClure 1974).

**Dispersal from breeding site.** Renests within previous breeding territory or nearby if first nest is depredated; replacement nests built 17–100 m from first nest site (European subspecies; Dittberner and Dittberner 1984).

**Home range.** Movements on wintering grounds: Of 309 banded wagtails, 172 recorded within 9.7 km of banding site, 6 within 12.9 km, 41 at 23.4 km, 37 at 29.0 km, and 53 >34 km away (McClure 1974). On wintering grounds, daily movements between foraging and roosting sites often  $\geq 30$  km (Ali and Ripley 1973). Summer communal roost sites used for extended time: by adults, for average 19.5 d, by juveniles, for average 13 d (Dittberner and Dittberner 1984, 1987).

#### POPULATION STATUS

**Numbers.** Most common or second most common passerine at Umiat, AK, during 1950s; third or fourth most common along Colville River (Kessel and Cade 1958); sixth most common breeding passerine on Seward Peninsula in late 1960s–early 1970s (Kessel 1989). One of the most common landbirds in St. Michael in late nineteenth century (Nelson 1887). In suitable habitats, breeding densities reach 1.5–2.2 pairs/10 ha (BK and DDG). Numbers in linear habitats have varied from 0.6 bird/km on coastal plain of n.-central Alaska to 1.6 pairs/km in nw. Alaska to 7 pairs/km farther south at lower edges of brush zone adjacent to tundra and marsh in Askinuk Mtns. (Kessel et al. 1964, BK and DDG). Average density in n. and central Europe: 2.92 pairs/10 ha of suitable habitat (Dittberner and Dittberner 1984).

**Trends.** Decrease in populations supplying Taiwan wintering areas presumably due to low adult survival (see Life span and survivorship, above) and to disturbance and harvesting of birds on wintering grounds (McClure 1974).

#### POPULATION REGULATION

No information for North American populations. See Conservation and management: effects of human activity, below.



## CONSERVATION AND MANAGEMENT

### EFFECTS OF HUMAN ACTIVITY

**Habitat alteration.** Intensive logging during nineteenth century considerably aided range expansion in w. Palearctic populations (e.g., Mal'chevski and Pukinski 1983). As result of logging, breeding densities increased from 0.2 pair/km<sup>2</sup> in virgin pine forests to 3.0 pairs/km<sup>2</sup> in thinned pine forests (n. Finland; Virkkala 1987). Breeding density declines locally after changes in agricultural practices that result in tall, dense ground vegetation (Smith 1950, Mal'chevski and Pukinski 1983). For effects of deforestation on wintering grounds, see Gatter and Mattes 1987.

**Pesticides and other contaminants/toxics.** Wintering individuals apparently avoid fields treated with pesticides in Sahel and Senegal River valleys, w. Africa. Often share night roosts with several granivorous bird species on wintering grounds in w. Africa, and often killed there by avicides such as phosdrin, toritox, and parathion, as well as by explosives used for control of granivorous species (Mullié et al. 1991). For other effects of pesticides, see De Snoo and De Leeuw 1996.

**Disturbance at nest and roost sites.** Frequently disturbed by trappers on wintering grounds in Taiwan; 1 night of trapping was sufficient to cause birds to desert roost. Also disturbed by agricultural operations on roost sites in sugarcane fields (McClure 1974). Pronounced trap shyness; previously captured birds are 6–7 times less likely to be captured again at same roost (Buckland and Hereward 1982); see Buckland 1980 for capture-recapture models based on roost arrivals and tenure.

### MANAGEMENT

No data from Alaska. Intensive logging considerably aided range expansion (see Effects of human activity, above). Commercial trapping for food on wintering grounds may cause population declines (McClure 1974). See Wood 1992 for conservation of migrating Yellow Wagtails in w. Palearctic.

## APPEARANCE

### MOLTS AND PLUMAGES

**Hatchlings.** Drying down of hatchlings changes from dark gray to yellowish by end of first day, to dark yellowish by end of second day, and to yellowish brownish (10 mm long) by end of fourth day (Dittberner and Dittberner 1984). Gabrielson and Lincoln (1959) described nestling down as buffish white. See Neifeldt 1970 for details of natal down distribution.

**Juvenal plumage.** Little information on timing or sequence of Prejuvenal molt. In *flava*, feather growth continues for 10–15 d after departure from nest (Mal'chevski and Pukinski 1983). In *tschutschensis*, "top of head and back nearly uniform fulvous brown, varying to olive brown; wings and tail as in the adult. The white chin patch is much extended, frequently reaching far down on the throat, where it is more or less washed with pale fulvous. The sides are washed with dingy olive-brown" (Gabrielson and Lincoln 1959: 691). Juvenal plumage described as follows in European populations: "Upperparts variable, pale buff-brown with darker feather-centers—olive-brown, dark gray-brown, or dull olive-gray; side of crown with black stripe, Lore mottled gray and buff, often with a dark spot in front of eye. Supercilium from above eye backwards and narrow eye-ring pale buff or off-white. Upper cheek and ear coverts brown or dull gray with fine buff or off-white specks and streaks. Broad stripe running backwards from gape pale buff or off-white, bordered by distinct black malar stripe below; black of malar stripe extends up into short black band at rear of cheek and down into boldly spotted black band across upper chest. Underparts pale yellow-buff, pale yellow, buff-white, or dirty white. Tail, flight feathers, tertials, and greater upper wing-coverts like upperparts; median and greater coverts dull black with pale yellow-buff tips which soon bleach to white (coverts blacker than in adult, pale tips more sharply demarcated; tips buffier or whiter, less yellowish" (Cramp 1988: 429).

**Basic I plumage.** Prebasic I molt partial, extent of molt variable and depends strongly on geographic location (see below). Feathers replaced include all contour body-feathers, usually all marginal and median upperwing-coverts (about 10% retain variable numbers of these feathers); less than 1% of birds replace all greater upperwing-coverts, about 30% of birds replace 1–4 greater-coverts; less than 6% of birds (but see Dittberner and Dittberner 1987) replace 1–3 rectrices and rarely 1–3 tertials (Ginn and Melville 1983, Jenni and Winkler 1994). No primaries or secondaries replaced.

All Juvenal-plumaged Yellow Wagtails collected at Umiat, AK, after 25 Jun (16 males, 12 females) were molting; molt "nearly complete" on 1 juvenile female on 23 Jul (Baldwin 1955). In w. Palearctic populations, Prebasic I molt begins when birds are 25–30 d old, lasts 35–40 d (Mal'chevski and Pukinski 1983), longer in some populations (average 43 ± 5 d, according to Dittberner and Dittberner [1987]).

In European populations, Basic I male varies in appearance. May be similar to Definitive Basic male or Definitive Basic female (see below). Basic I female similar to Definitive Basic female or duller.

All immatures distinguished from adults by presence of retained Juvenal flight-feathers and wing-coverts (see below; Cramp 1988).

Best ageing criteria of immatures after Prebasic I molt until fall migration is skull pneumatization (Serra 1992, Jenni and Winkler 1994). Other characteristics include pronounced differences in wear and color between retained Juvenal feathers and new Basic I feathers within greater-coverts, alulae, rectrices, and tertials. In late summer, adults can be distinguished from juveniles by lack of white on fringes of all greater-coverts, lack of differences in wear and color that result from molt, and much greater feather wear (see Dittberner and Dittberner 1987 and Jenni and Winkler 1994 for illustrations).

**Alternate I plumage.** In European populations, Prealternate I molt of second-year birds identical to Definitive Prealternate molt, but more greater secondary-coverts might be replaced (Jenni and Winkler 1994). Plumage identical to Definitive Alternate plumage (see below), except in males underparts slightly paler and retained outer greater wing-coverts worn and have white margins, and female variable, resembling Definitive Alternate female or Definitive Basic female (see below; Cramp 1988).

**Definitive Basic plumage.** Definitive Prebasic molt complete. In most subspecies, proceeds as follows: Primaries replaced in order P1 to P10, P10 sometimes replaced together with P9 or P1-P10; P1-P5 phase is considerably faster than P6-P10 phase (Sondell 1993, Spina and Massi 1992). First secondary shed with P6; secondaries molt in sequence S1-S6. Tertials replaced rapidly, with no particular relationship to molt of other feathers; shed in sequence T2, T1, T3. Molt of alula-feathers begins with P8 and lasts until after primary molt is completed (Spina and Massi 1992). In *flavissima*, molt pattern of rectrices normally is symmetrical (37% of birds); central pair shed first (R1 first, R6 last); 33% of birds shed R1 and R6 together, 13% show asymmetrical molt pattern (Ginn and Melville 1983); see Sondell 1993 for details of tail molt in *flava*.

In *flava*, primaries and secondaries replaced in 34.7 d in males and in 35.5 d in females on average (Sondell 1993). Feather growth as follows ( $n = 78$  birds; Sondell 1993): Tertials and rectrices start to molt when primaries are 0-30% grown; secondaries start to molt when primaries are 30-50% grown. Tertials completely replaced when primaries are 50-70% grown; tail fully regrown when primaries are 80-90% regrown. Secondaries are 50-60% grown when all primaries are fully grown. Number of primaries and secondaries usable for flight averages 12.4 (83%) of total 15 wing-feathers; if tertials and

tail considered, 15.7-19.2 feathers of nominal 24 remain usable during molt (Sondell 1993).

None of the 18 adults (11 males and 7 females) collected at Umiat, AK, had begun molt during period 14-24 Jun; 5 of 7 males and 5 of 6 females had begun molt between 25 Jun and 14 Jul; 1 male was in advanced molt on 13 Aug, 2 females collected 26-28 Jul were molting (Baldwin 1955). In central and n. European populations, molt begins right after breeding and lasts 45-55 d (Mal'chevski and Pukinski 1983, Spina and Massi 1992). Molt lasts 43-53 d in males and 40-48 d in females (Dittberner and Dittberner 1987), and fall migration begins immediately thereafter (Sondell 1993). In subarctic populations (farther north than 67°N), molt often overlaps with breeding; 8 of 10 males and 2 of 10 females feeding nestlings were molting primaries; in these birds, onset of molt coincided with hatching of young (n. Russia; Ryzhanovskii 1987). In most Yellow Wagtails in this population, intensive molt coincides with feeding of fledglings; female-biased ratio among late-molting birds (Ryzhanovskii 1987).

"Adults are nearly uniform olive-brown above, with a grayish shade on the crown and grayish on the rump. Tail and wing feathers are of a softer shade than in the spring, and tinted with a mixture of olive. Superciliary line white, sometimes yellow shaded. White chin patch extends to the breast and the yellow or fulvous of breast surrounds it posteriorly; this fulvous-brown shade extends across the breast. Abdomen dingy yellowish; sides and flanks dingy olive" (Gabrielson and Lincoln 1959: 691).

**Definitive Alternate plumage.** Definitive Prealternate molt incomplete. Feathers replaced include contour body-feathers, all rectrices, 2-3 tertials, 5-8 greater-coverts (10-6), all (47.7% of birds) or some (43.0%) marginal coverts, and all (42.5% of birds) or some (46.8%) median-coverts (Jenni and Winkler 1994). Takes place on wintering grounds and lasts 50-90 d, often in 2 stages. Innermost greater-coverts, some marginal and median-coverts, tertials 8-9, and many feathers of head, throat, and mantle molt during first stage; central greater-coverts, rest of marginal and median-coverts, tertial 7, and all rectrices are replaced during second stage. Head- and neck-feathers may be replaced again during second stage. See Jenni and Winkler 1994 for ageing criteria of adult and 2-yr-old birds after Definitive Prealternate molt.

Sexes alike. "Crown and nape, extending down the sides of the neck, clear ashy, becoming shaded more or less with brown in poor or worn plumage; back rich olive green, especially upon the rump and upper tail feathers, and extending to just back of the ashy crown patch; intermediate region between the shoulders and on the scapulars shaded

more or less strongly with brown, becoming ashy brown; wings brown; tertiaries and coverts edged with pale yellowish white, the tips of the coverts forming two dull wing bars. Middle tail feathers dark-brown, becoming nearly black in some specimens; two outer feathers have their basal quarter brown, with a narrowing band of the same extending from the dark base along the inner half of inner web, reaching nearly to the tips; remainder of these feathers white, including the entire tip of each and their shafts. Narrow white superciliary stripe usually commences at the nostril and reaches to the nape, but in some specimens it is obsolete in front of the eye, and is frequently barely discernible. A dark brownish ashy line includes the lores, eye, and ear coverts. Chin white, shading into rich greenish yellow, which occupies the entire under parts, including the under tail coverts. Olive green of back extends on the sides of neck and breast, forming a more or less obsolete and slightly clouded band across the breast, the basal half of each feather being olive green with a yellowish tip. A strong wash of olive green extends along sides and flanks" (Gabrielson and Lincoln 1959: 961).

#### BARE PARTS

**Bill and gape.** In nestlings, inside of mouth orange yellow, gape-flanges pale yellow. In juveniles, bill pale fleshy horn color; in adults, bill black in spring and horn color in fall (Gabrielson and Lincoln 1959).

**Iris.** Dark or very dark hazel (Gabrielson and Lincoln 1959, University of Alaska Museum).

**Legs and feet.** In juveniles, legs are pale fleshy horn color; in adults, feet black in spring and horn color in fall (Gabrielson and Lincoln 1959).

#### MEASUREMENTS

See Appendix. Measurements of wing (flattened; Vaurie 1959): male *tschutschensis*—76–80 mm (mean 78,  $n = 8$ ); male *simillima*—80–85 mm (mean 83,  $n = 10$ ). Intergrade male *simillima* × *tschutschensis* from w. Aleutian Is. (passage migrant): mass, 18.2 g; wing-chord length, 80.2 mm; tail length, 66.7 mm; tarsus length, 23.4 mm (University of Alaska Museum). See also Bhattacharyya 1985 for morphology of tongue muscles.

#### PRIORITIES FOR FUTURE RESEARCH

Although the Palearctic subspecies of the Yellow Wagtail are well studied, many aspects of the biology of the North American Yellow Wagtail remain unknown. Especially needed are research

on energetics and metabolism in arctic conditions and data on nestling growth and development. The entire wintering range of Alaska wagtails remains unknown.

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**Appendix.** Linear measurements (mm) and mass (g) of adult Yellow Wagtails from Alaska. Specimens of *M. f. tschutschensis* from Alaska mainland (breeding range), those of *M. f. simillima* from w. Aleutian Is. (passage migrants). Specimens from University of Alaska Museum and U.S. National Museum. Data shown as mean (range, *n*).

	<i>M. f. tschutschensis</i>	<i>M. f. simillima</i>
Mass		
Male	16.04 (15.1–17.5, 5)	21.4 (21–21.7, 3)
Female	17.06 (15.4–20.4, 7)	
Wing-chord		
Male	76.6 (74.5–78.5, 17)	82.8 (81.2–83.6, 3)
Female	74.5 (72.0–77.8, 11)	
Tail		
Male	65.5 (63.5–67.7, 16)	68.6 (66.7–71.4, 3)
Female	64.02 (57.3–66.7, 9)	
Tarsus		
Male	24.3 (22.7–25.2, 15)	24.7 (23.2–25.9, 3)
Female	23.9 (23.2–24.6, 9)	
Culmen		
Male	9.1 (8.2–9.8, 15)	9.8 (9.5–10.2, 3)
Female	9.1 (8.8–9.5, 6)	

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