

White Wagtail

Motacilla alba

FRENCH: *Bergeronnette grise*
RUSSIAN: *Belaya Tryasoguzka*

Black-backed Wagtail

Motacilla lugens

FRENCH: *Bergeronnette lugubre*
RUSSIAN: *Kamchatskaya Tryasoguzka*

Although the well-known White Wagtail complex includes some of the most thoroughly studied birds in the western Palearctic (e.g., *Motacilla alba alba* and *M. a. yarrellii*), two eastern palearctic forms that occur annually in North America (Alaska)—and that are the focus of this account—remain poorly known. The easternmost subspecies of the White Wagtail, *M. a. ocularis* Swinhoe 1860, reaches the western perimeter of Alaska in the Bering Strait region, and the Black-backed Wagtail, *Motacilla lugens* Gloger 1829, does so in the western Aleutian Islands.

Originally described as a full species but long treated as a subspecies of the White Wagtail, the Black-backed Wagtail has been segregated again as a full species by the American Ornithologists' Union (1983) based on work in Asia (e.g., Nazarenko 1968).

Breeding widely in remote parts of Asia, these two taxa are among the least studied forms of the *Motacilla alba* complex.

Both White and Black-backed wagtails occur near rivers and along sea coasts. White Wagtail also inhabits more inland areas and is

associated more with human settlements than is Black-backed Wagtail. The latter occurs mostly within one to two kilometers of sea coastline and on oceanic islands. In addition to breeding habitat, the two species differ in phenology of nesting, song, and courtship displays.



White Wagtail



Black-backed Wagtail

The Birds of North America

Life Histories for the 21st Century



Figure 1.

Distribution of the White Wagtail in North America. The Black-backed Wagtail is only known to breed at two localities in North America, Nome and Attu Island, Alaska. These species also breed in Asia (see text for details). Birds breeding in North America winter in Asia, and occasionally are reported during fall, winter, and spring along the West Coast of North America.

Differences in phenology of breeding may be caused by greater dependency of Black-backed Wagtail on availability of flying insects than in other wagtails. A growing number of human settlements, roads, and other industrial constructions along coastlines and in northern regions increases suitable breeding and foraging habitats for both species and most likely will lead to the expansion of the wagtails' range in North America. Many aspects of the wagtails' biology, especially territoriality, physiology, and breeding behavior, are better studied in eastern palearctic populations, and the Old World literature sheds much light on the biology of these species. Thus, understudied North American populations of White and Black-backed wagtails provide excellent opportunities for comparative studies of breeding biology of these species in relation to Asian populations.

DISTINGUISHING CHARACTERISTICS

Medium-sized (19 cm, 25–30 g) passerines with characteristic black-and-white pied plumage, long, often wagged tail, and strongly undulating flight. Adults sexually dimorphic in plumage and wing length. Alternate-plumaged immature (second year [SY]) and adult (after second year [ASY]) male Black-backed Wagtail best distinguished from male of White Wagtail (*M. a. ocularis*) by much more black on back and rump; all-gray upper rump always indicates White Wagtail. Both sexes of White Wagtail have clearer and brighter blue-gray back than the darker gray back of Black-backed Wagtails. Adult Black-backed Wagtail has mostly-white primaries, especially noticeable in flight, in contrast to adult White Wagtail and to immature (SY) Black-backed Wagtail, which have mostly dark wings. Only Black-backed Wagtail has pure white chin and only adult White Wagtail has solidly black chin. Black-backed and White wagtails in Juvenal plumage, and immature birds before the second Prebasic molt, are indistinguishable in the field (see Morlan 1981, Howell 1990). Occurrence of hybrids complicates identification of extralimital birds of this complex in North America.

DISTRIBUTION

THE AMERICAS

Breeding range. Figure 1. White Wagtail (hereafter meaning *M. a. ocularis* unless otherwise noted) confined to w. Alaska; breeds annually in small numbers from St. Lawrence I. and the Norton

Sound coast of Seward Peninsula north along coasts of Bering and Chukchi seas to capes Thompson and Lisburne (Kessel and Gibson 1978). May breed occasionally on coast south of Norton Sound (Yukon-Kuskokwin Delta; BK and DDG).

Black-backed Wagtail (hereafter meaning *M. lugens*) has nested several times on Attu I. in the w. Aleutians, AK, where it occurs annually in spring in small numbers (Gibson 1981, Wagner 1991). Elsewhere in Alaska, a Seward Peninsula (Nome) breeding pair (Kessel 1989) apparently comprised both a male and a female Black-backed Wagtail (Univ. Alaska Mus. photos), although this nesting took place within the Alaska breeding range of White Wagtail and thus might have been expected to involve a hybrid pair.

Winter range. Few winter records of these species from the Americas. Transients of both species recorded casually in spring and fall along Pacific Coast from British Columbia south to s. Baja California; also winter records (but very few) within this area from Oregon to s. Baja California (Roberson 1980, Small 1994, Howell and Webb 1995). See Migration, below.

OUTSIDE THE AMERICAS

Breeding range. **WHITE WAGTAIL.** All mainland e. and ne. Siberia from coast of the Arctic Ocean southward. Southern boundary: north of Lake Baikal, ne. Kamchatka Peninsula, upper reaches of Kolyma River, along the Sea of Okhotsk coast, including Yablonovyi and Stanovoi ranges; western boundary: n. Taimyr coast (Dement'ev and Gladkov 1954). Regular visitor on Novosibirskie and Wrangel islands (Kistchinski 1988). Several sightings at Geraldton, w. Australia (Storr et al. 1982).

BLACK-BACKED WAGTAIL. S. and central Kamchatka Peninsula, Commander and Kuril islands, Sakhalin I., Shantar I., lower reaches of Amur River and Ussuriland; s. China, n. India, ne. Burma, North Vietnam; n. and central Honshu, Japan (Dement'ev and Gladkov 1954).

Winter range. **WHITE WAGTAIL.** Sw. China, Philippines, Hainan, Cameroon Highlands, Selangor, and Singapore. Uncommon winter visitor in the Malay Peninsula (McClure 1974, Medway and Wells 1976), Assam, Nagaland, Manipur, Bangladesh, and w. and central Nepal (Ali and Ripley 1973).

BLACK-BACKED WAGTAIL. Se. Asia. Mainly Japan: common winter visitor to Hokkaido and very common winter visitor south of Honshu to Nansei Shoto (Brazil 1991). Also winters south of Yangtze, China, and in Taiwan. Fifteen wagtails from n. Sakhalin and Kuril islands wintered in Okazaki and Yahigi, Japan (McClure 1974). Accidental in Queensland, Australia, May–Sep 1987 (Ross 1987).

HISTORICAL CHANGES

Since 1930s, Black-backed Wagtail has been extending its breeding range southward, colonizing n. Honshu, central Japan, and thereby coming in contact with Japanese Wagtail (*M. grandis*; Nakamura 1985). Increasing number of towns along sea coast has brought *M. a. leucopsis* to the coastline and thereby increased its contact zone with Black-backed Wagtail in s. Ussuriland (Nazarenko 1968).

FOSSIL HISTORY

No information.

SYSTEMATICS

GEOGRAPHIC VARIATION

Marked variation in plumage patterns and coloration along ranges of 9–13 strongly morphologically distinct subspecies of *M. alba*. See Nakamura 1985 for review of variation in plumage characteristics among the subspecies. See Johansen 1944, Dement'ev and Gladkov 1954, and Cramp 1988 for geographic variation in w. palearctic *M. alba*, see Étchécopar and Hüe 1983 for e. palearctic subspecies.

SUBSPECIES; RELATED SPECIES

Unresolved taxonomic relations within *M. alba* complex (see below). *Motacilla [a.] personata* and *M. [a.] dukhunensis* may have reached species level. Nine to 13 subspecies of *M. alba* include *M. a. yarrellii* (British Isles, nw. Europe), *M. a. alba* (Europe), *M. [a.] dukhunensis* (w. Siberia and Caucasus), *M. a. baicalensis* (Far East and China), *M. a. ocularis* (see Distribution, above), *M. [a.] lugens* (see Distribution, above), *M. [a.] personata* (central and Middle Asia), *M. a. persica* (Iran), *M. a. subpersonata* (nw. Africa), *M. a. alboides* (s. Tibet, nw. Sinkiang and North Vietnam), and *M. a. vidua* (Johansen 1944, Dement'ev and Gladkov 1954, Ali and Ripley 1973, Étchécopar and Hüe 1983, Nakamura 1985, Cramp 1988). Closely related species (formerly races of *M. alba*): Japanese Wagtail, African Pied Wagtail (*M. aguimp*), and Large Pied Wagtail (*M. madaraspatensis*).

M. lugens has apparently differentiated from *M. alba* at species level; differs from *M. alba* in breeding habitat, phenology of nesting, song, and courtship displays (see below). Area of infrequent hybridization of *M. lugens* and *M. a. leucopsis* limited to 2–3 km along coastline in s. Ussuriland. No hybridization occurs in typical habitat of each form (Nazarenko 1968). See Nazarenko 1968 and Panov 1973 for list of known *M. lugens* × *M. a. leucopsis* pairs in the field and in museum collections. Also, twice on St. Lawrence I., AK, male *M. lugens* ×

female *M. a. ocularis* (J. L. Dunn in litt.) Despite extensive overlap in breeding ranges, *M. lugens* and *M. grandis* do not interbreed in central Honshu, Japan (Higuchi and Hirano 1989). In part of its range, *M. a. ocularis* interbreeds with *M. a. dukhunensis* (Dement'ev and Gladkov 1954).

MIGRATION

NATURE OF MIGRATION IN THE SPECIES

Migratory. Black-backed Wagtail occasionally resident in central Japan (n. and central Honshu). In *M. a. yarrellii* more adults than hatch-year birds winter in northern parts of winter range (Dougall and Appleton 1989).

TIMING AND ROUTES OF MIGRATION

North American breeding populations migrate southwest–northeast to and from wintering grounds in Asia (see below).

White Wagtail. Arrives on the Seward Peninsula, AK, late May; migration continues to mid-Jun (Kessel 1989). First birds arrive in ne. Siberia early May, the last mid-May (Kistchinski 1980). Northbound birds pass s. Ussuriland (extreme ne. China and adjacent Russia, north of Vladivostok) mid-Apr to mid-May (Panov 1973). Males arrive ne. Yakutiya (extreme ne. Asia) 25–27 May, females 7–10 d later, 4–6 Jun (Gavrilov 1991a). Arrives Yakutiya about 21 Apr, Sea of Okhotsk coast (west of Kamchatka Peninsula and Kuril islands) and upper reaches of Kolyma River (ne. Siberia) end of May (Dement'ev and Gladkov 1954).

Fall departure from Seward Peninsula late Aug to mid-Sep (Kessel 1989). Last birds leave ne. Siberia late Sep (Kistchinski 1980). Birds from north pass the coast of Ussuriland late Sep–Oct (Panov 1973). A bird with an injured tarsus stayed in s. Ussuril and until mid-Dec, foraging along ice-free river areas (Panov 1973). Common on passage in the Nepal Valley in Mar–Apr and Oct (Ali and Ripley 1973). Recorded in Malaysia 8 Sep–6 Apr (Medway and Wells 1976).

Casual migrant in Pribilof Is., AK (22 May 1966; Thompson and DeLong 1969) and lone gray-backed birds reported—but species not substantiated—in the Aleutian Is., AK (Byrd et al. 1978, Gibson 1981). Regarded as accidental in central and se. Alaska (Kessel and Gibson 1978), but in absence of specimens from Alaska east of the Bering Sea as well as from North American localities beyond Alaska, identification of many extralimital birds is problematic (see Phillips 1991). In North America outside Alaska, casual or accidental records of adults in California (fall and winter; Roberson 1986, Pyle

and McCaskie 1992, Heindel and Garrett 1995) and Michigan (Apr; Powell 1985). A specimen from Baja California Sur (9 Jan 1882; Ridgway 1882) may be no longer extant (Phillips 1991). Additional records of unidentified white wagtails (either *M. a. ocularis* or Black-backed Wagtail) in British Columbia (Weber and Shepard 1975, Godfrey 1986), Oregon (Weber and Shepard 1975), Arizona (Stejskal and Witzeman 1986 [including photo]), and Sonora, Mexico (Alden and Mills 1974). An 1883 sighting in n. Quebec (Turner 1885) has been discussed under *M. a. alba* (Am. Ornithol. Union 1931, Phillips 1991), as has been a 1987 (Norton 1987) report from Barbados (Phillips 1991), but there are no substantiated New World records of nominate *M. alba*.

Black-backed Wagtail. Arrives w. Aleutian Is., AK, early May (BK and DDG). First birds arrive s. Ussuriland late Mar, peak early Apr (Panov 1973); in s. Kuril Is., first birds arrive first days of Mar, n. Kuril Is., end of Mar (Dement'ev and Gladkov 1954, Nechaev 1969); on Sakhalin I. and Kamchatka Peninsula end of Apr to early May (Dement'ev and Gladkov 1954). Transient birds pass Kuril Is., during Apr (Nechaev 1969). Black-backed Wagtails from Sakhalin and Kuril islands winter on average 1,920 km southwest (range 1,481.6–3,259.5 km, SD 437.6, $n = 15$; data from McClure 1974). Departs w. Aleutian Is., by late Sep (BK and DDG). Peak fall migration in s. Ussuriland is second half of Oct (Panov 1973). In Kamchatka Peninsula, peak is first 10 d of Sep; last transient bird 28 Nov (Dement'ev and Gladkov 1954). In Kuril Is., birds leave end of Sep; transients pass Oct–Nov, last on 25 Nov (Nechaev 1969). Wintering birds from Sakhalin I. recorded in Japan from 5 Nov to 9 Apr (McClure 1974).

In North America outside of Alaska, casual records of adults on the Pacific Coast in British Columbia (male, Apr 1982 [Mattocks and Hunn 1982]), Washington (male, May 1985, [Rogers 1985]; adult, May 1986, [Mattocks 1986]; male, May 1993, [Tweit and Gilligan 1993]), and California (adult female, Aug–Sep 1979 and Jul–Sep 1980, [Binford 1985]; adult male, May 1980, adult male, May 1985, [Bevier 1990]; adult bird, Aug–Sep 1987, [Pyle and McCaskie 1992]; 1 unknown, Sep 1994, [Yee et al. 1995]). Accidental on Atlantic Coast, in N. Carolina (male [photos examined by H. E. LeGrand, Jr.; in litt.], May 1982 [LeGrand 1982]).

MIGRATORY BEHAVIOR

White Wagtail. In spring and fall, migrates singly or in groups of 3–10 birds, rarely in larger flocks (Panov 1973, Kistchinski 1980). Males arrive when 1–3% and females when 5–10% of ground is snow free (Gavrilov 1991a). Nominate *M. alba* usually migrates along coastline of large water basins; small

groups fly at 30–70 m altitude (Mal'chevski and Pukinski 1983).

Black-backed Wagtail. Spring migration in groups of 7–10 birds (Nechaev 1969), often in single-sex flocks (Panov 1973). In Sakhalin I., flies along coast to far north part of island, and with warm weather flies south to nesting sites. Commonly arrives when area still snowbound (Dement'ev and Gladkov 1954). Flock of 120 birds seen in Okinawa, Japan, on 1 Mar (Brazil 1991). Fall migrations in flocks of 4–30 birds (Panov 1973); in family groups of 5–7 or small flocks of 10–12 birds (Nechaev 1969). Lone migrating wagtails common during Oct–Nov in Kuril Is.; transient birds stay at same site for no longer than 1–2 d (Nechaev 1969).

Both White and Black-backed wagtails are territorial during spring and fall migrations. See Behavior: agonistic behavior and spacing, below, for displays.

CONTROL AND PHYSIOLOGY

Premigratory period of White Wagtail characterized by increased activities of glucose-6-phosphate and malic enzymes in the liver. These enzymes facilitate high lipogenic activities during premigratory period which results in significant increase in body mass (Patel et al. 1977, Shah et al. 1978).

HABITAT

BREEDING RANGE

White Wagtail. In Alaska, sea cliffs and coastal villages (Kessel 1989). Elsewhere, also river banks. In ne. Siberia along sand and gravel areas of mountain rivers to subalpine (up to 500–750 m). Favors level areas of river basins. Along sea coasts, occupies grassy terraces with overhanging vegetation. Commonly associates with seabird colonies. Most numerous bird in human settlements of ne. Siberia (Kistchinski 1980; see Breeding: nest site).

Black-backed Wagtail. Ins. Ussuriland and Kuril Is., strictly along seacoast and rock cliffs of islands; rarely, also on islands along lake shores (Nazarenko 1968, Nechaev 1969, Panov 1973). Even in suitable habitats, distribution limited to 2 km from sea coastline (Nazarenko 1968). In Kamchatka Peninsula, up to 800 m above sea level (Nechaev 1969, Panov 1973). In Honshu, Japan, nests along streams without gravelly shores and along waterways in towns (Nakamura et al. 1984). In Alaska has nested in a shed, under a dilapidated river bridge, and under a seacoast pier.

SPRING AND FALL MIGRATION

Both White and Black-backed wagtails occur along gravel banks of rivers, shallow river areas,

and coastlines (Panov 1973, Kistchinski 1980) especially where some larger rocks or other similar structures (e.g., empty oil drums, cabins, bridges, driftwood) are present. Also see Food Habits: feeding, below.

WINTER RANGE

As during migration. Also see below, Food Habits: feeding; Demography and Populations: population status; and Watanabe and Maruyama 1977. In winter, Black-backed Wagtails form large communal roosts on buildings, in trees along streets, under bridges, and in industrial parks (Brazil 1991).

FOOD HABITS

FEEDING

Main foods taken. Mainly terrestrial and water invertebrates; occasionally seeds and berries. In winter, nominate *M. alba* occasionally consumes barley seeds and bread crumbs (Zahavi 1971).

Microhabitat for foraging. In prenesting period, White Wagtail forages primarily near human settlements, farms, and dumps (especially fisheries); often follows agricultural machinery. Also on washed-out logs along seacoasts, on muddy banks of rivers and lakes, and on dry moss-lichen tundra (Kistchinski 1980, Gavrilov 1991a). During nesting season, forages mostly along gravelly areas of rivers, shallow-water areas along seacoast, and in towns. In Jun often gathers insects on snowfields. Later in summer, some birds forage along lake shores, where birds run on floating leaves and vegetation debris up to 50 m from shoreline (Kistchinski 1980). Also, in Aug, forages near seabird colonies, picking Diptera pupae from cormorant (*Phalacrocorax*) and kittiwake (*Rissa*) nests that have fallen on ground. On rivers usually forages along water's edge, but sometimes flycatches for Tipulidae above water or digs in mud in search of mosquito larvae. Early in fall also forages in subalpine bushes (Kistchinski 1980).

During fall migration, Black-backed Wagtail commonly feeds along seacoast on wave-deposited invertebrates (AVB). In winter, in central Japan, 37% of 3,047 foraging attempts were along water's edge and in shallow water, 63% on sand and gravel of river banks (Higuchi and Hirano 1983).

Food capture and consumption. No data for *M. a. ocularis*. Of 995 foraging attempts during breeding season by Black-backed Wagtail, 77.4% on ground, 13.2% flycatching in air above water surface, 6.5% picking insects off walls and buildings while flying, and 2.9% feeding while flying at water surface; adult caddisflies (Trichoptera) and mayflies (Ephemeroptera) taken by flycatching, whereas larvae of these taxa taken by ground-feeding (Higu-

chi and Hirano 1989). On winter grounds, 92.7% of all foraging attempts on ground, 5.0% flycatching above water surface, and 2.3% feeding while flying at water surface (Higuchi and Hirano 1983). Flycatches significantly more often during breeding season than in winter (Higuchi and Hirano 1989). On sea beaches during fall migration, forages by moving along water's edge against surf direction, periodically flying back to beginning of foraging route and repeating the cycle; in small harbors often moves from one end to another and then flies back; in large bays or on particularly warm days with abundant food supply, interrupts feeding movements and flies back every 15–20 min of foraging (AVB).

M. a. yarrellii near Oxford, England, consumes on average $7,550 \pm 1020$ SD (range 4,790–15,160) prey items/day during winter foraging, or 15.4 ± 1.8 items/min; feeding rates lower and more variable when foraging within territory than when foraging in flocks; solitary birds use greater variety of prey-capturing techniques than birds in flocks (Davies 1976, 1977). See Rezanov 1981 for detailed account of foraging techniques of nominate *M. alba* in different habitats. In summer, consumes on average 15.19 ± 0.63 items/min (maximum 115 items/min near site of mass emergence of Diptera) including (items/min): on roads 11.31 ± 0.41 ($n = 219$), on ploughed fields 9.40 ± 0.87 ($n = 25$), along seacoast 13.28 ± 1.06 ($n = 36$), on meadows 6.75 ± 0.56 ($n = 16$), along water's edge of lakes and ponds 63.39 ± 6.36 ($n = 9$) (Rezanov 1981). Average run before picking prey on flat surface = 1.6 m (range 0.2–9.0, $n = 65$), on plowed fields 0.55 m ($n = 11$); average speed traveled while foraging on flat surface = 11.3 m/min (Rezanov 1981). When foraging in tall grass, groups of 2–6 birds often associate with moving groups of 10–20 domestic sheep. Birds perch on back of sheep for an average of 3.6 s ($n = 121$) before darting down to pick insects disturbed by moving sheep; also pick insects directly from animals and flycatch while perching on sheep (Rezanov 1981).

When flycatching, *M. alba* often follows large prey for up to 20 m (takes 15–20 s), usually ascending to 6–7 m (mean 0.97 m, $n = 33$), sometimes to 20 m for *Libellula* dragonflies (Rezanov 1981). Flycatching rate 2.3 ± 1.1 (SD) flights/30 s; number of captured prey 1.1 ± 0.8 (range 0–10); 97% of flights successful; average flight time 4.3 \pm 2.6 s/captured prey (Cuadrado 1994). Hovers for about 5 s when foraging on flying insects (Cramp 1988).

Large dragonflies captured with feet. Small prey swallowed whole. Butterfly (Lepidoptera) with 3-cm wingspan eaten over 45 s; large (up to 8 cm in length) *Aeschna* dragonflies held about 1.5 min on ground, then killed by about 52 pecks during 3 min and carried away using feet. Large prey usually

beaten against ground before being swallowed (Rezanov 1981).

DIET

Major food items. *WHITE WAGTAIL.* Stomachs of wintering birds in the pre-Saharan steppe of Tunisia contained mostly beetles, followed by caterpillars, ants, Tenebrionidae, and weevils (Coleoptera); also contained 1–5 stones. One stomach had many leaf fragments (Heatwole and Muir 1982).

BLACK-BACKED WAGTAIL. In s. Ussuriland during spring and summer, small Diptera; during fall migration, large caddisfly larvae, mayflies, amphipods (*Gammarus*), and water scorpions (Nepidae) (Panov 1973). On Kuril Is., in 12 stomachs: Diptera (adults and pupae), Aphrophoridae, earwigs (Dermaptera), beetles (Coleoptera) including Elateridae, Chrysomelidae, Staphylinidae, and small Melolonthinae; bugs (Hemiptera); *Sipha subrugosa*; hill ants (*Formica rufa*); Ichneumonidae; caterpillars (Lepidoptera); spiders (Araneae); small seeds; and sand particles (Nechaev 1969).

Quantitative analysis. See Breeding: parental care, below, for quantitative analysis of nestling diet. In winter, diet of *M. a. yarrellii* 96.7% Chironomidae, 1.2% various Coleoptera, and 2.1% Diptera other than Chironomidae (Davies 1977); in summer, 30% larvae Odonata, 15% larvae Lepidoptera, 30% Carabidae and Chrysomelidae beetles, 20% Diptera, Hymenoptera, and other insects, and 5% vegetative matter (Ptushenko and Inozemsev 1968). For geographic variation in diet of w. palearctic subspecies of *M. alba*, see Cramp 1988. In 9 wintering *M. alba*, mass of gizzard stones averaged 0.003 g (SD 0.0043, range 0–0.011; Heatwole and Muir 1982).

FOOD SELECTION AND STORAGE

See Davies 1977 for prey selection in wintering *M. a. yarrellii*.

NUTRITION AND ENERGETICS

In winter, territory owner *M. a. yarrellii* feeds for 90% of 8.5 h daylight, mean caloric value of prey approximately 3.5 cal; to maintain energy balance bird must consume 1 prey/ 3.3 s (Davies 1976, 1981). Energy intake depends on size of prey (handling time); varies from 117.1 cal/min when foraging around flooded pool (feeding rate 72.3 items/min, 1.6 cal/item) to 78.8 cal/min (10.1 items/min and 7.8 cal/item) when feeding around dung pats (Davies 1977). For caloric value of *M. a. yarrellii* prey items, see Davies 1976. In wintering *M. alba* in pre-Sahara steppe of Tunisia, oven-dry weight of food in 9 stomachs averaged 0.15 g (SD 0.09, range 0.01–0.28); mean food intake is 5.9% of dry body weight/day, highest estimate 8.2% (Heatwole and Muir 1982).

METABOLISM AND TEMPERATURE REGULATION

Metabolism and time budget of activities (hours spent per 24 h/kJ spent per 24 h) after pair formation and before nest building in White Wagtail in ne. Siberia (after Gavrilov 1991a) as follows. Display flights: male 2.78/50.04, female 0.36/5.96; other flight: male 0.21/3.78, female 0.28/4.64; bathing: both sexes 0.01/0.02; foraging: male 11.55/27.72, female 14.13/31.20; courtship displays: both sexes 0.01/0.02; preening: male 0.33/0.64, female 0.26/0.47; perching on vegetation: male 1.07/2.09, female 0.42/0.75; perching on ground: male 2.43/4.74, female 2.22/3.98; loafing: male 1.82/3.06, female 2.93/4.53; night roosting: male 3.79/5.69, female 3.38/4.66. Total energy of activities for male 97.8 kJ/d, for female 56.2 kJ/d. Thermoregulation energy during this period ($T_a = 0^\circ\text{C}$) for male 52.3 kJ/d, for female 53.26 kJ/d. Total daily expenditure for male 4.17 basic metabolisms (BM)/d, for female 3.31 BM/d. Basal metabolism for male 1.5 kJ/h, for female 1.38 kJ/h; Temperature coefficient HEM for male 0.083 kJ/h, for 1 degree centigrade, for female 0.076 kJ/h, for 1 degree centigrade (Gavrilov 1991a). Energy balance of wintering *M. a. yarrellii* is approximately 20–25 kcal/d (Davies 1981).

Metabolism and time budget of activities (percent of 24 h period/kJ spent per 24 h) of *M. a. alba* during nestling feeding as follows (after Dol'nik and Gracheva 1990). Night roosting: male 33.3/8.63, female 33.2/8.60; day sleeping: male 0.2/0.08, female 0.1/0.03; loafing: male 6.2/0.77, female 10.1/3.042; preening: male 0.8/0.29, female 2.0/0.62; vocalizing: male 0.4/0.46, female 0.6/0.21; display flights: male 0.3/0.91, female 0.2/0.68; territory defense (activities combined; AVB): male 21.3/12.05, female <0.1/0.02. nestling feeding, long-distance flights: male 0.9/2.91, female 1.5/4.72; nestling feeding in the nest: male 1.6/0.346, female 4.4/1.48; perching: male 3.9/1.11, female 5.9/1.69; picking: male 11.1/ 3.77, female 15.8/5.30; walking and running: male 15.6/6.47, female 19.5/8.06; short-to-medium range flights: male 4.0/9.52, female 5.9/14.20; hovering: male 0.5/2.21, female 0.9/3.45.

Total energy of activities for male 50.4 kJ/d, for female 52.1 kJ/d. Basal metabolism during this period 26.0 kJ/d. Total daily expenditure for male 1.94 BM/d, for female 2.00 BM/d. Thermoregulation energy during this period ($T_a = 15^\circ\text{C}$) for male 20.4 kJ/d, for female 20.2 kJ/d (= 0.78 BM) (Dol'nik and Gracheva 1990).

DRINKING, PELLET CASTING, AND DEFECATION

Drinks by sipping and dip-and-tilt action.

SOUNDS

VOCALIZATIONS

Development. No information.

Vocal array and behavior. Classification follows that of Cramp 1988 for *M. alba*.

SONG. In Black-backed Wagtail described as *chichit chichit chuy chuy chuku chuku chi chi chi* (5–15 s in duration, Fig. 2a); sings while feeding (Higuchi and Hirano 1989). As in other wagtails, apparently is not related to territorial behavior (e.g., Cramp 1988); in *M. a. alba* song given on wintering grounds while walking or resting (Zahavi 1971). *M. [a.] personata* sings most often during dangerous situations near nest or when aerial predators are in sight (Kovshar 1979).

ADVERTISING CALL. Fig. 2b. In Black-backed Wagtail repeated several times in sequence, *chiffee* (Higuchi and Hirano 1989) or *chuchun...chuchun* (Brazil 1991) while advertising a male's presence on conspicuous perch in territory or while reacting to intruders (Higuchi and Hirano 1989, AVB). In *M. alba che-wee* often given in response to Contact Call of potential intruders flying overhead (Zahavi 1971, Davies 1981, AVB).

CONTACT CALL. In *M. alba*, a monosyllabic *zit* or *psit* or 2–3 syllables *zittip* or *zillip* (Cramp 1988), or *tschizzik* in *M. a. ocularis* (Gabrielson and Lincoln 1959). Continuously given in flight and by caged birds toward passing flocks (AVB). Sometimes given while perched (Cramp 1988), or while foraging in flocks during migration (AVB); also used by males to attract females to territory in spring (Cramp 1988).

APPEASEMENT/SOLICITING CALL. Similar among subspecies, in *M. alba* a repeated, quiet *zrrrip* or variant *pee pee pee* given by female during male's pre-copulatory display, while inviting copulation, or while appeasing territory owner in winter (Cramp 1988).

ALARM CALL. In *M. a. ocularis*, *chtri chvchiv* given when intruder is near nest (Portenko 1989). In Black-backed Wagtail, *chubi chubi* given during physical fights on overlapping parts of neighboring territories (Watanabe and Maruyama 1977). In *M. alba*, repeated *quizzick* given in territory disputes; *chick, ki...ki...ki, or tic...tic...tic* given by birds near nest in reaction to intruder (Cramp 1988).

NESTLING AND FLEDGLING CALLS. Similar for both species. Nestlings give high-pitched *sisisisi* call; fledglings give stronger and lower-pitched *zississi* (Cramp 1988). Nestlings start to give fledgling call when 10 d old (Leinonen 1973).

Phenology. Male White Wagtail starts to sing about 1 wk after spring arrival to ne. Siberia (Kistchinski 1980). In central Japan, Black-backed Wagtail sings early Jan to late Jun. Peak early Mar

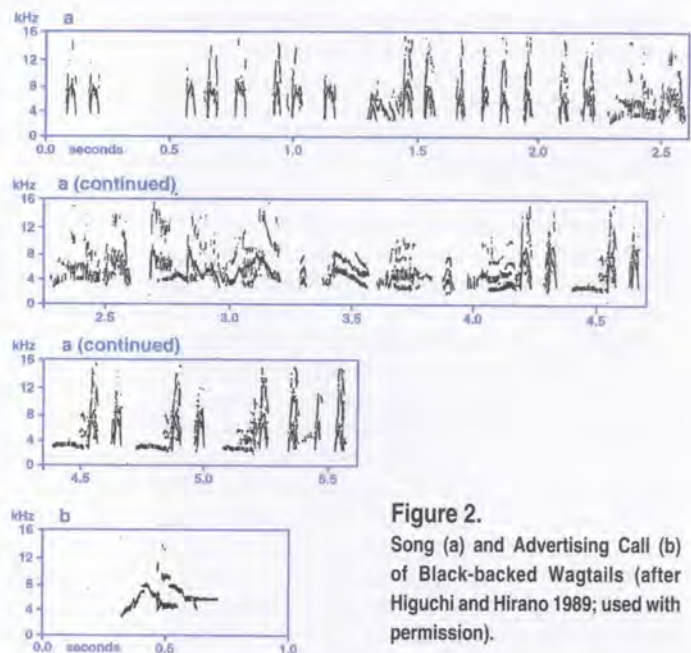


Figure 2. Song (a) and Advertising Call (b) of Black-backed Wagtails (after Higuchi and Hirano 1989; used with permission).

to late Apr. Seasonal variation in frequency of Advertising Call is greater than in Song (Higuchi and Hirano 1989). Seasonal singing activity (songs and Advertising Calls combined; number of songs/10 min [data from Higuchi and Hirano 1989]): Jan 0.7–3; Feb 3–6; Mar 12–19; early Apr 26; late Apr 10; May 3–7; Jun 0–1.7.

Daily pattern of vocalizing. No data for *M. a. ocularis*. Black-backed Wagtail first calls on average 13.9 ± 2.5 (SD) min before sunrise, 15.9 ± 0.7 min before sunrise on clear days and 12.1 ± 1.0 min before sunrise on cloudy days (see Yamadera and Yamadera 1991 for phenological changes in time of first calling).

NONVOCAL SOUNDS

Bill-snapping. *M. alba* snaps bill towards females and "satellites" (see Behavior: spacing, below) on winter territories, and often during disputes on communal roosts (Cramp 1988).

Wing-beating. In *M. alba* described as part of distraction display when human is near fledglings; accompanied by intense Alarm Calling (see Vocalizations, above; Cramp 1988).

BEHAVIOR

LOCOMOTION

Walking, hopping, climbing. Walks, runs, and hops on ground. Head moves back and forth when walking. Wags tail when walking, especially at end of runs.

Flight. Distinctive, strongly undulating flight.
Swimming and diving. Not known.

SELF-MAINTENANCE

Preening, head-scratching, stretching, bathing, anting. Preens most often on pre- and post-roosting gatherings. Scratches head by bringing foot over wing; walks in shallow standing water and bathes, especially on sunny days (see Food Habits: metabolism and temperature regulation, above, for time budgets).

Sleeping, roosting, sunbathing. Incubating and brooding female often sleeps on nest (AVB). Birds always roosts communally outside breeding period. In wintering Black-backed Wagtails, up to 2,000 birds at a single roost and up to 7,000 birds at 11 closely located sites (Brazil 1991). Birds never clump together at winter roosts even on the coldest night (Broom et al. 1976). Some *M. a. yarrellii* (including breeding birds) roost communally throughout breeding season; behavior at roost well studied in European subspecies (e.g., Zahavi 1971, Chandler 1979, Broom et al 1976, Fleming 1981, Cramp 1988); similar to that noted for Black-backed Wagtail (Watanabe and Maruyama 1977). Here briefly described for *M. a. yarrellii* after Broom et al. 1976. Birds start to gather near feeding areas about 1 h before sunset; at pre-roost gathering birds commonly walk or preen, maintaining visual or auditory contact with center of gathering; some birds make circular flights just before departure. Pattern of entry to roost depends on characteristics of site. Start to leave roost about 30 min before sunrise; often spend 10–15 min at post-roost gatherings, mostly preening, before departing to foraging areas.

Spreads tail and wings, raises nape feathers, and opens bill while sunning (observed in captivity; AVB).

Daily time budget. See Food Habits: metabolism and temperature regulation, above. Wintering territorial male *M. a. yarrellii* spends 90.1% of daylight feeding, 6.2% resting and preening, and 3.7% defending; in 24 h in midwinter, 64.6% spent sleeping, 31.9% feeding, 2.2% preening, and 1.3% defending (Davies 1976, Cramp 1988).

AGONISTIC BEHAVIOR

Physical interactions. Highly aggressive on foraging (migration and wintering) and breeding territories. Fighting and threat displays common along territory boundaries. Fights for sheltered positions common on communal roosts (Broom et al. 1976).

Communicative interactions. THREAT DISPLAYS. Head-bobbing Display similar for both species: body held horizontally, head stretched, and bill pointed up (see Panov 1973 for illustrations of

Black-backed Wagtail). Performed when 2 males meet on boundary of their territories.

Aggressive Bowing Display similar for both wagtails. Here described for male *M. a. ocularis* during spring migration. Birds stretch their bodies horizontally and simultaneously bow face to face. One of the birds periodically gives Advertising Call (see Sounds: vocalizations, above). This display may develop into aerial fight at about 0.5 m from ground (also known for Black-backed Wagtail; Watanabe and Maruyama 1977). When 1 bird loses, winner chases it long distance in the air and then returns to his foraging patch (Panov 1973).

APPEASEMENT DISPLAYS. Similar in both species. Most often shown by female towards conspecific male on wintering and breeding grounds (e.g., Watanabe and Maruyama 1977). Female lifts her tail and bill, lowers and quivers her wings, while giving Appeasement Call (see Panov 1973 for illustration of female Black-backed Wagtail display). Sequence of behaviors before pair formation apparently similar on wintering and breeding grounds in both species (Zahavi 1971, Watanabe and Maruyama 1977). In winter, female initiates pair formation when she lands on male's territory and does not fly away after being attacked, but retreats slowly and performs intensive Appeasement Displays. These continuous displays progressively increase male's tolerance of female presence on the territory; Appeasement Displays also commonly performed after pair formation when female is near male, or in response to his attacks (Zahavi 1971, Watanabe and Maruyama 1977).

SPACING

Territoriality. Both White and Black-backed wagtails are territorial during breeding season; mostly territorial on winter grounds, depending on food availability. For territory defense, time allocation between territories and flocks, and optimal territory size in *M. a. yarrellii* see Davies 1976, 1977, Davies and Houston 1981, 1983, and Watanabe and Maruyama 1977. In *M. a. alba*, females have exclusive territories within male territory when >1 female uses male's winter territory (Zahavi 1971; see also Ohsako and Yamagishi 1989). In Black-backed Wagtail, in central Japan, winter territories were $3,364 \pm 2,941$ (SD) m² and $4,519 \pm 5,001$ m² (Watanabe and Maruyama 1977). In *M. a. yarrellii*, winter territory was about 300 m long along the River Themsa banks; in Israel, territory size depended on food supply and varied from 10 m in diameter around abundant food supply to 100 m in diameter in a city (Zahavi 1971). Breeding territory of White Wagtail in ne. Yakutiya 0.75–2 ha; availability of snow-free gravelly areas for

foraging seems to be a criterion for selection of territory in spring (Gavrilov 1991a).

NATURE AND EXTENT OF TERRITORY. Territory serves for feeding and nesting. All food collected on nesting territory in *M. a. yarrellii* (Davies 1976). In subalpine habitats, pairs of *M. [a]. personata* often nest 30 m from each other in villages, with no aggressive interactions >10–15 m from nest; food collected on shared foraging territories 300–500 m away from nests (Kovshar 1979). Wintering Black-backed Wagtail often feeds outside of established territory along river (Watanabe and Maruyama 1977).

MANNER OF ESTABLISHING AND MAINTAINING TERRITORY. In both species, winter territory established and defended by male, which, depending on food supply, can form temporary (up to several weeks) association with a "satellite," i.e., a young bird or a female (see Agonistic Behavior, above, for Appeasement Displays used by satellites to allow use of male territory; see also Watanabe and Maruyama 1977). If allowed to stay, satellite assists in territory defense against intruders (up to 53.6% of all defenses in *M. a. yarrellii*; Davies 1981).

Pre-nesting male White Wagtail performs display flights along boundaries of his territory on average 2.78 h/24h (Gavrilov 1991a). Display flights conducted either by pair or by male alone (12% of all flights; Gavrilov 1991a). During migratory stopover in Black-backed Wagtail, dominant bird occupies suitable foraging territory and then suppresses all trespassers by swiftly flying just above ground toward approaching intruder, which commonly runs away (Panov 1973).

INTERSPECIFIC TERRITORIALITY. Winter territories of Black-backed Wagtail overlap with those of Japanese Wagtail in central Honshu, Japan; centers of activity and foraging areas of the 2 species are separated, and interspecific distance of >50 m is maintained during foraging (Higuchi and Hirano 1983). Black-backed Wagtail nested 250–300 m from *M. a. leucopsis* nest; both pairs shared same foraging territory (Nazarenko 1968). On winter territories, *M. a. yarrellii* always chases Gray Wagtail (*M. cinerea*), Meadow Pipit (*Anthus pratensis*), and European Robin (*Erithacus rubecula*) from the territory; does not chase Dunlin (*Calidris alpina*), Mistle Thrush (*Turdus viscivorus*), European Starling (*Sturnus vulgaris*), Linnet (*Acanthis cannabina*), or House Sparrow (*Passer domesticus*) (Davies and Houston 1981).

WINTER TERRITORIALITY. Both species usually territorial on winter grounds. In contrast to nominate *alba* (Zahavi 1971), no clear boundaries among winter territories of Black-backed Wagtail in central Honshu, Japan (Higuchi and Hirano 1983). Of 10 winter territories, 3–4 occupied by temporary pairs (some about 25 d in duration) and

the rest by single males (Higuchi and Hirano 1983). Owner and satellite association presumably always conspecific in areas of sympatry with other wagtails (Higuchi and Hirano 1989), but see Higuchi and Hirano 1983 for example of Black-backed Wagtail forming an apparent satellite association with male Japanese Wagtail. In territorial disputes on winter territories of *M. a. yarrellii*, female satellite often confronts female of other "pair" while male threatens other male; female sometimes appeases 2–3 males simultaneously and feeds on their territories (Zahavi 1971).

DOMINANCE HIERARCHIES. No data for *M. a. ocularis*. On winter territories, male Black-backed Wagtail dominates female in all encounters ($n = 194$; Hirano and Higuchi 1986). During spring and fall migrations, older birds in flocks of Black-backed Wagtails dominate young birds, thereby determining the order of foraging; dominant birds become very territorial and aggressive once foraging territories established on migration stopovers (Panov 1973).

Individual distance. In flocks of *M. alba* during migration or on winter grounds, birds often feed <1 m apart. Individual distance in flocks depends on food concentration (Zahavi 1971, Davies 1976). In pre-roost aggregations, birds stand 20–100 cm apart; birds usually roost 10–20 cm from each other (minimum 7 cm, mean 17 cm), the shortest distance when birds are positioned bill to tail (Zahavi 1971, Broom et al. 1976).

SEXUAL BEHAVIOR

Mating system and sex ratio. Socially monogamous. In *M. [a]. personata*, male once provided food to nestlings in his nest and to nestlings in another nest located 40 m from his own (Kovshar 1979). In closely related Japanese Wagtail in 225 breeding attempts over 4 yr of observations: 12.5% of males solitary, 85.2% monogamous, and 2.3% bigamous (Ohsako and Yamagishi 1989).

In nominate *M. alba* in nw. Russia, sex ratio at fledging (males:females) = 1.02 (69:67 nestlings, $n = 28$ broods, 3 yr of data); male-biased, late summer-early fall ratio = 1.53 (151:99 birds); sex ratio changes significantly between fledglings and first-fall birds, presumably owing to differential postfledgling mobility or mortality between sexes (Chemyakin 1988).

Pair bond. Pairs form during migration or after arrival on breeding grounds. Most pairs remain together throughout a breeding season, occasionally re-pairing in subsequent seasons (Cramp 1988). In *M. [a]. personata*, partners often change between nesting attempts within breeding season (Kovshar 1979). Sexes sharing winter territory usually do not form a breeding pair. In closely related Japanese Wagtail, males spend 50% of time within 10 m of

female during copulation stage and only 6% of time during incubation stage (Ohsako and Yamagishi 1989). Courtship feeding unknown, but male brings food to female while she broods nestlings (see Breeding: parental care, below).

Courtship displays. *BOWING DISPLAY.* See Cramp 1988 for *M. alba*. Here described for Black-backed Wagtail after Higuchi and Hirano 1989. Male approaches female while moving his head up and down and raising his body feathers slightly. At 0.5–1 m from female, bowing movements become more active and male starts to quiver his wings. Female stays motionless or shows no particular posture to male. Bowing Display precedes Precopulatory Display.

PRE-COPULATORY DISPLAY. Apparently similar in Black-backed and White wagtails. Markedly differs from sympatric *M. a. leucopsis*. In Black-backed and White wagtails, male flies down to female on hovering wings, landing 2–3 m away. Male lowers body, tilts head toward female, fluffs flank feathers, and opens both wings and tail while approaching female. Male spreads and sometimes twists tail and wings on side closest to female. Open wings kept at about 10° below horizontal level. Female posture similar to intensive Appeasement Display (see Agonistic Behavior, above). Facing male, female lowers her body, keeping it horizontal, points bill upward, and lifts tail almost vertically while intensively quivering wings. Copulation follows (Panov 1973, Higuchi and Hirano 1989). Pairs copulate several times in succession (Cramp 1988). In Black-backed Wagtail, copulations observed during egg-laying period and immediately after clutch completion (Panov 1973).

Extra-pair copulations. Forced extra-pair copulations observed twice in Black-backed Wagtail (Higuchi and Hirano 1989). In one case, female (during egg-laying stage) was mounted by floater male. In other, male from neighboring territory forcibly copulated with female (during nest-building stage) while she was foraging on the overlapping part of their territories. Neighboring or floating males sometimes sing near nest sites of other pairs while owner is absent (Higuchi and Hirano 1989).

SOCIAL AND INTERSPECIFIC BEHAVIOR

Degree of sociality. Both White and Black-backed wagtails are solitary and territorial during breeding season and usually migrate in small flocks. In winter, birds' dispersal varies from solitary and territorial to gregarious, depending on food concentration (e.g., Cramp 1988). Outside breeding season, always forms large communal roosts (see Self-maintenance, above). Stays in family groups after breeding until fall migration (Nechaev 1969).

Play. No information.

Nonpredatory interspecific interactions. Japanese Wagtail very aggressive towards Black-backed Wagtail during breeding season in central Japan (Nakamura et al. 1984). Most aggressive behavior of Japanese Wagtail directed towards male Black-backed Wagtail (91.9% of all chases; 40.9% of chases towards female or pair of Black-backed Wagtails), in 1 instance continuously preventing male Black-backed Wagtail from approaching his own nest for incubation (Nakamura et al. 1984). Black-backed Wagtail always defeated by Japanese Wagtail (Nakamura et al. 1984). Both sexes of Japanese Wagtail chase Black-backed Wagtail on winter territories in central Honshu, Japan; Japanese Wagtail dominates Black-backed Wagtail in all chases, except 5.7% of encounters between female Japanese Wagtail and male Black-backed Wagtail (Hirano and Higuchi 1986). Frequency of chases depends on segregation of foraging territories of 2 species and ranged from 3 to 11 times/h. Contrary to situation when chased by conspecifics, Black-backed Wagtail when chased by Japanese Wagtail does not show appeasement behavior towards the latter (Higuchi and Hirano 1983). In s. Ussuriland early in season, territorial males of *M. a. leucopsis* chase both sexes of later-nesting Black-backed Wagtail (Nazarenko 1968, Panov 1973). On winter territories, both sexes of Black-backed Wagtail dominate in all encounters with Gray Wagtail and with Buff-bellied, or American, Pipit (*Anthus spinoletta* [= *rubescens*]; Hirano and Higuchi 1986). *M. alba* seen repeatedly attacking European Dipper (*Cinclus cinclus*) (Cramp 1988). Also see Spacing, above.

Sympatric Japanese Wagtail and Black-backed Wagtail form separate roost flocks on winter grounds (Higuchi and Hirano 1989). *M. alba* sometimes roosts with Bank Swallow (*Riparia riparia*), Barn Swallow (*Hirundo rustica*), Common Raven (*Corvus corax*), Eurasian Blackbird (*Turdus merula*), Yellow Wagtail (*Motacilla flava*), House Sparrow, and Spanish Sparrow (*Passer hispaniolensis*) (Cramp 1988).

PREDATION

Kinds of predators. Eurasian Sparrowhawk (*Accipiter nisus*) and Boreal Owl (*Aegolius funereus*) known to prey on roosting wagtails (Broom et al. 1976). Domestic cats (*Felis silvestrus*) account for 9.8% of predation in urban areas (Dougall and Appleton 1991). Eurasian Kestrel (*Falco tinnunculus*), Hooded Crow (*Corvus corone*), and Bull-headed Shrike (*Lanius bucephalus*) elicit mobbing responses (Broom et al. 1976, Watanabe and Maruyama 1977).

Response to predators. *M. alba* detected mount of Eurasian Sparrowhawk on its territory 3.8 ± 2.2 (SD) min after it was presented; flew to it and

circled it several times at 3.1 ± 2.1 m for about 1 min; then landed 8.9 ± 11 m away (Götmark 1993).

BREEDING

PHENOLOGY

Differs markedly between Black-backed Wagtail and other sympatric wagtails, including *M. a. ocularis*, *M. a. leucopsis*, and Japanese Wagtail (see below).

Testicular/ovarian cycle. Testes (mm) of White Wagtail collected on 27 May at Chukchi Peninsula (extreme e. Asia): left 10×7 , right 9×6 ; on 9 Jun, left 10×7 , right 8×6 ; on 13 Jul, left 11×8 , right 9×8 ; on 7 Sep, left 3×2 , right 2×2 (Portenko 1989). Female collected 19 Jun 1989 on St. Lawrence I., AK, had ova up to 10 mm in diameter (DDG). In s. Ussuriland on 28 Mar, testis of Black-backed Wagtail significantly enlarged 4.5×3 mm (Panov 1973); female collected on 18 Jul had well-developed ovary, with largest follicles of 0.7×0.5 mm (Panov 1973). In Aleutian Is., AK, male collected on Shemya I. on 1 May 1977 had enlarged testes: left 10.2×8 mm, right 10×8.8 mm (Univ. Alaska Mus.). See Panov 1973 for hybrids' data.

Pairformation. In White Wagtail near northernmost part of distribution range, pairs form during first half of Jun (Gavrilov 1991a). In Black-backed Wagtail in s. Ussuriland, in second half of Apr (Nazarenko 1968). Also see Behavior; sexual behavior, above.

Nest-building. *M. a. ocularis* initiates nest-building within 10 d of arrival (Dement'ev and Gladkov 1954, Kessel 1989). In ne. Siberia, nests completed by mid-Jun (Kistchinski 1980). Nest initiation in Black-backed Wagtail starts much later in season, about 3–4 wk after arrival (e.g., Dement'ev and Gladkov 1954, Nechaev 1969, Nakamura et al. 1984). In Kuril Is. and on Kamchatka Peninsula, nest-building by Black-backed Wagtail starts during first half of May (Dement'ev and Gladkov 1954, Nechaev 1969). On Honshu, Japan, Black-backed Wagtail builds during Apr (Nakamura et al. 1984). Late nesting of Black-backed Wagtail may be caused by greater dependency on availability of flying insects than in other wagtails (Higuchi and Hirano 1989).

First/only brood per season. **WHITE WAGTAIL.** On Seward Peninsula, AK, nest initiation starts early Jun, within 7–10 d of arrival, and continues over 3+ wk; hatching starts late Jun (Kessel 1989). In ne. Siberia, egg-laying during second half of Jun; first independent young mid-Jul (Kistchinski 1980). In Yakutiya, eggs during May–Jun; first fledglings end of Jun; in Provideniya Bay (extreme ne. Asia)

incubation begins early Jul (Dement'ev and Gladkov 1954).

Renests if first nest destroyed; repeated clutches occur until end of Jul (Kistchinski 1980). One brood raised/yr (Dement'ev and Gladkov 1954).

BLACK-BACKED WAGTAIL. On Attu I. (Aleutian Is.), AK, first egg of one clutch was laid 8 June 1990 (DDG); adult male feeding 2 fledglings 4 Aug 1983 and female was feeding 5 young in nest 7 Aug 1983 (Wagner 1991). On Seward Peninsula, a pair feeding 6 nestlings in shed, near Nome, 7 Jul 1973 (Kessel 1989). In s. Ussuriland, earliest nest with eggs 8 May; nestlings in nests Jun–Jul; first independent fledglings 5 Jul (Panov 1973). In Kuril Is., egg-laying end May–Jun, nestlings mid-Jul, first fledglings mid-Jul (Nechaev 1969). Repeated clutches occur until mid-Jul (Nechaev 1969). Building of second nest starts 2–5 d after failure of first breeding attempt in nestling stage (Higuchi and Hirano 1989). In Honshu, Japan, first eggs late Apr, incubation May–Jun, fledglings late Jun (Nakamura et al. 1984, Higuchi and Hirano 1989). In s. Ussuriland, hybrid pairs male *M. lugens* x female *M. a. leucopsis* hatched nestlings 5 Jul, and male *M. a. leucopsis* x female *M. lugens* initiated incubation 22 May (Nazarenko 1968, Panov 1973).

Second/late brood per season. In central Honshu, Black-backed Wagtail usually produces 1 brood/yr; 2 broods recorded for 2 out of 14 pairs (Nakamura et al. 1984). Second clutch presumably common in s. Ussuriland (Nazarenko 1968); observations, however, might refer to reneesting after predation.

NEST SITE

Selection process. In Black-backed Wagtail, both parents select nest site (Nechaev 1969). Male first brings nest material to future nest site; female follows closely behind (Nakamura et al. 1984). In *M. [a.] personata*, male leads female to prospective sites and starts to collect nest material before female; male often carries material to several potential sites and, at the same time, pair prospects new sites (Kovshar 1979; the same behavior for *M. a. alba* [Leinonen 1973]). Almost-completed nests can be abandoned in favor of new sites (Kovshar 1979, AVB).

Site characteristics. White Wagtail nests in cavities and crevices of rock cliffs or abandoned buildings, as well as in ditches along roads (Kistchinski 1980, Kessel 1989). Often forced by spring floods to nest on high banks (Dement'ev and Gladkov 1954). Nests found in occupied Golden Eagle (*Aquila chrysaetos*) nest (Kistchinski 1980), in walrus (*Odobenus rosmarus*) skull, in old fuel drums (Kessel 1989), and in tree stumps (Dement'ev and Gladkov 1954). Nesting of *M. a. alba* in ne. Europe

often associated with muskrat (*Ondatra zibethica*) and beaver (*Castor fiber*) activities; every examined beaver dam contained a nest (Mal'chevski and Pukinski 1983). Nests in nest boxes (Bragin and Gilyazov 1984).

Black-backed Wagtail nests on coastline rock cliffs (up to 30 m height), under washed-out logs on beaches, under rails of railroads, in burrows, in buildings and other human constructions (Nechaev 1969, Nakamura et al. 1984, Kessel 1989). Also may nest openly on ground next to a tussock (Panov 1973). On Attu I., AK, nested under dilapidated river bridge 800 m upstream from seacoast (Wagner 1991, DDG). In central Honshu, Japan, 23 out of 26 nests were in roofs and crevices of buildings; 3 in crevices of bridges (Nakamura et al. 1984, Higuchi and Hirano 1989).

NEST

Construction process. Male starts to build, both partners build together in later stages, and only female builds in final stages. In *M. [a.] personata*, only female builds nest for second clutch because male is provisioning the first-brood fledglings (Kovshar 1979). Both sexes build in *M. a. ocularis*, nest-building lasts 9 d (Dement'ev and Gladkov 1954). In Black-backed Wagtail, nest-building takes 16 d for first nests, 10 d for first nests using old nests, 5 d for repeat nests. Frequency of carrying nest material <10 times/d for both parents until 6 d of building, up to 61 times/d thereafter (nest-lining stage); peak building on day 9. Peak time of building 0900 h; less material brought in afternoons. Male does 8% of building; only female builds after day 13 (Nakamura et al. 1984).

Structure and composition matter. In White Wagtail, nest built of dry, thick stems of graminoids, dwarf willow (*Salix*), leaves of sedges (*Carex*), and twigs. Lined with rootlets and leaves of graminoids, deer and dog hair, or ptarmigan (*Lagopus*) feathers; in some nests in ne. Siberia, hair of ground squirrel (*Citellus*) (Kistchinski 1980, Portenko 1989). Occasionally dry grass held with mud (Dement'ev and Gladkov 1954). In Black-backed Wagtail, nest is large and loose structure. Built of dry leaves, soaked rootlets and graminoid stems. Lined with vegetative fluff, fur and wool, deer and horse hair, and some feathers (Dement'ev and Gladkov 1954, Nechaev 1969).

Dimensions. Overall dimensions (cm) of *M. a. ocularis* nest 18.0 x 11.5, inside diameter 7.5 x 6.5, depth: 4.5 (Portenko 1989); overall dimensions (cm) of Black-backed Wagtail nest 9-13.5 x 13-16.5, inside diameter 6.4-7.4 x 6.7-7.3, height 5.3-8.2, inside depth 4.2-4.6 ($n = 4$, Nechaev 1969). Mean dry weight of 10 *M. a. alba* nests from natural cavities 44 g (range 13-74), 10 nests from artificial sites

108 g (47-164); differences due to greater framing of nests in artificial sites (Leinonen 1973).

Microclimate. No data.

Maintenance or reuse of nests; alternate nests. When nesting in human-made constructions with repeated similar architectural structures, *M. a. alba* often builds multiple nests (4-6; Leinonen 1973, AVB). *M. [a.] personata* often uses same sites for repeated clutches within season; in one case birds laid second clutch in nest used for first nesting, with only lining changed (Kovshar 1979). In mountains, *M. alba* often uses unfinished nests built in beginning of breeding season for second or replacement nests (Kovshar 1979, AVB). Four records of nominate *M. a. alba* using first-brood nests for second nesting; in 8 cases, second-brood nests were in same building as first ones (Leinonen 1973). *M. a. alba* known to build nests in old nests of about 15 other bird species (Mason and Lyczynski 1980).

Nonbreeding nests. None known.

EGGS

Shape. Subelliptical. In *M. a. ocularis*, shorter and rounder than in other *M. alba* subspecies (Dement'ev and Gladkov 1954).

Size. WHITE WAGTAIL. In *M. a. ocularis* length x breadth (mm): 17.1-18.0 x 14.1-14.6, mean 17.63 x 14.42 mm ($n = 6$ eggs; Dement'ev and Gladkov 1954); 19.2-20.1 x 14.7-15.3, mean 19.78 x 14.95 ($n = 4$ eggs; Portenko 1989).

BLACK-BACKED WAGTAIL. Length and breadth (mm): 20-23 x 15-17, mean 21.6 x 15.9 ($n = 3$ clutches, 13 eggs; s. Kuril Is., Nechaev 1969); 20-21.3 x 14.8-16.5, mean 21.48 x 15.88 ($n = 20$ eggs; n. Kuril Is.; Dement'ev and Gladkov 1954); mean 22.78 x 16.44 ($n = 1$ clutch, 5 eggs, Honshu, Japan; Nakamura et al. 1984).

Mass. No data for *M. a. ocularis*. For Black-backed Wagtail, 2.62-3.5 g, mean 2.92 g ($n = 20$ eggs, n. Kuril Is.; Dement'ev and Gladkov 1954); mean 3.28 g ($n = 1$ clutch, 5 eggs; Honshu, Nakamura et al. 1984). Mass decreases as incubation progresses: 3.1 g ($n = 5$ eggs) on day 4 of full incubation, 2.8 g on day 9, and 2.67 g on day 12 (data from Nakamura et al. 1984).

Color. Similar in both species (Dement'ev and Gladkov 1954). Ground color bluish white or light green with light brown spotting; speckles dense and sometimes concentrated to solid color at larger end (Nechaev 1969, Panov 1973).

Surface texture. No data.

Eggshell thickness. No data.

Clutch size. WHITE WAGTAIL. In *M. a. ocularis* 5 eggs, range 4-7 (Dement'ev and Gladkov 1954). On Seward Peninsula, AK, 5-7 eggs ($n = 2$; Kessel 1989); in ne. Siberia, 5 eggs (range 4-6, $n = 3$), 2 repeat clutches contained 5 eggs (Kistchinski 1980).

BLACK-BACKED WAGTAIL. On n. Kuril Is., 6 eggs, repeat clutches 4–5 eggs (Dement'ev and Gladkov 1954); on s. Kuril Is., 4.3 eggs ($n = 3$; Nechaev 1969); in s. Ussuriland, 4 eggs, (range 3–5, $n = 4$; data from Panov 1973). See also Demography and Populations: measures of breeding success, below.

Egg-laying. Pause between nest completion and egg-laying early in season = 2–15 d; later in season = 0–1 d (*M. a. personata*, Kovshar 1979). For *M. a. alba*, in 67% of cases the interval between nest completion and egg-laying = 1–3 d; in 26%, 4–6 d; in 7%, 7–10 d (Leinonen 1973).

Eggs laid daily in both White and Black-backed Wagtails. In Black-backed Wagtail, eggs laid at 1000–1100 h (Dement'ev and Gladkov 1954) or 0418–0432 h (Nakamura et al. 1984). In one nest, female Black-backed Wagtail stayed on nest 17 min to lay first egg, 33 min for second, 38 for third, and 43 for fourth. Female quivers her wings and moves her body up and down slightly just before laying egg (Nakamura et al. 1984).

INCUBATION

Onset of incubation in relation to laying. Black-backed Wagtail incubates little during egg-laying; full incubation starts after last egg laid or day before (Panov 1973, Kistchinski 1980, Nakamura et al. 1984).

Incubation patch. Female with single abdominal brood patch. When male incubates, he raises abdominal feathers for better contact with eggs (Leinonen 1973).

Incubation period. No data for *M. a. ocularis*. For Black-backed Wagtail, 13–15 d (Nakamura et al. 1984, Brazil 1991). For *M. a. yarrellii*, average 12.4 d (range 10–16, $n = 59$; Mason and Lyczynski 1980); in *M. a. alba*, 12.6 d (range 11–16, $n = 69$), incubation period shortened 0.03 d per day of the breeding season (Leinonen 1973).

Parental behavior. No data for *M. a. ocularis*. In Black-backed Wagtail, both parents incubate: female in morning, evening, and at night; either sex during midday (Nechaev 1969, Nakamura et al. 1984). The following account for Black-backed Wagtail based on Nakamura et al. 1984. Seventy percent of male incubation at 1100–1300 h. When female leaves nest to forage on her own, average incubation interval is 20.7 min followed by 6.7 min of absence; when accompanied by male or called from nest by male, average of 29.5 min on nest alternating with 15.9 min of absence. Overall, female leaves nest on average every 22.1 min for 8.2 min. Male incubation rhythms irregular. Total incubation time (min) for first brood: 1,275 on day 3 of incubation; 1,168 on day 5; 1,172 on day 8; 1,175 on day 10; 1,308 on day 12; 1,219.6 min/d on average. Male incubation time min/day increases as

incubation progresses: 12 (day 3), 24 (day 5), 16 (day 8), 44 (day 10), and 119 (day 12). Male contributes 6% to incubation in first broods and much less in repeated clutches. Incubating parents turn eggs up to 10 times/h, 3.4 times on average. Female sometimes covers eggs with lining material when leaving nest. Three types of incubation change-over: (1) by approach and/or (2) call of incoming partner, or (3) spontaneous departure from the nest without waiting for alternation (males only; Nakamura et al. 1984).

Incubating *M. alba* often sleeps; periods of day-sleeping last on average 3.9 min (Leinonen 1973, AVB). When *M. a. alba* approaches nest, it commonly flies to nest vicinity and then runs to nest; when leaving nest, often flies directly from nest or runs several meters and then flies (Leinonen 1973).

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

HATCHING

No data for *M. a. ocularis*. Entire clutch of Black-backed Wagtail hatches same day or within 2 d, depending on whether incubation started with last or penultimate egg. Female either eats hatched eggshells or carries them out (Nakamura et al. 1984). Hatching in *M. a. alba* lasts average of 12 h; about 2 d before hatching, adults, apparently searching for eggshells, begin to peck nest bottom, often picking pieces of leaves or bark as a substitute (Leinonen 1973).

YOUNG BIRDS

Conditions at hatching. Altricial and nidicolous. Weight of Black-backed Wagtail at hatching 2.32 g ($n = 3$; Nakamura et al. 1984).

Growth and development. **WHITE WAGTAIL.** Growth described by following equations (Gavrilov 1991b): Body Mass = $22(1 - 1.09e^{-0.4D})^3$ (where D is day after hatching); tarsus length = $23.3 / (1 + 9.16e^{-0.57D})$; linear growth of skull (from occipital complex to end of bill) = $31.2 / (1 + 2.93e^{-0.39D})$; bill length growth (from skull) = $8.82 - 7.17e^{-0.61D}$. Eyes open on day 4; the same day ensheathed feathers erupt in all tracts; on day 6–7, feathers break from sheaths in all tracts, except for capital where they break on day 8 (Gavrilov 1991b). See Leinonen 1973 for growth curve of *M. a. alba* nestlings. See Yakovleva et al. 1987 for exhaustive study of *M. a. alba* development.

Additional details of *M. alba* development (after Yakovleva et al. 1987): ear passages open on day 2; alular quills appear on day 4, open on day 7–8; rectrices appear on day 4, start to open on day 6–7, open completely either on day 17–23 in nestlings from late broods, or on day 23–28 in nestlings from early broods; and ensheathed contour feathers

appear on day 2, start to open on day 5. Growth of primaries and secondaries quite variable among individuals and nests. Nestlings from later broods achieve maximum body mass and gain length in wing, tarsus, and most feathers significantly faster than nestlings from early broods; development apparently controlled by photoperiod. Early and late broods differ mostly in development of greater-primary coverts (Yakovleva et al. 1987).

BLACK-BACKED WAGTAIL. Nestlings ($n = 4$) grow as follows: weight (g) 4.7 on day 3 after hatching; 6.0 on day 5; approximately 8.9 on day 6; 13.0 on day 7; 16.8 on day 8; 20.0 on day 10; 24.1 on day 11; 23.9 on day 12; and 23.7 on day 13 (day of nest departure). Wing length (mm): 14.4 on day 3; 28.0 on day 6; 30.7 on day 7; 45.7 on day 9; 56.0 on day 11; and 63.8 on day 13. Tarsus length (mm): 8.4 on day 3; 15.0 on day 6; 20.2 on day 8; 21.8 on day 9; 23 on day 11; and 23.9 on day 13; eyes open on day 5; nestlings begin to flap wings on day 10 (Nakamura et al. 1984).

PARENTAL CARE

Brooding. Only female broods. In Black-backed Wagtail, female broods after feeding nestlings during daytime and all night until nestlings 6 d old (Nechaev 1969, Nakamura et al. 1984). Total brooding time during daytime: 339 min (22.6 min/h) for 3-d-old nestlings and 28 min (4.6 min/h) for 6-d-old; brooding most frequent in mornings and evenings (Nakamura et al. 1984).

Feeding. By both parents. Nestling foods in one nest of Black-backed Wagtail were insects (85.4% of all items) and spiders 14.6%; Tipulidae (Diptera) composed the largest part of the diet (56.1%) (Nakamura et al. 1984). Items included Tipulidae, Tabanidae, Bibionidae (Diptera); Scarabaeidae (Coleoptera); Pyralidae (Lepidoptera); Chrysopidae (Neuroptera); Agrionidae, Libellulidae (Odonata); Gerridae (Hemiptera), and Attidae (Aranea) (Nakamura et al. 1984).

Mostly adult Diptera (49.0%) in diet of *M. [a.] personata* nestlings, including Calliphoridae 23.1%, Muscidae 10.8%, and Tipulidae 6.1%; also Ephemeroptera 27%, Lepidoptera 6.7% (Noctuidae), Orthoptera (including *Chortippus* and *Gomphocerus*) 8%; Hemiptera (including Miridae and Tingitidae) 3.4%; Coleoptera 1.5%, and mollusks (including *Pupilla* and *Bradybaena*) 2.9% (Kovshar 1979). In 11 nests, Diptera 45% of nestling diet (mostly Tipulidae), Lepidoptera 10.5%, Orthoptera 4.8%, and others (dragonflies, beetles, spiders, earthworms, and bread crumbs) 2.8% (Kovshar 1979).

As Black-backed Wagtail nestlings age, frequency of food deliveries to nest increases from 51 times/d for 3-d-old nestlings to 63 times/d for 13-d-old; on average 55.4 times/d for nestling stage

(Nakamura et al. 1984). Frequency of food transfers during nestling stage: female to nestlings 64.6% of all transfers, male to nestlings 32.5%, and male to female (when female broods) 2.9% (Nakamura et al. 1984).

Nest sanitation. No data for *M. a. ocularis*. Following based on Nakamura et al. (1984) for Black-backed Wagtail. Fecal sacs either eaten or carried away and dropped in the air. Of all sac removals, female eats them on 38.1% of occasions (almost all sacs eaten until nestlings 3 d old) and carries them away on 61.9% of occasions. Male never eats fecal sacs; just carries them away. Male contributes 28% to fecal sac removal during nestling period. Frequency of fecal sac removal 15 times/d for 3-d-old nestlings, 11 times/d for 6- and 10-d-old, and 12 times/d for 13-d-old. Ratio of defecation to feeding is 1/4.3 (Nakamura et al. 1984).

In *M. a. alba*, 10-d-old and older nestlings defecate over rim of nest (Leinonen 1973). If nestling does not gape and remains quiet, adult keeps pushing it with bill; if nestling does not react it is carried out of nest; dead nestlings removed until 5-6 d old (Leinonen 1973).

COOPERATIVE BREEDING

Not known.

BROOD PARASITISM

Identity of the parasitic species. *M. a. ocularis* is most common host of Common Cuckoo (*Cuculus canorus*) in ne. Siberia. In s. Ussuriland, *M. a. leucopsis* and Black-backed Wagtail also parasitized by this cuckoo (Litun et al. 1986, Mal'chevski 1987). Long nesting season, frequent repeated nesting attempts, and diversity of nest sites apparently contribute to high level of parasitism.

Frequency of occurrence; seasonal or geographical variation. Of all cuckoo-parasitized nests found in USSR, 18% were those of *M. alba*. Of 294 nests of *M. a. alba* found over 25 yr in a region in central Europe, 97 contained eggs and nestlings of cuckoo; on some cuckoo territories, up to 90% of all *M. alba* nests were parasitized (Mal'chevski 1987).

Timing of laying in relation to host's laying. Usually during host's egg-laying or in early stages of incubation; cuckoo rarely lays in empty nest immediately after nest-building. Usually lays in late afternoon. Since cuckoo arrives in spring after most wagtails have initiated their nests, it mostly parasitizes repeat and second clutches (Löhrl 1979). In central Europe, duration of cuckoo egg-laying in *M. a. alba* nests 1.5-2 mo (Mal'chevski 1987).

Response to parasitic mother, eggs, or nestlings. Parents intensively attack female cuckoo approaching nest. Female cuckoo often approaches nest and lays egg in parents' presence. *M. alba* almost never

rejects cuckoo eggs, regardless of cuckoo eggs' coloration and race. Rejection rate appears to be higher in European races than in Asian races of White Wagtail. Forty-one cuckoo eggs found in nominate *M. a. alba* nests belonged to 3 known races of coloration; none was similar to that of the host wagtail.

Effect of parasitism on host. Female cuckoo consumes 1 of host's eggs when she lays her own. Cuckoo nestling pushes all eggs or nestlings of host over rim of nest during first few days. Also see Demography and Populations: measures of breeding success, below.

Success of parasitism with this host. Nesting success (young fledged/eggs laid) of Common Cuckoo in *M. alba* nests is 45%, apparently higher than with most other hosts. Major cause of nest failure is predation on wagtail nests; also, rarely, competition between cuckoo nestlings when 2 eggs are laid in the same nest instead of usual 1. Young cuckoos leave *M. alba* nests 19–21 d after hatching; host parents intensively feed them for at least 17 d after departure from nest (Mal'chevski 1987).

FLEDGLING STAGE

Departure from the nest. Both White and Black-backed wagtails normally leave nest when 13–14 d old (Nakamura et al. 1984, Gavrilov 1991b). *M. a. yarrellii* and *M. a. alba* also depart nests on day 13–14 (*M. a. yarrellii*: mean 13.8, range 11–15, $n = 31$; [Mason and Lyczynski 1980]; *M. a. alba*: mean 13.7, range 11–16, $n = 44$; [Leinonen 1973]). Can leave nests prematurely when 11 d old if 1 or several disturbed nestlings give Alarm Call (Leinonen 1973; see Sounds: vocalizations, above). Both parents present when young leave nest; they accompany the first fledgling, calling intensively, as it jumps from nest to where it lands; then 1 parent returns to nest and keeps calling, as if to stimulate others to leave; fledging can last up to 1 d (Leinonen 1973).

Growth: mass, proportions, structures. At fledging, Black-backed Wagtail weight is 89% of adult weight, wing length 67% of adult, tarsus length 98% (Nakamura et al. 1984).

Association with parents or other young. *M. a. alba* brood reassembles for roosting during first several days after fledging (Leinonen 1973). In *M. [a.] personata*, both parents feed fledglings for 14–18 d after departure from nest; fledglings stay together and within 50 m of nest during this time (Kovshar 1979). If second clutch is initiated, only male feeds fledglings of first brood after day 7; 7–8 d after nest departure, young attempt to forage by themselves; they fly well at this time, and brood drifts up to 1.5–2 km from nest 18 d after departure from nest (Kovshar 1979).

DEMOGRAPHY AND POPULATIONS

MEASURES OF BREEDING ACTIVITY

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

Clutch size. For *M. a. ocularis*, 5 eggs, range 4–7 (Dement'ev and Gladkov 1954). On Seward Peninsula, AK, 5–7 eggs ($n = 2$; Kessel 1989); in ne. Siberia, 5 eggs, (range 4–6; $n = 3$), 2 repeat clutches contained 5 eggs (Kistchinski 1980). For clutch size of w. palearctic subspecies of *M. alba*, see Cramp 1988.

Clutch size decreases as season progresses in *M. [a.] personata* from 5.36 in May ($n = 11$), to 5.08 in Jun ($n = 12$), to 4.62 in Jul ($n = 8$) (Kovshar 1979); in *M. a. alba* from 5.8 to 5.3 eggs (Leinonen 1973). For Black-backed Wagtail in n. Kuril Is., 6 eggs, repeat clutches 4–5 eggs (Dement'ev and Gladkov 1954); in s. Kuril Is., 4.3 eggs ($n = 3$; Nechaev 1969); in s. Ussuriland 4 eggs (range 3–5, $n = 4$; data from Panov 1973). Clutch size of a hybrid pair, male *M. a. leucopsis* x female *M. lugens*, was 5 eggs (Nazarenko 1968).

Annual and lifetime reproductive success. For *M. alba* in central Finland, 78.9% eggs hatch ($n = 270$ nests) and 77.0% of those result in fledglings ($n = 153$ nests); number of unhatched eggs higher in later clutches (Leinonen 1973).

In England 1,186 nests contained 5,747 eggs, and 2.55 young fledged/nest, hatching success 63.8%, fledgling success 82.6%; young fledged from eggs laid 52.7%. Clutches of 3 eggs produced 1.59 fledglings, 4 eggs 2.32, 5 eggs 2.80, and 6 eggs 3.29. Causes of nest failure: predation 49.9%, desertion 33.5%, weather 5.8%, agricultural activities 5.2%, infertility (all eggs) 0.6%, cuckoo parasitism 1.7%, adult death 2.6%, and other 0.6% ($n = 463$ nests; Mason and Lyczynski 1980).

In subalpine population of *M. [a.] personata*, of 96 eggs from 19 nests, 7 eggs (7.3%) were infertile; of 46 clutches, 3 abandoned during incubation, 3 destroyed by human activities, and in 40 (86.9%) all nestlings fledged (Kovshar 1979). Overall nesting success higher in human landscapes (88%, $n = 39$ nests) than in natural habitats (75%, $n = 68$ nests) (Mal'chevski and Pukinski 1983). No data on lifetime success.

Number of broods normally reared per season. **WHITE WAGTAIL.** *M. a. ocularis* raises 1 brood/yr (Dement'ev and Gladkov 1954).

BLACK-BACKED WAGTAIL. In central Honshu, Japan, usually 1 brood/yr; 2 broods recorded for 2 out of 14 pairs (Nakamura et al. 1984). Second clutch presumably common in s. Ussuriland (Nazarenko 1968). See Breeding: phenology, above.

LIFE SPAN AND SURVIVORSHIP

Oldest known *M. alba* 9 yr 11 mo (Cramp 1988). Of 260 *M. a. yarrellii* recovered dead, 44.2% were in their first year and 55.8% in later years; 46.1% of first-years' deaths were in their first winter and 24.3% in their first fall; of adult deaths, 34.5% were in summer, 29.7% in winter, and 17.9% in each fall and spring (Dougall 1991). Of 134 *M. alba* nestlings banded, 79.8% recovered the first year of life, 9.7% in second year, 8.2% in third, 1.5% in fourth, 0.8% in fifth (Cramp 1988). See Cramp 1988 for additional data.

For geographic and temporal variation in age structure of wintering *M. a. yarrellii*, see Dougall and Appleton 1989. In Aichi Prefecture, Japan, usual wintering site for Black-backed Wagtails from Sakhalin I., Kamchatka Peninsula, and Kuril Is., the numbers of banding recoveries as follows: 1,752 birds recaptured 3 mo after banding; 1,240 after 6 mo; 1,171 after 9 mo; 987 after 12 mo; 627 after 18 mo; 343 after 24 mo; 224 after 30 mo; 128 after 36 mo; 65 after 42 mo; 34 after 48 mo; 8 after 54 mo; and 1 after 60 mo (McClure 1974).

DISEASE AND BODY PARASITES

Of 73 adult white wagtails (probably Black-backed Wagtails) examined in coastal Japan, 3 infested with *Yersinia enterocolitica*, 1 with *Y. intermedia*, and 1 with *Y. pseudotuberculosis* (Hamasaki et al. 1989). Of 46 *M. alba* examined in w. Europe, 18 infested with *Leucocytozoon* spp., 5 with *Trypanosoma* spp., 2 with *Haemoproteus* spp., and 1 with *Alaroplasma (Lankestrella)* (Peirce 1981). In Central Asia, of 13 migrating White Wagtails, 1 infested with *Haemoproteus anthi* (Subchonov et al. 1981); *H. motasillae* found in *M. alba* collected in South Korea, *H. motacillae* in White Wagtail from India (Bennett and Peirce 1990). Trematode *Sinobilharzia motacillae* described from *M. alba* in Nei Mongol Region (Qui and Li 1986); nematode *Capillaria corvorum* found in digestive tract of White Wagtail from Central Asia (Sergeeva and Borgarenko 1985). Feather mites *Analges pollicipatus*, *A. pachynemis*, and *Pteromyssoides motacillae* have been found in *M. alba* (see Mironov 1985 for details of feather mites localization in plumage). Also see Kurbanova 1973 and Mousa et al. 1988.

CAUSES OF MORTALITY

Of 335 banding recoveries of *M. a. yarrellii*, 260 found injured or dead; mortality due to following: 60.4% unknown, 17.7% collision with traffic, windows, or wires; 7.3% predation, 6.9% trapped inside buildings, and 5.0% weather (Dougall 1991). Farmland population of *M. a. yarrellii* reduced by 55% after severe winter (Dougall 1991). Owing to owner-satellite association on winter territories (see

Behavior: spacing, above), sexes behave differently in periods of adverse weather: males (owners) tend to remain on their territories and forage intensively, whereas females undertake local movements (Dougall 1991).

RANGE

Initial dispersal from natal site. In *M. a. alba*, young males more mobile than females in post-fledging movements; male:female ratio in late summer-early fall 0.93 for captures <400 m from natal site and 1.44 for captures >400 m from natal site (3 yr of data; Chemyakin 1988). *M. a. yarrellii* remains within 40 km of nests at least until 103 d old, but some 115-d-old birds were already >200 km from nests, and by age 207 d some birds were 1,500-2,000 km from their nests. Sixteen first-year *M. a. yarrellii* bred an average of 20.4 km from their natal sites (SD 24.5, range 0-100; data from Dougall 1991). Of 100 marked *M. [a.] personata* nestlings, 1 recovered 2 yr later at 300 m from natal site and 7 more birds recovered the next year >1 km from natal sites (Kovshar 1979).

Fidelity to breeding site and winter home range. Black-backed Wagtail from Sakhalin I. wintering in Japan used the same roost area for up to 60 mo (McClure 1974). Of 5 marked breeding females and 3 males of *M. [a.] personata*, all but 1 female nested within 100 m of their nests of previous year; 1 female nested 1 km away; a marked male nested in 1 site for 4 consecutive years (Kovshar 1979). Of 27 marked wintering *M. a. alba*, 11 occupied same territory next winter; high fidelity to previous winter range in flocks as well (Zahavi 1971).

Dispersal from breeding site. In *M. a. alba*, 49 of 64 unsuccessful pairs abandoned their territories after nesting; 15 pairs re-nested on same territory (Leinonen 1973). In *M. [a.] personata*, replacement and second-brood nests built within 20-30 m of first nest site (Kovshar 1979).

Home range. In winter, most *M. a. yarrellii* feed within 12-15 km of night roost site (Broom et al. 1976).

POPULATION STATUS

Numbers. WHITE WAGTAIL. Very common in Yakutsk (ne. Asia); casual on Commander Is. (Dement'ev and Gladkov 1954); rare in coastal w. Alaska (Kessel and Gibson 1978, Kessel 1989), maximum numbers 5-6 breeding pairs at Gambell, St. Lawrence I., Jun 1989 (M. E. Islieb pers. comm.), 3-4 pairs annually at both Wales and Nome (Kessel 1989). Seven nesting pairs along 15 km of river banks in ne. Siberia; minimum distance between nests 1 km (Kistchinski 1980).

BLACK-BACKED WAGTAIL. Fairly common on Kamchatka Peninsula and abundant on Sakhalin I.;

up to 5 pairs on <10-ha islands (Dement'ev and Gladkov 1954). On Kunashir I., Kuril Is., 2–3 nesting pairs on 1 km of sea coastline, but only 1 pair on 10 km of lake shores (Nechaev 1969). Densities of adults (per kilometer) in Tochigi Prefecture, Japan, in Jun–Aug: 0.5 along streams without gravelly areas, 0.7 on factory areas with waterways, 0.3 in towns; distances between nests (m): along streams without gravelly areas about 800 and in factory area with narrow waterways about 30, 550, 1,500, and 2,000 (Higuchi and Hirano 1981). On Sea of Okhotsk (west of Kamchatka Peninsula) 2.0–2.9 nesting birds/kilometer of coast; after nesting season, 3.5 birds/km (Elsukov 1984).

Trends. No information.

POPULATION REGULATION

No information for North American populations. Both White and Black-backed wagtails are too scarce to be managed in North America. See Conservation and Management: effects of human activity, below.

CONSERVATION AND MANAGEMENT

EFFECT OF HUMAN ACTIVITY

Growing number of human settlements, roads, bridges, and other industrial constructions along coastlines and in northern regions increases suitable breeding and foraging habitats. This commonly increases numbers and leads to occupation of inland areas (Nazarenko 1968, Mal'chevski and Pukinski 1983, Nakamura 1985). In ne. Russia, extensive logging resulted in expansion of *M. alba* breeding range because logging provided abundant suitable nest sites, including stumps, piles of trunks, and logging wastes (Mal'chevski and Pukinski 1983). Comparison of spring arrival times between nineteenth and twentieth centuries revealed earlier arrival and nesting at present compared to 100–150 yr ago, possibly owing to more extensive utilization of human landscapes in the late twentieth century (Mal'chevski and Pukinski 1983). Nesting success in human settlements also higher compared to natural conditions (Mal'chevski and Pukinski 1983; see Demography and Populations: measures of breeding success, above). *M. alba* easily attracted to nest boxes, especially those under bridges near human settlements (Mal'chevski and Pukinski 1983, Bragin and Gilyazov 1984).

Pesticides and other contaminants. For impact of pesticides see Mullie et al. 1991. In wintering *M. alba*, average accumulation of heavy metals in body ($\mu\text{g}/\text{dry g}$) as follows: lead: in brain 13.5, feathers 5.9, kidneys 5.1, bones 3.9, heart and muscle 3.7 each, liver 0.7; mercury: in brain 14.2, heart 11.3,

feathers 10.6, kidneys 9.4, muscles 9.2, liver 5.6, bones 2.8; selenium: in liver 20.0, kidney 19.9, heart and bones 5.5 each, brain 4.2, feathers 2.0, muscles 1.1; copper: in feathers 77.0, heart 45.7, kidneys 29.0, brain 28.6, liver 20.6, muscles 11.7, bones 6.4; manganese: in feathers 65.1, heart 32.1, liver 27.5, kidneys 23.7, bones 18.2, brain 4.2, muscles 3.9; zinc: in feathers 96.0, liver 73.2, kidneys 71.8, heart 55.6, muscles 26.6, brain 14.2, bones 5.5 (see Saleh et al. 1988 for details).

Disturbance at nest and roost sites. *M. [a]. personata* easily abandons nests when disturbed or often without any visible reasons; 2 nests in advanced stage of incubation deserted after 1–2 nest checks (Kovshar 1979). Repeated disturbance at traditional roost sites in *M. a. yarrellii* caused roost abandonment in following years (Dougall and Appleton 1989). At roost, 1 h of disturbance sufficient to cause drop of about 200 birds in following nights; return to previous level takes up to 2 wk (Broom et al. 1976).

MANAGEMENT

M. a. alba population increases when suitable nest boxes provided (Bragin and Gilyazov 1984). White Wagtail colonized new habitats (e.g., forest creeks and extensive reed areas) following reintroduction of beavers and muskrat in ne. Europe (Mal'chevski and Pukinski 1983; see Breeding: nest site, above).

APPEARANCE

MOLTS AND PLUMAGES

Molt cycle similar in *M. a.ocularis* and *M. a. alba*. Black-backed Wagtail less studied, but apparently also similar to *M. a. alba* (Dement'ev and Gladkov 1954). See Appendix for tail measurements.

Hatchlings. Skin flesh-colored. Neossoptiles on 8, rarely 9 feather tracts; see Neifeldt (1970) for details of natal down distribution.

Juvenal plumage. Development of Juvenal plumage starts on day 23–25 and ends on day 48–52 in young from early broods and starts on day 28–33 and ends on day 42–46 in late broods (Yakovleva et al. 1987).

WHITE WAGTAIL. For *M. a.ocularis*. "Entirely dull gray on the upper parts, the forehead gray of a lighter tint, a white eyebrow and a blackish transocular stripe; the sides of the head are mottled with gray, the throat feathers are edged with black and the breast has a blackish crescent-shaped patch. The face and throat are generally suffused with yellow" (Gabrielson and Lincoln 1959: 690).

BLACK-BACKED WAGTAIL. "The hind crown gray, the forehead, fore crown, and sides of head, chin,

and throat white washed with yellow, very much less white on wings than adults, the quills being white only internally and narrowly on the outer edges" (Gabrielson and Lincoln 1959: 690).

Basic Plumage. Prebasic I molt partial. Feathers replaced include all contour body feathers, all marginal and lesser secondary coverts, 4-10 greater secondaries, some tertials, and rarely rectrices, depending on geographic location (Ginn and Melville 1983, Yakovleva et al. 1987, Jenni and Winkler 1994). Molt proceeds on major tracts as follows: starts on ventral sternal, crural, spinal cervical and pelvic, and humeral; then malar part of capital, ventral cervical and abdominal, anal cirlet, femoral, marginal-coverts, greater-primary coverts, lesser-secondary coverts, and undermedian secondary-coverts; then upper- and undertail-coverts, crown and auricular parts of capital, and tertials; then eye region of capital, greater-secondary coverts; and finally, upper median secondary-coverts (Yakovleva et al. 1987).

Molt is faster and less extensive in late-hatched than in early-hatched birds. In *M. alba*, molt begins 35-40 d after hatching and ends at 125-135 d in early broods, begins 41-47 d after hatching and ends at 110-115 d in late broods (Yakovleva et al. 1987). In *M. [a.] personata*, young birds of first broods started to molt 33-39 d after nest departure; young of second broods after 20-21 d (Kovshar 1979).

Except for retention of Juvenal feathers, Basic I plumage practically identical to Definitive Basic plumage; see Jenni and Winkler 1994 for plumage characteristics useful for aging of *M. a. alba*. Young Black-backed Wagtail gain black hind crown gradually during first winter (Gabrielson and Lincoln 1959).

Alternate I plumage. In White Wagtails Prealternate I molt of second year (SY) birds identical to Definitive Prealternate molt but more greater-secondary coverts might be replaced (Jenni and Winkler 1994). Plumage similar to Definitive Alternate plumage; see below.

Definitive Basic plumage. Definitive Prebasic molt complete and lasts 45-78 d. Females with late broods can start molt before nestlings leave nest (Ginn and Melville 1983). First secondary shed with primaries P5 and P6; tertials molt between shedding of primaries P2 and P8; body feathers molt between shedding primaries P2 and P10 and proceed with lesser-secondary coverts, mantle, scapulars, and rump (Ginn and Melville 1983, Cramp 1988, Jenni and Winkler 1994); rectrices shed with primaries P3-P4, regrow during growth of primaries P7-P8 (Cramp 1988) or molt throughout; greater-secondary coverts replaced in 3 groups: 9-7, then 6-4 (or 3), then 2 (or 3) -1;

secondaries replaced in sequence S1-6-2-5-4-3 (Ginn and Melville 1983, Jukema and Rijpma 1984).

WHITE WAGTAIL. For *M. a. ocularis*. Plumage same as Definitive Alternate. In addition, in male: "chin and throat are white, the pectoral black being restricted to a more or less broad patch; female "has less white on its wings" (Gabrielson and Lincoln 1959: 690).

BLACK-BACKED WAGTAIL. Plumage same as Definitive Alternate. In addition, in male "black on the throat is restricted to the sides of the gular region and to more or less broad breast-band, the back turns gray [after molt], but generally with traces of black and even with good-sized black patches"; female: "grayer than male, practically pure gray above, with black hind crown and nape" (Gabrielson and Lincoln 1959: 690).

Definitive Alternate plumage. Definitive Prealternate molt partial. Feathers replaced include 0-7 greater-secondary coverts, 3-4 median lesser secondary-coverts, 1 or 3 tertials, sometimes 1-2 (usually central) rectrices, and some body and head feathers (Ginn and Melville 1983, Jenni and Winkler 1994).

WHITE WAGTAIL, MALE. For *M. a. ocularis*. Chin, throat, breast, a transocular stripe, hind crown, and nape black; upperparts clear gray to uppertail-coverts which are chiefly black, with the outer webs of the side, middle, and lesser uppertail-coverts white; outermost pair of rectrices white edged narrowly with black on the inner web, the next pair also white with a broader black edge on inner web, rest of tail black, the central rectrices with outer webs edged with white; lesser wing-coverts gray, outermost feathers blackish, more or less broadly edged with white; wings blackish or grayish black, primaries and secondaries very narrowly edged with white on outer webs; innermost tertials grayish white; underparts below breast entirely white with some gray on flanks (Gabrielson and Lincoln 1959).

WHITE WAGTAIL, FEMALE. Slightly smaller than male with less white on wings (Gabrielson and Lincoln 1959).

BLACK-BACKED WAGTAIL, MALE. Forehead, forehead, superciliary region, sides of head and neck, chin, upper throat, outer webs of uppertail-coverts, and underparts below breast white; transocular stripe and upperparts from hind crown to tail black, except 2 outermost rectrices which are white, outermost with a very narrow and incomplete black edge on inner web, next pair with a broader inner black edge; wing remiges, median-coverts, and greater-coverts nearly all white, only tips of primaries, and inner parts of 3 innermost tertials brownish black, lesser-coverts being entirely black (Gabrielson and Lincoln 1959).

BLACK-BACKED WAGTAIL, FEMALE. Summer females of *M. lugens* are gray-backed and resemble female *M. a. ocularis*, particularly in the first year when the white in the wing is not yet fully developed (Morlan 1981). Most female *lugens* have more black on the nape and may show some dark shading on the back, but even lacking this they can be distinguished by their white chin and upper throat, virtually all *ocularis* exhibit a black chin at this season (Morlan 1981).

BARE PARTS

Bill and gape. In nestlings, bill flesh-colored, gape orange-yellow; in adults, bill black, gape dark gray (Gabrielson and Lincoln 1959, Cramp 1988).

Iris. Dark brown.

Legs and feet. Flesh-colored in nestlings, black in adults.

MEASUREMENTS

BLACK-BACKED WAGTAIL

See also Appendix. Culmen length (from skull, mm): males 17.7 ± 0.2 (SD) ($n = 21$), females 17.7 ± 0.1 ($n = 8$) (Higuchi and Hirano 1983). Wing length (mm): males 96.6 ± 0.6 ($n = 21$; Honshu, Higuchi and Hirano 1983), 93–101 ($n = 5$; s Kuril Is.; Nechaev 1969), 93.5 (range 91–96, $n = 12$; s. Ussuriland; Nazarenko 1968), and 94.6 (range 87–99, $n = 19$; e. Palearctic; Dement'ev and Gladkov 1954); females 89.9 ± 0.9 ($n = 8$; Honshu; Higuchi and Hirano 1983), 89.4 (range 87–92, $n = 6$; s. Ussuriland; Nazarenko 1968), 90.7 (range 85–97, $n = 9$; e. Palearctic; Dement'ev and Gladkov 1954). Tail length (mm): males 98.3 ± 0.5 ($n = 21$), females 92.3 ± 0.9 ($n = 8$) (Honshu; Higuchi and Hirano 1983). Body mass (g): males 30.4 (range 27.9–33.8, $n = 5$; s. Kuril Is.; Nechaev 1969), 25.3 (range 24.5–29.6, $n = 4$; e. Palearctic; Dement'ev and Gladkov 1954); females 25.3 (range 23.4–28.4, $n = 4$; e. Palearctic; Dement'ev and Gladkov 1954). Beak depth (mm) at anterior edge of nostril: males 3.90 ± 0.04 (SE) ($n = 21$), females 3.81 ± 0.06 ($n = 8$) (Honshu; Higuchi and Hirano 1983). Wing length (mm) of *M. lugens* x *M. a. leucopsis* hybrids: males 91.7 (range 88–95, $n = 3$), females 87.0 (range 85–89, $n = 2$) (s. Ussuriland; Nazarenko 1968).

WHITE WAGTAIL

For *M. a. ocularis*. See also Appendix. Wing length (mm): males 95.7 (range 90–98, $n = 7$), females 89.8 (range 88–92, $n = 7$) (e. Palearctic; Dement'ev and Gladkov 1954). For measurements of *M. a. alba* and other w. palearctic subspecies, see Cramp 1988. For review of winter weight dynamics in *M. a. yarrellii*, see Dougall and Appleton 1989. Mean 60%

(SD 3.57, range 53.7–65.3) of water content in body mass of 9 wintering *M. alba* (Heatwole and Muir 1982).

In both Black-backed and White wagtails, males have significantly longer wings than females (Appendix). Difference especially prominent in *M. a. ocularis*. Male *M. a. ocularis* also has significantly longer tail than female. No differences between sexes in weight, tarsus length, or bill length for either both species.

PRIORITIES FOR FUTURE RESEARCH

North American populations of White and Black-backed wagtails provide excellent opportunities for comparative studies of breeding biology of these wagtails as related to better-studied Asian populations. Molecular studies are needed to clarify phylogenetic relationships in the wagtail complex.

ACKNOWLEDGMENTS

AVB thanks E. K. Kupriyanova for help with a worldwide literature search. AVB was supported in the field by the Ornithology Laboratory of Moscow University (Prof. R. L. Boehme, director). Cover photo of White Wagtail by Rick and Nora Bowers; Black-backed Wagtail by C. Speegle/VIREO.

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Appendix. Body mass (g) and linear measurements (mm) of White and Black-backed wagtails (collections of Burke Museum, Univ. of Washington, Seattle). Shown are mean value and (range). ASY = after-second year birds; HY = hatching year birds.

Sex (age)	<i>n</i>	Culmen length	Wing	Tail	Tarsus	Mass
Black-backed Wagtail						
Males (ASY) ¹	11	10.8 (10.1–12.3)	90.2 (80.9–94.1)	92.0 (80.8–101.3)	21.3 (20.2–23.0)	27.2 (24.0–29.1)
Males (ASY) ²	4	11.3 (10.2–13.0)	93.3 (90.5–97.5)	94.4 (90.0–100.0)	21.1 (20.2–22.1)	32.1 (31.4–32.9)
Females (ASY) ¹	5	11.1 (10.7–11.6)	86.8 (84.2–90.2)	88.9 (85.3–91.1)	22.7 (22.1–23.6)	26.1 (23.8–29.0)
Females (HY) ¹	2	9.3 (9.2–9.3)	85.3 (84.5–86.1)	74.7 (72.5–76.8)	22.1 (21.3–23.0)	25.8 (24.5–27.0)
White Wagtail						
Males (ASY) ³		10.7 (10.5–10.9)	93.1 (90.4–98.1)	96.9 (95.6–97.7)	22.6 (22.0–22.9)	25.1 (23.0–26.7)
Females (ASY) ³	5	10.8 (10.0–11.7)	85.9 (84.0–87.9)	88.5 (83.5–95.3)	22.1 (20.8–22.9)	23.7 (17.7–28.5)
Females (HY) ³	2	10.0 (9.7–10.2)	88.0 (85.9–90.0)	95.7 (94.1–97.4)	22.6 (22.5–22.6)	23.3 (21.8–24.8)
Black-backed Wagtail x White Wagtail hybrid						
Males (ASY) ¹	3	11.0 (10.6–11.5)	90.2 (89.5–91.0)	95.9 (95.8–96.1)	22.6 (22.4–22.8)	25.3 (24.0–26.5)

¹ Kamchatka Peninsula.
² Sakhalin I.
³ Coast along Sea of Okhotsk.

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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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RECOMMENDED CITATION

Badyaev, A. V., D. D. Gibson, B. Kessel. 1996. White Wagtail (*Motacilla alba*) and Black-backed Wagtail (*Motacilla lugens*). In *The Birds of North America*, No. 236-237 (A. Poole and F. Gill, eds.). The Academy of Natural Sciences, Philadelphia, PA, and The American Ornithologists' Union, Washington, D.C.

