DISTINGUISHING CHARACTERISTICS

Large and deliberate in its movements compared to other *Dendroica*. Pumps its tail. Male is bluish gray above with dark streaks in the feathers. Yellow below with black spots or streaks confined to the sides. Male has blackish area in front and below the eye (missing in female), with prominent white crescents outlining the top and bottom of the eye. Markings less pronounced in females, some males, and immatures. Wing bars present but not conspicuous. Sometimes confused with Prairie Warbler (*Dendroica discolor*), which also bobs its tail but is smaller, 8 g compared to 14 g, and is yellowish on face; also with Magnolia Warbler (*D. magnolia*), which has prominent white wingbars and tail marks, and does not pump its tail.

DISTRIBUTION

AOU CHECK-LIST REGION

Breeding range. Nests on scattered tracts within 13 contiguous counties (but as few as 6 at one time) in n. Lower Michigan (Fig. 1), mainly in drainage system of Au Sable River. Singing males without mates found in some years in Wisconsin and Ontario near same latitude as Michigan nesting grounds, but always in stands of small jack pines. Confirmed record in Upper Peninsula of Michigan (Probst 1985) as well as unpublished sightings, and in Quebec (Chamberlain and McKeating 1978). All outside normal nesting range have been males. Summering in most depauperate lands of northern forests and wintering in most depauperate lands of West Indies, this warbler finds a measure of sanctuary from enemies and competitors at all seasons.

Nonbreeding range. Apparently winters throughout Bahama Islands (Fig. 1), but difficult to find. Most reports from places with most human visitors. Sightings also in Turks and Caicos Islands, which are politically but not geologically separate (Mayfield 1960, Clench 1978). Claimed sightings in Mexico and Dominican Republic have not been fully documented.

HISTORICAL CHANGES IN DISTRIBUTION

Probably survived near extinction for many centuries, limited by highly specialized and transitory nesting habitat. Lightning-caused forest fires that produced good habitat were fewer but larger in extent than in modern times. Native Americans probably not a significant factor since they were not numerous in these pinelands. Modern limitations include better control of wildfires and new menace of Brown-headed Cowbirds (see Breeding: brood parasitism) that entered nesting range about 1880 and steadily increased, putting pressure on warblers in this century, without affecting range.

At height of Wisconsin glaciation, 17,000 yr BP, Atlantic Ocean was more than 100 m lower than at present, and land area of Bahamas was vastly greater than now. Then jack pine forests were limited to se. corner of continent and warblers' habitat probably lay on coastal plain much nearer the wintering grounds than at present. Species probably originated in West Indies, achieving its distinctness during Pleistocene and adapting to forest changes on its nesting ground during the ice ages (Mengel 1964). Jack pine spread west and north to present range within past 10,000 yr (Mayfield 1988b). No fossils known.

As a result of extensive lumbering of Michigan forests and accompanying forest fires, peaking in 1871, nesting habitat was at its historical maximum in 1880s and 1890s.

SYSTEMATICS

The phylogenetic relationships among the Dendroica warblers have not been well studied, and the close relatives of Kirtland's Warbler remain obscure. It is usually placed in classifications between Pine Warbler (*Dendroica pinus*) and Prairie Warbler (e.g., Sibley and Monroe 1990). Mengel (1964) suggested that it might be a relict species related to the Yellow-throated Warbler (*D. dominica*), although Mayr and Short (1970) voiced some uncertainty about this.

MIGRATION

NATURE OF MIGRATION OF THE SPECIES

Entire population migrates from nesting ground in early fall to Bahama Islands and returns to Michigan in late spring. Most probably make the trip in one hop unseen, with only strays and stragglers observed (Mayfield 1988a).

TIMING AND ROUTES OF MIGRATION

Spring migration. See Fig. 4. Departure from Bahamas not observed but probably in late Apr or early May. Scanty records from se. U.S. may not represent main body of migrants. Sight records, usually of single birds, are often publicized and noted in most states e. of Mississippi River.

Earliest mainland record 12 Apr 1902, on Georgia coast (Van Tyne 1951). Records increase near destination in s. Michigan and n. Ohio in mid-May. Apparently migrates in narrow band between Bahama Islands and nesting ground, traversing S. Carolina, N. Carolina, w. Virginia, W. Virginia, Ohio, and s. Michigan.

Spring arrivals on breeding ground not detected until they sing; hence actual arrival may be earlier than noted, 3–18 May, mean 12 May (Mayfield 1960).

Fall migration. Postbreeding birds in nesting habitat until migration. Numbers in breeding ground decline through Aug, with hatching-year birds gone by mid-Sep and a few adults lingering into early Oct (Sykes et al. 1989, Sykes and Munson 1989; Fig. 4). Birds examined on nesting grounds in late Aug and Sep showed little subcutaneous fat deposition. Fall migrants sometimes wander outside migratory path (Clench 1973). First arrivals noted in Bahamas in Aug.

MIGRATORY BEHAVIOR

Individual birds usually forage in low vegetation and stay in one area for a few days. Males in spring often sing. Little association with other birds in same area.

CONTROL OF MIGRATION No information.

HABITAT

BREEDING RANGE

Nests in extensive stands of jack pine. Region is level or gently rolling, covered mainly by expanses of pine of various sizes interspersed with openings and clumps of pin oak (Quercus ellipsoidalis), red maple (Acer rubrum), and quaking aspen (Populus tremuloides). Prefers homogeneous tracts of great size, but has nested in tracts < 30 ha although more successful on tracts >200 ha. Jack pine is firedependent species, dominating forest on sandy soil where fire has cleared the land, fertilized the surface, and opened serotinous cones to spread the seed. Jack pine ranges from British Columbia to Nova Scotia and northward almost to the arctic, but Kirtland's Warbler utilizes only the southernmost extensive tracts, which extend across about 190,000 ha in Lower Michigan (Zimmerman 1956). Here jack pine is dominant only on poorest of loose sandy soils giving way to deciduous trees in more fertile soils.

These conditions occurring naturally only after forest fire can be approximated by plantings of jack pine and red pine (*Pinus resinosa*), which warblers will occupy. Warblers first appear about 6 yr after fire where the new growth is most dense and the prevailing height is 1.5–2.0 m. Tracts then continue to be occupied for about 15 yr when trees are 3–5 m or taller and lower limbs dying where shaded. Warblers occupy densest stands first but persist longer in more open tracts. Last residents of a tract are unmated males (Mayfield 1960).

Females are more selective than males in choice of habitat, so better habitat may attract excess of females, encouraging polygyny (see Demography and Populations).

Amount and quality of available habitat is difficult to estimate. Some tracts that appear promising are not occupied, and tracts that do not appear ideal are occupied. Exactly why some tracts are more attractive and perhaps more productive is not always understood, although accurate predictions of warbler occupancy have been made using measures of jack pine stem density and canopy cover (Nelson 1992). Subtle factors of microclimate may be involved. Tracts may be unsuitable because the nature of soil and elevation produce surface temperatures below freezing on cold mornings in June when the female is selecting a nest site (Barnes et al. 1989). The same factors may help explain why nesting range is limited to the most southerly portions of jack pine range.

Bird life is generally sparse in jack pine plains. No other species of warbler is characteristic of this habitat. The closely related Pine Warbler nests in branches of large pines nearby, the Prairie Warbler (*D. discolor*) nests in small pines but favors an admixture of broad-leaved shrubs, and the Nashville Warbler (*Vermivora ruficapilla*), which nests on the ground like Kirtland's Warblers, prefers openings and larger trees.

Vegetation preference in migration. Usually seen in low broad-leaved scrub in semi-open locations.

WINTER RANGE

Rare and difficult to find in winter. Quiet, no song, only faint chirps. Inhabits dense scrub. Almost always solitary. Unique habitat requirements not known. Many observers have searched unsuccessfully on various islands. Radabaugh (1974) spent 800 hr searching on 11 islands in 2 winters, using playback of recorded song to attract warblers, and found 1 male on Crooked Island. Site was 900 m inland from sea in sparse broadleaved scrub, thickets interspersed with openings. General height of woody vegetation was 1.0-1.5 m, with scattered taller trees. Exposed ground surface was mostly limestone. Male spent 70% of time on ground gleaning small insects. Clench (1978) reported similar sighting on Caicos. Last wintering specimen collected in 1965 on San Salvador on former farmland, as on New Providence where Maynard collected 24 specimens in 1884 (Mayfield 1972b).

Visiting bird watchers on Grand Bahama have reported Kirtland's Warblers frequently among

tall pines but always in the understory. Never reported in tall broadleaf woodlands (coppice) of Bahamas.

FOOD HABITS

FEEDING

Forage for insects through ground cover and midlevels of small pines and adjacent oaks on breeding grounds. Gather food mainly by gleaning among pine needles, leaves of deciduous trees, and ground vegetation. Sometimes hover to snatch flying insects and to gather insect food in terminal clusters of pine branches. Occasionally ingest matter of doubtful nutritive value such as twigs, rotten wood, pine needles, grass, and globules of pitch. Appear to get food in summer with small effort, except perhaps during cold weather early in the season.

Food usually seems abundant, but drought may reduce food supply at times (Radabaugh 1974; See Demography and Populations: mortality and disease).

DIET

Summer diet chiefly small crawling and flying insects and larvae, including sawfly (Tenthredinidae) adults and larvae, grasshopper (Acrididae) nymphs, flying moths and dipterans. Young are fed same assortment. When blueberries (*Vaccinium angustifolium*) ripen in midsummer, adults eat them avidly and feed soft fruit to young.

In winter also feed on insects and small fruits like many other warblers wintering in the Neotropics (Radabaugh 1974, Sykes 1989).

Water apparently sipped from dew on leaves. Standing water seems to be ignored, but is rarely available on porous soils of summer and winter habitats.

NUTRITION AND ENERGETICS No information.

METABOLISM AND TEMPERATURE REGULATION No information.

SOUNDS

VOCALIZATIONS

Phenology. Females and immature males do not sing ordinarily, but partial song noted in late summer by hatching-year male (Walkinshaw 1983), by captive male at 40 d, with whisper songs from 77 d onward (Berger 1968). Males sing in spring migration from South Carolina northward.



Figure 2. Adult male Kirtland's Warbler in typical breeding habitat. By J. H. Dick.

Singing becomes sporadic in early Jul, but a few males still sing in early Aug. These late singers often feeding fledglings.

Daily pattern of vocalizing. Male on nesting territory sings loudly and persistently (Fig. 2). Songs (Fig. 3) uttered 6–9 times per minute, each song lasting l.0–l.5 s. Singing courses often last 15 min or more followed by a few minutes of silence. Singing most frequent early in morning, dwindling in late forenoon, and becoming desultory in afternoon, especially on hot days. Often resumes early in evening but less actively. Song ceases in cold or blustery weather. Unmated males sing more often than mated males (Hayes and Probst 1986), and also males unaccompanied by females because of incubation duties.

In censusing under good weather conditions on a June morning, the probability of song by a male is 85% in any 5–min period. In calm weather song can be heard by human ears more than 400 m. One male with mate in 13th day of incubation sang 2,212 times in a day (Mayfield 1960).

Song clear and emphatic with none of buzzy quality of some other warblers. Tempo and quality suggested by English syllables *chip-chip-che-way-o* with slight individual variation. Some resemblance to song of Northern Waterthrush (*Seiurus noveboracensis*), but some variants may resemble fragments of song of Indigo Bunting (*Passerina cyanea*), House Wren (*Troglodytes aedon*), or final notes of Vesper Sparrow (*Pooecetes gramineus*) heard at a distance.

Repertoire and delivery of songs. Primary songs (Fig. 3) differ slightly among individuals, allowing recognition with practice, like a friend's voice identified quickly on the telephone. The differences are not always sufficient to allow reliable identification on sonograms (David Ewert unpub.). Some idiosyncrasies have been recognizable from



year to year, but whether primary song changes significantly over time has not been studied.

"Chatter songs" are brief. Unmusical syllable repeated rapidly, *chu-chu-chu-chu*. Sometimes given under stress, but also for no discernible reason. A few males use this variant regularly. "Whisper" songs may be either of the two types, but given so softly they can be heard only within 10 m or so. Often noted when two males are near each other or when a male is investigating song playback.

Other vocalizations. Generally quiet except for males on territory. May not utter a sound for many minutes at a time. Communicate with one another by high-pitched, faint note, *zeet* like other warblers. Apparently a signal to other birds not within sight. Heard on breeding ground, migration, and wintering ground. A few other single notes under varying degrees of apparent stress, as in distraction display at the nest. Fledglings beg for food by single notes uttered rapidly, *Chi-chi-chi-chi.*

BEHAVIOR

LOCOMOTION

Moves on ground by hopping, but capable of moving feet alternately as in "Rodent Run" of distraction display. Hops quickly from twig to twig in thickets.

Swift, agile flyer, darting through dense foliage.

SELF-MAINTENANCE

After eating food or giving food to young, often wipes its bill on branch, presumably to remove food particles. In early mornings sometimes bathes in dew, placing itself in a cluster of dripping leaves, fluffing plumage, shaking wings and tail vigorously, and then preening. Captive 19 d old bathed in shallow pool on the floor of aviary, dipping its breast into water and fluttering wings (Van Tyne 1953, Berger 1968).

Female incubating eggs or brooding young at night (examined by flashlight) sleeps with head turned back into scapular feathers. In daytime on Figure 3. Primary song of Kirtland's Warbler. nest she dozes with head forward and eyes closed. Adults on night perches not observed. Fledglings choose perches close to one another for sleeping until about 9 mo old, then choose isolated perches (Berger 1968).

Anting not seen in wild, but noted in captive warblers (Berger 1968). Both sexes sunbathe. Warbler selects sunny perch on twig or open space on ground, fluffing its feathers, raising tail and spreading wings. Basks facing sun or turned away from it for several minutes at a time, alternating periods of preening and foraging (Mayfield 1960). Male may sing at times. Sunbathing noted in captive birds at 17 d (Berger 1968).

AGONISTIC BEHAVIOR

After territorial boundaries are established, little conflict with same or other species. Tolerant of bird neighbors except very near nest. Brief chases of other small birds may be play rather than defense.

Captive young birds gave hoarse call, spreading wings and tail and advancing on companions at 70 d. Dominant individuals displaced others at food dish at 5 mo. Aggressor advanced with halfopen bill, spread and lowered wings, and pursued displaced bird with short chase. These episodes were infrequent but perhaps stimulated by confinement. Usually perched near each other with no sign of hostility. At 8 mo of age most interaction ceased (Berger 1968).

Territorial and nest defense. Male on territory challenges approach of another male by flying toward him and uttering song. Both sing. Actual combat is rarely seen except at the beginning of nesting season when boundaries are not yet established. Males then fight fiercely in the air, their mandibles locked together until they tumble to the ground (Mayfield 1960).

When a small mammal or bird approaches nest, brooding female may dart at it on ground or in flight with noisy wing motion and snapping bill (Mayfield 1960). Small intruders, including cowbirds, are usually repulsed. Males also dart at intruders near nest (Walkinshaw 1983).

SPACING

Territoriality and colonies. Territory defended by male is larger than that reported for most warblers and may be affected by density of tree stand. Territories larger in thinner vegetation. Estimates of territory size based on apportionment of available habitat larger than those based on actual movements of males. Species does not seem to use all the suitable habitat available. Territories from 0.6 ha to more than 10 ha, mean 8.4 ha (Walkinshaw 1983) and 3.4 ha (Mayfield 1960). Nest may be placed anywhere within territory.

6 KIRTLAND'S WARBLER

Female usually forages near nest. Male sometimes leaves territory for brief periods.

Territories tend to be grouped in "colonies," each male within hearing of at least one neighbor. Isolated pairs rarely found. Territories sometimes loosely distributed over terrain like a bunch of grapes, not always touching nor filling intervening spaces. Road-building has divided most of this region into mile squares, and a mile (259 ha) may hold 6–22 males.

Some colonies are small (< 6 males) but the greater part of the population is gathered into a few large colonies (Burgoyne and Ryel 1978). Large colonies may be advantageous, but reasons not fully understood. Presence of singing males may attract and stimulate other males and females. In new habitat among small pines, the buildup of a colony is gradual, reaching its peak in about 10 years and then declining for about 5 years (Probst 1986).

SEXUAL BEHAVIOR

Mating system. Usually monogamous during nesting season. Polygyny occurs sporadically and at times may involve 15% or more of males (Radabaugh 1972b). Reason for this variability not fully understood, but may be influenced by quality of habitat.

Pair bond. Male and female of pair stay near one another until young are independent. Male does not touch female except in copulation, which occurs before eggs are laid. Witnessed examples occurred in clusters of pine branches before first egg was laid. The act lasted only 1–2 s while pair communicated by soft twittering. If both birds return in the following year, about half find the same mate.

No instance of males with more than 2 mates simultaneously nor females with more than 1 mate in a season. Occasionally males mate with 2 females successively in one season (Radabaugh 1972b).

Sex ratio. See Demography and Populations.

SOCIALITY

Usually appears to be unaccompanied on nesting ground, in stops during migration, and on wintering ground, yet shows some gregarious tendencies. As noted before, the pairs aggregate in colonies, and when fledglings are attended by adults, a family remains in loose association within tract that held nest. The species carries signals of recognition: distinctive call note, flash of white in tail, and active tail bobbing.

Some individuals on breeding ground are remarkably tame, allowing human beings to approach closely without alarm. Adults near nest have been photographed on hand and foot of visitor. Females on nest captured easily by net, and after capture return quickly and silently. Other individuals more wary and some females difficult to find and trace to nests. Tolerate more disturbance at nest than most warblers without deserting. Tameness may have developed because little threatened by mammals in summer or winter.

Tail bobbing. One of the field marks of the species is its frequent moving of its tail, variously described as bobbing, wagging, jerking, and flicking. Habit is shared in breeding region by Palm Warbler and Prairie Warbler. Movement is up and down, not sideways. Tail is jerked downward and then more slowly returns. Noted in field on short-tailed fledglings as early as 18 d and among captives at 12 d (Berger 1968). Perhaps valuable as a recognition signal in shrubbery.

PREDATION

No predation on adults witnessed. Identity of predators speculative and circumstantial, including Sharp-shinned Hawk (*Accipiter striatus*), Northern Harrier (*Circus cyaneus*), Great Horned Owl (*Bubo virginianus*), and domestic cat (*Felis domesticus*). For predation on nests and eggs, see Demography and Populations: mortality and disease.

Response to predators. Faced with overwhelming danger at nest, female often gives elaborate distraction display, scuttling away several meters like a mouse, in "rodent run" with wings lowered and quivering, body turning from side to side, tail spread showing white in rectrices, head raised and thrown backward. Although seeming out of control, she is actually alert and ready to take flight rapidly if pursued. Male also gives distraction display under similar circumstances, but not as intensely.

In presence of distant danger, like noisy jay or crow, warbler sometimes freezes for minutes at a time absolutely rigid.

BREEDING

PHENOLOGY

Pair formation. Females arrive on breeding ground a few days after males in mid-May. Pair formation begins within 1 wk.

Nest building. First nests may be started as early as 16 May or as late as 2 Jun. Date determined not by arrival time on the nesting ground, but by weather. All nesting activities suspended by cold, wet weather.

First brood. Fig. 4. First eggs appear in last week of May, but most clutches not started until first week in Jun. Mean, 4 Jun. First eggs usually hatch between 9 Jun and 26 Jun.