Introduction

The Kirtland's Warbler (*Setophaga kirtlandii*), one of the rarest songbirds in North America, was first discovered when Charles Pease shot a migrant on 13 May 1851 on the farm of his father-in-law, Jared P. Kirtland, near Cleveland, OH. The new species was identified by Spencer Baird, who named it for the renowned Ohio naturalist (Baird 1852). The species' wintering grounds were discovered as additional specimens were collected from throughout the Bahamas, but it took 52 years before Norman Woods followed the lead of a graduate student from the University of Michigan and pursued the species along the Au Sable River in northeast Oscoda Co., MI, where he discovered the first nest of this elusive species in July 1903 (Wood 1904, Rapai 2012).

Breeding male Kirtland's Warbler; Mio, MI; 25 May.

Breeding male Kirtland's Warbler; Mio, MI; 19 June.

Throughout the first half of the twentieth century, the Kirtland's Warbler was studied by several of ornithology's finest naturalists, including N. Leopold, L. Walkinshaw, J. Van Tyne, H. Mayfield and others, who shared details of the species' life history. Their work laid the foundation for recovery, as the species became the victim of its own habitat specificity, and the conservation movement sought to save declining species.

The 1971 decennial census confirmed the population crash that ornithologists had predicted (Mayfield 1972), documenting the decline in population size from estimates of 1000 individuals to around 400. The large areas of dry, sandy soil with dense stands of young jack pine (*Pinus banksiana*), upon which the species depended, had declined owing to fragmentation and fire suppression, but the most imminent threat was nest parasitism by the Brown-headed Cowbird (*Molothrus ater*, Mayfield 1960, Walkinshaw 1983).

Figure 1a. Breeding and non-breeding (winter) ranges of the Kirtland's Warbler.

Owing to its natural rarity and apparent decline,

Kirtland's Warbler was included on the first list of endangered species in 1967 under the Endangered Species Conservation Act (Office of the Secretary 1967). Following the enactment of the Endangered Species Act in 1973, the Kirtland's Warbler Recovery Team was created, and they produced a recovery plan in 1976 (Byelich et al. 1976). The plan established a recovery goal of 1000 breeding pairs distributed across the original breeding range of the species, and the revised plan (Byelich et al. 1985) identified and prioritized recovery strategies to achieve this goal, including habitat management, cowbird control, annual monitoring, research, and education. In the late 1980's, the population began to respond to the recovery efforts, and by 2012 the population had reached about 4000 individuals.

Figure 1b. Breeding range of the Kirtland's Warbler.

Kirtland's Warblers are now considered biologically recovered, but the species is dependent on perpetual management to establish the early successional habitat it needs, and to remove the cowbird threat on that restricted landscape. In fact, all five recovery strategies must continue, making the species entirely conservation-reliant (Scott et al. 2010). The Kirtland's Warbler Recovery Team is attempting to develop a public/private conservation partnership to safeguard annual management of the species after removal from the protection of the Endangered Species Act (Bocetti et al. 2012). The species has been above the recovery goal of 1000 breeding pairs for more than a decade, and as long as management continues, its future appears secure. Efforts to secure this rare and unique species may provide a conservation model for other conservation-reliant species as well.

Distinguishing Characteristics

Adult males have dark black stripes on blue or blue-gray back and head. Younger adult males have a more gray-brown head and back with brownish stripes. The stripes become darker on a more distinct blue-gray back with age (Probst et al. 2007). Younger males have rusty rather than brown or nearly black primary feathers. Adult males have bright, intense solid yellow throats, breast, and abdomen. These areas are lighter or faded yellow in younger males, and appear almost white in juveniles. The breast often has black streaking or spots, but it is not indicative of age (Probst et al. 2007). Adult males have distinct black lores or a black band across and below the eyes that looks like a mask. This mask is thin or vague in juvenile

Breeding male Kirtland's Warbler; Mio, MI; 19 June.

males and can appear missing in females. Adult females are much duller in color. Both males and females have white eyelids that form an incomplete eye ring, and there are white spots on the outer two tail feathers near the tips (Walkinshaw 1983). Wing bars present but not conspicuous.

Female Kirtland's Warbler; Adams County, WI; 1 July.

One of the larger wood warblers and is similar to the Connecticut Warbler in size. Deliberate in its movements compared to other *Setophaga* and has the distinct behavior of pumping its tail up and down. Similar species such as the Yellow-throated Warbler do not pump their tails. Sometimes confused with Prairie Warbler (*Setophaga discolor*), which also bobs its tail but is smaller, 8 g compared to 14 g, and is yellowish on face; also with Magnolia Warbler (S. magnolia), but this species has prominent white wingbars, white spots midway down the tail, a black band on tip of tail and does not pump its tail. The Yellow-rumped Warbler (*S. coronata*) is similar and often found in the jack pine habitat, but is black below with a white breast, and has a yellow rump.

Distribution

The Americas

eBird data provide detailed looks at the range of this species throughout the year: [eBird Year-round Range and Point Map for Kirtland's Warbler].

Figure 1a. Breeding and non-breeding (winter) ranges of the Kirtland's Warbler.

Breeding Range

Restricted range (see [eBird data]). Primary nesting grounds are early-successional jack pine forests on well-drained, sandy soils found within 13 contiguous counties in n. Lower Michigan ([Fig. 1a]and [Fig. 1b]). Increasing breeding population has expanded recently into 4 counties in the eastern Upper Peninsula of Michigan and 3 counties in Wisconsin (Probst 1985, Probst et al. 2003, Anich et al.

Figure 1b. Breeding range of the Kirtland's Warbler.

2011;http://www.uwgb.edu/birds/wbba/species/maps/KIWA.htm), as well as into s. Ontario (Richard 2008).

Singing males without mates or probable nesting activities have been historically recorded in regions of n. Wisconsin, Ontario, and Quebec (Harrington 1939, Tilghman 1979, Ryel 1981, Probst 1985, Chamberlain and McKeating 1978). There was a single nest record from Ontario in 1944 (Speirs 1984). Male migrants have been recorded in May and June across a broad range from Missouri and Minnesota in the west to Massachusetts and Virginia in the east, but migrants are presumed to be off the migration route and not breeding (Mayfield 1988b, Probst et al. 2003). The species forms lose breeding 'colonies' across breeding habitat, rather than continuously distributed across an area.

Winter Range

Restricted range (see eBird data). Winters throughout the Bahamian archipelago (Fig. 1) in early-successional broadleaf scrub or shrubby habitats (Sykes and Clench 1998, Wunderle et al. 2010). Most reports are from the island of Eleuthera, where considerable human habitation exists. Sightings also in the Turks and Caicos islands, which are politically but not geologically separate (Mayfield 1960, Clench 1978). Claimed sightings in n. Mexico, Cuba, and Dominican Republic have not been fully documented.

Historical Changes In Distribution

See above for expansion of breeding range in recent decades.

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

Historical records indicate wildfire habitat was most abundant when forest fires were rampant in n. Michigan shortly after the lumbering period of 1880s to 1890s, and it is estimated that Kirtland's warblers were probably at their highest densities during this time (Byelich et al. 1976, Kepler 1996). The drastic decline in Kirtland's Warbler numbers and concentration of their distribution was partly attributed to the substantial reduction in their suitable habitat after effective fire suppression and high precipitation in the 1950s and 1960s limited large fires in the jack pine barrens (Probst 1986, Kepler 1996). The jack pine forests of today are primarily maintained through timber harvesting and plantings. In the early 1980s, the majority of males were found in habitat naturally-regenerated from wildfire or prescribed burning due to lack of habitat from harvested, unburned jack pines by natural regeneration (Probst and Weinrich 1993). To attain 1,000 pairs on designated critical habitat, the amount and quality of habitat of unburned habitat was improved to augment habitat created by natural wildfires. To ensure a minimum amount of suitable habitat was available on the landscape through time, plantations with increased stem densities were used through a rotation schedule (Probst 1988).

By the mid-1990s, the amount of suitable habitat on the landscape had more than doubled from the 1980s, and the population responded by increasing numbers and widening their distribution across the landscape (Donner et al. 2008). By late 1990s and early 2000s, sightings increased outside their traditional breeding area including parts of n. Wisconsin, with breeding recorded in the e. Upper Peninsula of Michigan, and s.-central Wisconsin (Probst et al. 2003). Regular sightings of males in Ontario began in 2006.

Systematics

Geographic Variation

None described.

Subspecies

No subspecies have been described.

Related Species

The American wood-warblers (Parulidae) are a key component in a broad and, in geological terms, recent radiation of passerines with nine primaries that also includes the families Emberizidae, Cardinalidae, Thraupidae, and Icteridae (Klicka et al. 2007). Within the Parulidae, Lovette et al.'s (2010) comprehensive genetic study shook up generic relationships. A key finding was the genus *Dendroica*, in which *S. kirtlandii* was placed formerly, was paraphyletic with *Wilsonia citrina* (the Hooded Warbler) and *S. ruticilla* (the American Redstart). As a result, all species

of *Dendroica* warbler, as well as *W. citrina*, were merged into the genus *Setophaga* (Chesser et al. 2011), the oldest name and a genus that for many decades was thought to be monotypic. Thus, *Setophaga* went from being a monotypic genus to, with 34 species, the most speciose in the family, easily surpassing the Neotropical genus *Basileuterus* (26 species).

The nearest relative of *S. kirtlandii* is unclear. On the basis of gross morphology and plumage, the species was long treated as being near to *S. pinus*, the Pine Warbler, and *S. discolor*, the Prairie Warbler (e.g., Sibley and Monroe 1990), although Mengel (1964) posited that it is a relict species related to the *S. dominica* (Yellow-throated Warbler) complex, a hypothesis Mayr and Short (1970) doubted. A comprehensive molecular phylogeny places the species, with somewhat weak support, sister to a clade that includes*S. tigrina* (the Cape May Warbler), *S. cerulea* (the Cerulean Warbler), and *S. americana*/*S. pitiayumi* (the parulas) (Lovette et al. 2010).

Migration

Nature Of Migration In The Species

Complete migrant. Entire population migrates from nesting grounds in late summer and early fall to the Bahamas and Turks and Caicos islands (rarely elsewhere) and returns to the Michigan, Wisconsin and Ontario breeding grounds by May and early June (Petrucha et al. 2013). The reported range of migration dates in spring is 59 d, in fall 86 d (Petrucha et al. 2013). Males arrive on breeding grounds prior to females (Mayfield 1960). Males, especially young males, arrive later on the breeding grounds after dry winters in the Bahamas (Rockwell et al. 2012).

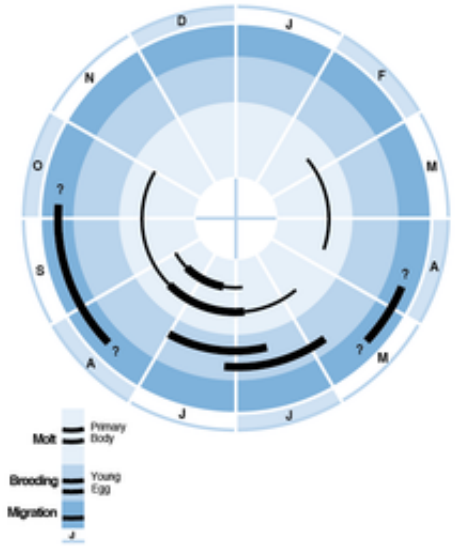

Figure 4. Annual cycle of breeding, molt, and migration of the Kirtland's Warbler.

Timing And Routes Of Migration

Spring Migration

See Fig. 4. Departure from the Bahamas is based primarily on the last observation of banded birds; most depart in late April, a few in very early May (Ewert et al. 2012, J. M. Wunderle et al., unpubl. data). Rarely migrates west of the Mississippi River; of 311 spring migration records accepted by Petrucha et al. (2013), there are more than 10 records in Florida (13), Illinois (12), Indiana (13), Michigan (50), Ohio (94), Ontario (74), and Wisconsin (10), and a smaller number of records from Arkansas and

Manitoba to Maine and Georgia (Clench 1973, Petrucha et al. 2013). Spring migrant males take as few as 13 d to migrate from Eleuthera to Michigan's northern lower peninsula (Ewert et al. 2012) and likely do not make the trip in one flight, as earlier thought (Mayfield 1988a).

Because males arriving on the breeding grounds are usually not detected until they sing, arrival dates could be slightly earlier than noted, 1–18 May, mean 12 May (Mayfield 1960, Petrucha et al. 2013); females arrive slightly later than males (Rockwell et al. 2012).

Fall Migration

Postbreeding birds are thought to remain in nesting habitat until migration but little is known about the post-breeding to pre-migration movement and distribution. A single hatch-year Kirtland's Warbler was captured in unsuitable habitat about 5 km from the nearest nesting area, possibly scouting for future breeding habitat (Bocetti 1993), and several cases of banded hatch-year birds moving from natal area to other suitable nesting areas suggests some movement does occur (C. Bocetti, C. Kepler, and P. Sykes, unpubl. data). Numbers on the breeding grounds decline through Aug, with most 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 may be more widely dispersed than spring migrants; of 114 fall records accepted by Petrucha et al. (2013) only two states/provinces had > 10 records: Florida (17) and Ohio (27). Fall migrants sometimes wander outside the main migratory path ranging from Manitoba and Louisiana to Quebec and Georgia (Clench 1973, Petrucha et al. 2013). Duration of fall migration is unknown but is being assessed with geolocators (P. Marra, pers. comm.). First arrival noted in the Bahamas on 20 Aug (Petrucha et al. 2013).

Migratory Behavior

From Petrucha et al. 2013, except where noted. Individual birds usually forage in low vegetation in shrub-scrub and stay in one area for 1-12 d; mean 1.23 d, pooled across years, seasons, and by sex. Invertebrates and fruit are eaten during migration by gleaning, fly-catching, and ground foraging. Males sing during spring migration and immediately prior to migration in the Bahamas (D. N. Ewert, J. M. Wunderle, Jr., pers. obs.); rarely appear to join mixed species flocks or associate with other birds in same area.

Migrating Kirtland's Warblers have been killed by colliding with lighted structures in Ohio (Mayfield 1960) and windows in North Carolina (M. Houston, pers. comm.) but little is known about sources and magnitude of mortality along the migration route. Mortality of adult birds is estimated to be higher during migration than during breeding and winter seasons (Rockwell et al. unpubl.).

Control and Physiology of Migration

No information.

Habitat

Breeding Range


Kirtland's Warbler WMA, MI; 12 April.


Kirtland's Warbler WMA, MI; 12 April.

Nests in dense, young (5-23 yr old) jack pine forests on nutrient-poor, sandy soils primarily in glacial outwash ecosystems of n. Lower Michigan (Mayfield 1960, Walkinshaw 1983, Kepler et al.1996), and limited areas in the Upper Peninsula of Michigan (Probst 1985, Probst et al. 2003). Nearly all breeding habitat is restricted to 23 established Kirtland's Warbler Management Areas (KWMAs) in n. Lower Michigan that cover approximately 90,000 ha (Radtke and Byelich 1963, Byelich et al. 1976). Here, the region is level or gently rolling, and the outwash sands are excessively well drained and generally lack weatherable minerals. Late-spring and fall freezes are common due to the area's inland location and relatively high elevation, contributing to the area's unfavorable growing conditions (Kashian et al. 2003).

Occupied jack pine forests tend to be nearly pure, even-aged stands interspersed with openings and scattered clumps of pin oak (*Quercus ellipsoidalis*), trembling and big tooth aspen (*Populus tremuloides* and *P. grandidentata*), black cherry (*Prunus serotina*), and choke cherry (*Prunus virginiana*) (Walkinshaw 1983, Probst 1988, Bocetti 1994). Ground cover in these forests is predominately moss/lichen, grass/sedge (*Carex pensylvanica*), and low shrubs such as blueberry (*Vaccinium angustifolium*), sand cherry (*Prunus pumila*), sweet fern (*Comptonia peregrine*), and bearberry (*Arctostaphylos uvaursai*) (Zou et al. 1992, Bocetti 1994, Houseman and Anderson 2002, Probst and Donnerwright 2003). In 2008, breeding activity was recorded in a red pine plantation with substantial natural jack pine recruitment in s.-central Wisconsin (Anich et al. 2011). Red pine plantations were used historically for nesting in n. Lower Michigan during periods of low population numbers (Radtke and Byelich 1963).

The suitability of habitat is a function of age and the associated habitat changes that occur with succession. Kirtland's Warblers enter jack pine habitat when the trees are near 1.7 m in height; numbers then rapidly increase with peak densities occurring

when jack pines are 8-15 yr old, and then numbers start to decline quickly as trees reach 5.0 m in height, which is when the lower live branches begin to die and break off (Probst 1986, Bocetti 1994). The lower branches provide nesting and fledgling cover, and forage space for the females. The last residents of a tract are usually unmated males (Mayfield 1960). Habitat is rarely occupied past 20 yr of age.

High quality nesting habitat has greater stem density (7,500 stems/ha) and between 35 – 65% canopy cover interspersed with small openings generally regenerated after wildfire events, but stands having at least 20-25% tree cover and at least 2000 stems per hectare, often associated with naturally regenerated jack pine following harvest, will be used (Probst 1988, Probst and Weinrich 1993, Bocetti 1994). Large wildfire events in jack pine are now rarer due to modern fire suppression and forest fragmentation, but when they occur, post-burn forests are consistently occupied by Kirtland's Warblers.

To create predictable areas of suitably-aged breeding habitat in the age of modern fire suppression, dense jack pine plantations (> 5,000 stems per hectare) with "opposing wave" strips to create small openings are used (Probst 1988, Kepler et al. 1996). The plantations are managed on a 50-year rotation for ecological and economic purposes (Byelich et al. 1976). The majority of the Kirtland's breeding population is found in these plantations currently, and male densities there are similar to densities found in wildfire-created habitat (Bocetti 1994). Warblers are beginning to use these areas as early as 3 yr after planting. However, pairing success and fledgling mortality are often dissimilar among the different habitat regeneration types (see Demography and Populations).

This area-sensitive warbler prefers larger habitat patches, typically > 80 ha, but warblers have used patches as small as 12 ha as long as the patches are surrounded by large complexes of suitably-aged jack pine habitat (Probst and Weinrich 1993, Donner et al. 2008). The average density of male warblers is greater in larger patches, and in wildfire-regenerated habitat and plantations compared to naturally regenerated habitat (Probst and Weinrich 1993, Bocetti 1994, Donner et al. 2009). Larger and more connected habitat patches are also colonized earlier and abandoned later, resulting in habitat being used for longer periods of time than smaller, isolated patches (Donner et al. 2010).

Bird life is generally sparse in jack pine plains. No other species of warbler is dependent on this habitat. The Prairie Warbler and Palm Warbler (*S. palmarum*) are regularly documented in earlier stages of succession in KWMAs, and the Nashville Warbler (*Oreothlypis ruficapilla*), which nests on the ground like Kirtland's Warblers, prefers the later stages of succession. The large, open areas created immediately after a fire or during the early stages of plantations prior to Kirtland's Warbler occupancy are used by other open land species of interest such as Upland Sandpipers (*Bartramia longicauda*), Sharptail Grouse (*Tympanuchus phasianellus*), American Kestrels (*Falco sparverius*), Eastern Bluebirds (*Sialia sialis*), and Grasshopper Sparrows (*Ammodramus savannarum*). The later seral stages of jack pine forests are important to species such as the Short-eared (*Asio flammeus*) and Barred owls (*Strix varia*), and Red-tailed Hawk (*Buteo jamaicensis*).

Spring And Fall Migration

From Petrucha et al. 2013, and others as noted. Relatively few observations have been made of Kirtland's Warblers during migration; most are from spring and are concentrated around Lake Erie's western shoreline (VanTyne 1951, Clench 1972). Most (83%) individuals were seen in low scrub/shrub habitat dominated by woody plants < 6 m in height, and they were observed foraging for insects from 0-6 m above ground. Most of the records (94%) indicate Kirtland's Warblers migrate alone relative to conspecifics, but some of the records indicate that individuals were found in the company of several other parulids (Clench 1972).

Winter Range

Wintering Kirtland's Warblers use upland, early-successional habitat with a low broad-leaved scrub component found in the Bahamian archipelago (Mayfield 1972, Radabaugh 1974, Sykes and Clench 1998, Wunderle et al. 2010). Radabaugh (1974) spent 800 h searching on 11 islands in 2 winters, using playback of recorded song to attract warblers, and found 1 male on Crooked Island. The site was 900 m inland from the sea in sparse broad-leaved 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. This male spent 70% of its time on the ground gleaning small insects. Clench (1978) reported similar habitat use on the Caicos Is.

Sykes and Clench (1998) described six broad habitats used on Eleuthera, Grand Turk, North Caicos, and Crooked I.: natural shrub/scrub, secondary shrub/scrub, low coppice, pineland understory, saline/upland ecotone, and suburban; tall broadleaf woodland (coppice) was not used. Comparing habitat among occupied (seven 3-28 yr old sites), random, and late-successional tall coppice sites on Eleuthera, Wunderle et al. (2010) found the average density of foliage was greatest at 0.5-1.0 m, and this density was consistent among capture plots despite significant variability in all other foliage-height classes below 3 m. Wunderle et al. (2010) also found that warblers were absent from mature forests. Wild sage (*Lantana involucrata*), snowberry (*Chiococca alba*) and black torch (*Erithalis fruticosa*) shrubs are important components of their wintering habitat. Greatest densities of birds in Eleuthra were found on goat farms where these shrubs were maintained by grazing. Using goats under power rights-of-ways is being explored as a way to create and maintain wintering habitat.

Food Habits

Feeding

Main Foods Taken

Observations of foraging birds in Michigan May – Sep recorded individuals taking insects such as moth larvae, flies, small beetles, sawflies, grasshoppers, cicadas, and also feeding on ripe blueberries (*Vaccinium* sp.) (Mayfield 1960, Walkinshaw 1983, Fussman 1997, Deloria-Sheffield et al. 2001). On wintering grounds, individuals consume fruit most often, followed by arthropods; a small portion of observations have included probing flowers (Wunderle et al. 2010).

Food Capture And Consumption/Microhabitat For Foraging

On breeding grounds, forage for insects through ground cover and mid-levels of small pines and adjacent oaks. Gather food mainly by gleaning among pine needles, leaves and buds of deciduous shrubs, and ground vegetation. Sometimes hover to snatch flying insects and to gather insect food in terminal clusters of pine branches. Appear to get food in summer with small effort, except perhaps during cold weather early in the season (C. Bocetti, pers. obs.) Females search for food within an area 91-122 m of nest (Walkinshaw 1972). When leaving the nest to forage, female flies to a nearby low branch, then hops among branches or dead logs on the ground, but remains in the denser middle branches.

On wintering grounds, males spend most of the time actively hunting food on the ground (Radabaugh 1974), or foraging from the ground up to 3 m (Sykes and Clench 1998, Wunderle et al. 2010). Fruit often seems abundant, but late winter drought may reduce local food availability at times (Radabaugh 1974, Sykes and Clench 1998, Wunderle et al. 2010; see Demography and Populations: mortality and disease).

Diet

Major Food Items

In n. Michigan, summer diet found to be primarily arthropods and blueberries from 202 fecal samples collected Jul to Sep (Deloria-Scheffield et al. 2001). Major food items are spittlebugs and aphids (61% of samples), ants and wasps (45%), blueberry (42%), beetles (25%), and moth larvae (22%).

In winter also feed on insects and small fruits (Radabaugh 1974, Sykes 1989). Fruit mostly consumed from wild sage (*Lantana involucrate*), black torch (*Erithalis fruiticosa*), and snowberry (*Symphoricarpos*), but fruit from another 7 species are known to be consumed as well (Wunderle et al. 2010).

Nutrition And Energetics

No information.

Metabolism And Temperature Regulation

No information.

Drinking, Pellet-Casing, And Defecation

Water apparently sipped from dew on leaves. Standing water is rarely available on porous soils of summer and winter habitats, and seems to be ignored. Drink white pitch-like fluid that secretes from branches of jack pine (Leopold 1924).

Food Selection And Storage

No information.

Sounds

Vocalizations

Figure 2. Adult male Kirtland's Warbler in typical breeding habitat.

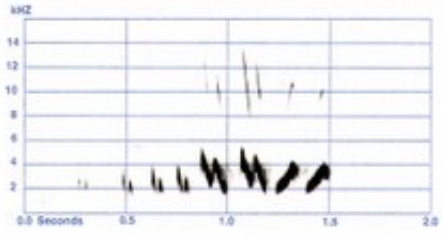

Figure 3. Primary song of Kirtland's Warbler.

Male on nesting territory sings loudly and persistently (Fig. 2). Songs (Fig. 3) uttered 6–9 times per minute, each song lasting 1.0–1.5 s. Singing courses often last 10 min or more followed by a few minutes of silence. Singing may persist if stimulated by disturbance or singing of nearby males.

Song clear, distinct, and loud compared to other birds in jack pine habitat. Song is typically 6-9 notes sung rapidly. It can be described as three couplets of notes, but variation is common with individuals adding or deleting syllables from the couplets. Tempo and quality suggested by English syllables *weche chee-chee-chee-cheer-r-r-r.*Mayfield (1960) described song as "*ch-ch-chatanooga-choo-choo*". Introductory notes low in pitch and may be hard to hear, slurred, or missing. Middle notes alternate from low to high pitch followed by loud, longer end notes. Song increases in volume and tempo and hits the highest pitch in the middle of the song. Wide variation in song observed that can be used to identify individuals in the field (C. Bocetti, D. Donner, pers. observation). 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*), yellow-throated warbler (*Setophaga dominica*) or final notes of Vesper Sparrow (*Pooecetes gramineus*) heard at a distance.

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). Singing becomes sporadic in early Jul, but a few males still sing in early Aug. These late singers are often feeding fledglings. Spring migrants reported singing (Petrucha et al. 2013). Males also sing occasionally on wintering grounds just prior to spring departure (C. Bocetti, D. Ewert, J. Wunderle, pers. observation).

Daily Pattern

Singing is most frequent early in the morning, dwindling in late forenoon, and becoming casual in the afternoon, especially on hot days. Often resumes early in the evening, but less actively. Song ceases in cold or blustery weather. Unmated males sing more often than mated males (Hayes and Probst 1986) 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 a mate in her 13th day of incubation sang 2,212 times in a day (Mayfield 1960).

Places Of Vocalizing

Male often sings while perched atop tall snags, in interspersed oaks or jack pine trees. Males use oaks more than expected, likely because oaks are taller in the early and mid-years of stand occupancy (C. Kepler, P. Sykes, C. Bocetti, unpubl. data). A male will fly to another tall snag or tree perch at the edge of its territory in response to another male singing nearby. Throughout the day, males often sing within their territory from a favorite tall perch, or from the middle branches of trees, often near the tips of branches. Males sing in lower branches when a tree is near grassy openings in a young jack pine forest. First vocalizations of the day are often directly above the nest; observers use this to locate nests.

Repertoire And Delivery Of Songs

When singing, the bill is pointed straight up, tail is down, and throat is expanding and contracting with the song. Primary songs (Fig. 3) differ slightly among individuals, allowing recognition with practice, like a friend’s voice identified quickly on the telephone. Variation is often the omission of notes, most notably the lower pitched introductory notes, but variation can also be added notes, often in the middle or end of the song. Individual males may vary the pitch or deliver a song more rapidly. Song may be slurred from males singing with food in their mouth. The differences are not always sufficient to allow reliable identification on sonograms (D. Ewert unpub.), but experienced observers can use variation to distinguish males in the field (C. Bocetti, D. Donner, pers. obs.). Some idiosyncrasies or ‘local dialects’ heard in distinct areas have been recognizable from year to year (C. Bocetti, D. Donner, pers. obs.). 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, when a male is investigating song playback, or when a potential mate is near.

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 a distinct loud “*chunk*” or “*chip*” note, lower in pitch than 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-chi*.

Nonvocal Sounds

Not known.

Behavior

Locomotion

Moves on ground by hopping, but capable of moving feet alternately as in “Rodent Run” of distraction display (Mayfield 1960, Walkinshaw 1983). Moves quickly from twig to twig in thickets.

Swift, agile flyer, darting through dense foliage. Females tend to fly lower than males. Measurements by D. Evered (pers. comm.) suggests short, rounded wings of females accommodate maneuverability required for such low flight.

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 (Mayfield 1960). 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). Males preen from perches between songs. Mostly use bill to preen body contour and flight feathers, but also use feet to preen head and nape contour feathers.

Female incubating eggs or brooding young at night (examined by flashlight) sleeps with head turned back into scapular feathers. In daytime on 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 the 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

Territories are primarily defended against conspecifics by male but occasionally female as well. Other species are well tolerated in territories. 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 half-open bill, spread and lowered wings, and pursued displaced bird with short chase. These episodes were infrequent but may have been 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 emitting agitated song, often partial song or full song at accelerated rate or as a “whisper” song. Territorial male is more apt to sing full songs whereas interloper often sings partial songs. 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 the nest, brooding female may dart at it on ground or in flight with noisy wing motion and snapping bill (Mayfield 1960). Male and female often join forces in response to threats near the nest. Small intruders, including cowbirds, are usually repulsed (Walkinshaw 1983, C. Bocetti pers. obs.).

Spacing

Territoriality And Colonies

Territory defended by the male is larger than that reported for most warblers and may be affected by density of the tree stand. Territories are larger in sparse vegetation. Estimates of territory size based on apportionment of available habitat are larger than those based on actual movements of males. Early estimates of territory size were from 0.6 ha to > 10 ha, mean 8.4 ha (Walkinshaw 1983) and 3.4 ha (Mayfield 1960). Estimate from 1987-1992 shows mean 6.7 ha based on actual movements (C.

Kepler, P. Sykes, and C. Bocetti, unpubl. data), and annual mean estimates from 2001-2012 from 5.7 ha to 60.9 ha; grand mean for all years 13.6 ha based on apportionment of occupied habitat in both n. Lower Peninsula and Upper Peninsula of Michigan (P. Huber et al. 2013). Nest preferentially placed about halfway between territory edge and center (Bocetti 1994).

Territories tend to be grouped in “colonies,” each male within hearing of at least one neighbor. Isolated pairs rarely found. Territories do not overlap and often have space between them (Mayfield 1960, Walkinshaw 1983, Bocetti 1994, Rockwell 2013). Road-building has divided most of this region into mile squares, and a mile (259 ha) may hold as many as 100 males in densely occupied core areas (J. Weinrich, pers. comm.).

Some colonies are small (< 6 males) but the greater part of the population is gathered into large colonies (Burgoyne and Ryel 1978, Donner et al. 2008). Large colonies appear advantageous, having both higher density of warbler use (Probst and Weinrich 1993, Donner et al. 2009) and longer duration of use (Donner et al. 2010). Presence of singing males may attract and stimulate other males and females. In new habitat of young pines, warbler occupation is gradual, reaching its peak in about 5 yr, stabilizing for 2-3 yr, and then declining rapidly for 2-3 yr (Donner et al. 2009, Donner et al. 2010). Type of habitat influences timing of colonization and duration of use, with wildfire sites (which are usually larger in size than plantations) occupied earlier and abandoned later for a longer duration of use (Donner et al. 2010).

Sexual Behavior

Mating System

Usually monogamous during the nesting season. Polygyny does occur (see Demography and Populations: sex ratio) and is almost always poly-territorial (Bocetti 1994, Rockwell 2013).

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 the vicinity of the nest before the first egg was laid. The act lasted only 1–2 s while the pair communicated by soft twittering. If both birds return in the following year, about half find the same mate.

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

Sex Ratio

See Demography and Populations.

Social And Interspecific Behavior

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

Predation

No predation on adults witnessed. Identity of predators remains 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 the nest, the female often gives an elaborate distraction display, scuttling away several meters 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. Males also observed plummeting into thicket from perch, sometimes mid-song, in response to overhead shadow, suggesting avian predation is significant (CB).

Some individuals on breeding grounds are remarkably tame, allowing humans to approach closely without alarm. Adults near the nest have been photographed on hand and foot of visitor. Females on the nest are captured easily by net, and after capture return quickly and silently. Other individuals are more wary and some females are difficult to find and trace to nests. Both members of the pair are most wary on the day their young fledge, showing agitation when an observer approaches (CB). In general, this species appears to tolerate more disturbance at the nest than most warblers without deserting.

Breeding

Phenology

Pair Formation

Females arrive on breeding grounds a few days after males. Pair formation begins within 1 wk.

Nest Building

First nests may be started as early as 11 May or as late as 18 Jun (Bocetti 1994). Date determined by arrival time on the nesting ground, and by weather. Arrival time is linked to winter habitat conditions (Rockwell et al. 2013). All nesting activities suspended by cold, wet weather (Mayfield 1960).

First Brood

Fig. 4. First eggs appear in the third week of May (earliest 20 May, Bocetti 1994), but most clutches are not started until the first week in June (Mayfield 1960). First eggs usually hatch between 9 Jun and 26 Jun (Mayfield 1960, Bocetti 1994).

Second Brood

If nest is destroyed or deserted, building of replacement may begin in 1–2 d. If first brood is fledged by late June, a second nesting may be attempted (Berger and Radabaugh 1968, Mayfield 1960). Latest second nest initiation 2 Jul (Bocetti 1994).

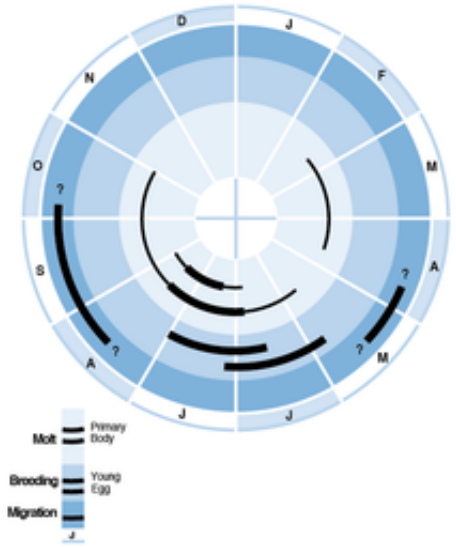

Figure 4. Annual cycle of breeding, molt, and migration of the Kirtland's Warbler.

Figure 5. Adult male Kirtland's Warbler, at the nest. By J. Zickefoose.

Nest Site

Site Selection

Female roams deliberately over the territory, penetrating the deepest ground cover, fitting her body into natural cavities in the vegetation. Male moves nearby, singing. Searching is most active in early morning. Searching may continue for 4 d or more at first nesting, but only 1–2 d for replacement nests.

Adult female Kirtland's Warbler, at its nest; Michigan, June

Site Characteristics

A ground nester. Nest is embedded in the ground concealed by grass and other low vegetation (seeFig. 5). Surrounding vegetation may include bluestem grass (*Andropogon* spp.), sedges (*Danthonia*: *Carex*), blueberry, northern dwarf cherry (*Prunus pumila*), bearberry (*Arctostaphylos uvaursi*), and sweet fern (*Comptonia peregrina*), generally 10–30 cm high (Buech 1980), but Bocetti (1994) showed preference for woody species such as blueberry, bearberry, and sweet fern and avoidance of sedge as nest cover. Ground also littered with pine needles and oak leaves.

Nest placed within a meter on either side of edge between jack pine thicket and opening, usually beside microstructure of ground such as down log, grass clump, or edge of plantation furrow.


Kirtland's Warbler nest, Michigan.

Kirtland's Warbler clutch, Michigan

Nest

Construction Process

Female shapes loose sandy soil into a shallow cup by rotating her breast against it. Female carries nesting material in her bill, dropping it into the cavity and pressing it into place with her breast, rotating her body through several turns, tail held high. She spreads wings slightly and flattens her tail over the edge. Male usually sings nearby. She brings coarser material at first: wisps of grass and sedge, long pine needles, pieces of oak leaf, slivers of crumbling wood. In one case 143 trips the first day, 59 trips the second, 7 trips third day, and 6 trips fourth (final) day. At the end of the second day, the nest looked complete. Final touches mainly involved lining with fine material: rootlets, deer hair, moss sporophytes, and grassy fibers.

Building most active between 07:00 and 12:00. Ceases in cold, wet weather. Building of first nest may require 6–8 d, and replacement nest 4 d.

Structure And Composition Matter

Analysis of finished nest shows 50% coarse sedge (*Carex pensylvanica*), up to 30% red pine needles (*Pinus resinosa*), and occasional twigs of blueberry or other woody plants (Southern 1961).

Dimensions

Outside diameter about 100 mm, inside diameter 58 mm, and depth 38 mm (Walkinshaw 1983).

Maintenance Or Reuse Of Nests

Former nest sites not reused.

Eggs

Egg Size

Mean 18.3 mm (15.5–19.9) x 14.2 mm (10.8–16.0; *n* = 253; Walkinshaw 1983). Mean mass 1.79 g (1.47–2.21; *n* = 50) weighed within two days of laying and all subsequently hatched (Mayfield 1960). Largest eggs in genus *Dendroica*, about 13% of female's body mass.

Shape And Color

Ovoid. Pale buff, whitish, or faintly pinkish with varying amounts of fine brown spots gathered in cap or wreath at larger end.

Egg Laying

First egg laid on day following completion of nest. All eggs laid soon after sunrise on successive days. Female sits on nest 0.5–1.0 h at each laying. Egg-laying period 5–6 d at first nest, 4 d at subsequent nests. Observations from concealment of blind have never revealed female at nest between completion of nest and start of incubation except to lay eggs.

Incubation

Role Of Sexes

Incubation by female only; 1 incubation patch. Incubation begins on day before laying of the last egg. Male rarely and briefly sits on eggs.

Some males feed the female regularly during incubation, but this is not always the case (Walkinshaw 1983; C. Bocetti, pers. obs). After observing 6 nests, males fed incubating females 24 times during approximately 46 h of observation (Mayfield 1960).

Incubation Period

Mean 14.2 d (13–15, *n* = 21) from laying of last egg to hatching of last egg (Walkinshaw 1983).

Incubation Routine

Females spend about 84% of daylight hours and all nighttime hours on nest. Mean attentive period in daytime 39 min (20–61). Mean period off the nest 9 min (5–13; Mayfield 1960). During attentive periods male brings food to female; occasionally visits unattended eggs with food. While female incubates, male roams territory, singing frequently.

Hatching

Emergence

At any time of day and perhaps at night. Nestlings emerge from egg 0.25–1.0 h after egg is pipped. Entire clutch usually hatches within 24 h.

Removal Of Eggshells

Both adults remove eggshell fragments, treating them like foreign objects such as twigs and pine needles. Fly ≥10 m to dispose of them (Mayfield 1960).

Young Birds

Description Of Nestlings

At hatching, mass about 1.30 g. Down brown, about 8 mm long on head but shorter on scapular, mid-dorsal, and femoral regions. (Distinguishable from cowbirds in nest, which have white down.) Weak, able to wriggle slightly, raise heads, and open mouths.

Day One. 2.6 g. Able to right themselves, using heels, wings, head. Mouth yellowish, becoming pink in throat. Wing 7.8 mm, tarsus 7.0 mm, culmen 4.0 mm. No egg tooth visible. Tip of mandible dark.

Day Three. 5.1 g. Yellow gape conspicuous. Feather tracts well defined. Juvenal ensheathed primary remiges visible. Wing 11 mm, tarsus 10 mm, culmen 5 mm.

Day Five. 9.4 g. Wriggle and stretch. Some preening motions. Jostle one another in nest. Eyes open. Make no attempt to retreat when handled. Basal one third of mouth edge conspicuously yellow. Remiges much grown but not yet burst at tip, “covered with pin feathers.” Tail not visible.

Day Seven. Juvenal plumage emerging. Responsive to approach of adult. Young pant when sun strikes them. Red of mouth cavity faded toward orange. Wing 34.2 mm. First primary 18.6 mm, tarsus 19.0 mm, culmen 8 mm, tail 2.0 mm.

Day Eight. 12.7 g (about 80% adult mass). Juvenal plumage well developed. May

leave nest if disturbed, but if not frightened will remain 1–2 d longer. Active. Some climb over others. At approach of adult with food, young strain wildly, calling *ti-ti-ti-ti-ti*. Raise yellow-edged mouth to adults, vibrating it energetically. Preen actively. Stretch and lean out of nest, pecking at tiny objects, perhaps ants, on edge or just outside nest (Mayfield 1960).

Day Nine to Ten. Mean weight of 9-10 day old nestlings (*n* = 19) in 1990 was 13.1 g (Bocetti 1994).

Parental Care

Brooding

Female spends about 80% of daytime hours and all of nighttime hours brooding small nestlings, but these attentive periods diminish as the nestlings grow. Male brings food to the brooding female. She eats some and passes some to the young. Male rarely broods young in the nest.

Feeding

Both parents share feeding duties to nestlings. Older nestlings observed being fed every 17 – 38 min (3 nests; Van Tyne 1953). Fledglings fed by both parents until 26-41 d old (Walkinshaw 1983).

More recent observations suggest adults bring food 2–16 times/h. Mayfield (original BNA) reported that the male brings food 3–5 times as often as the female, but C. Bocetti (unpubl. data) found males and females bring food at the same rate (3.2 times/h for the entire nestling period). Number of trips/h increases as nestlings grow (C. Bocetti, unpubl. data). If female is present, male usually offers food to her and she transmits it to the nestlings. Sometimes he reaches over the female and feeds nestlings directly. Food consists of flying insects, larvae, and ripe berries, similar to the food adults consume. Food items are larger later in the nestling period. Young present an open mouth as a colorful target, vibrating head and mouth. Adults seem to apportion food, sometimes reaching over begging nestlings to feed others.

Nest Sanitation

Immediately after being fed, the young bird turns away, lifts its posterior toward the adult, and voids a fecal sac. Adult removes the sac promptly, eating it during the first three days, and then transporting it intact. On the fourth day adults begin carrying away some of the sacs, by the sixth day all of them, flying out of sight ≥ 10 m (Mayfield 1960).

Brood Parasitism

Recent Problem

Brown-headed Cowbirds (*Molothrus ater*) first reached the Kirtland's Warbler nesting range about 1880 and have steadily increased throughout the formerly forested parts of the continent (Mayfield 1965a). Impact of cowbirds has been greater on Kirtland's Warbler than on other hosts in the same region (Walkinshaw 1972). Kirtland's Warbler is a receptive host, presenting little defense. The cowbird threat was first suspected in the 1920s (Leopold 1924), but not proven until the 1950s. Adequate samples showed that production of fledglings was reduced 40% when 55% of nests were parasitized. Activity of the cowbird has the effect of predation, but unlike the usual forms of predation it is not density-dependent. Pressure does not relent when prey (host) becomes rare (Mayfield 1961); damage accelerates when parasitism rate increases. Greater cowbird pressure results in more nests with ≥ 2 cowbird eggs each, which produce no warblers. In one sample of 29 nests, 70% were parasitized and only two fledgling warblers produced (Walkinshaw 1972). At those pressures, the Brown-headed Cowbird threatened extinction of the Kirtland's Warbler by 1980 (Mayfield 1975a).

Cowbird Behavior

Cowbirds arrive on the Kirtland's nesting grounds in April, before the warblers arrive. Female cowbirds watch female warblers building their nests, thus (apparently) synchronizing their own egg laying. Damage occurs in 3 ways: (1) cowbird removes approximately 1 warbler egg for each of its own laid in the nest; (2) the larger cowbird egg may sap heat from the incubating female and surrounding eggs, reducing the hatching success of warbler eggs; (3) the cowbird nestling hatches 2 d earlier than the warblers and, being larger, monopolizes food and space in the nest. Incubation period of cowbirds 12 d; warblers 14 d (Van Tyne 1953).

The female cowbird usually enters the warbler nest before dawn during the egg-laying period, when the nest is unattended, and sometimes after the clutch is completed. The cowbird slips in silently, lays its egg, and leaves within 15 s. In the same or previous day, the cowbird may visit the nest again, grasping the warbler egg by puncturing it with open mandibles and flying away with it. The cowbird takes only the host egg if both warbler and cowbird eggs are available, and does not take the only egg in a nest; apparently select the smaller eggs in a mixed set (Mayfield 1960).

Host nests most frequently have 1 cowbird egg, but often have 2, 3, in declining numbers. The distribution is random according to the number of cowbirds present and the availability of host nests, the numbers conforming to a Poisson series (Mayfield 1965b).

When a warbler hatches, weighing about 1.3 g, the 2-d-old cowbird in the nest may weigh 6–12 g. Two or more cowbird nestlings crowd the nest. Fledgling cowbirds usually leave the nest at about 9 d, about 2 d before the warblers. At departure, cowbirds may weigh up to 30 g, more than twice the weight of adult warblers.

In the nest and after leaving, cowbirds beg noisily for food with a quavering note different from rapid chips of young warblers. Adult warblers continue to feed fledgling cowbirds like their own young. Fledgling cowbirds move more widely than young

warblers, seeking open spaces and exposed perches, whereas young warblers seek the concealment of thickets. Cowbirds still beg and warbler hosts still feed them at 30 d, although cowbirds now fly beyond the territory limits where warblers do not ordinarily follow.

The probability that a cowbird egg laid in synchrony with warbler eggs will produce a fledgling is 0.41, which is slightly higher than the probability that a warbler egg will produce a fledgling without cowbird influence, which is 0.32 (Mayfield 1960). So Kirtland's Warbler is a good host for cowbirds.

See Conservation and Management for cowbird control and its impacts on Kirtland Warbler breeding success.

Fledgling Stage

Departure From Nest

Young leave the nest at a mean age of 9.4 d, but may do so at 8 d if disturbed. Usually leave in the morning. Most young leave within an hour, but sometimes 1 or 2 remain until the following day. Fledglings immediately flutter to concealment in ground cover. Within 12 h may be 20–40 m from the nest. Both adults chip with excitement when feeding fledglings. The brood may stay loosely together, or the brood is divided evenly between male and female and fed in disjunct areas within the territory (C. Bocetti). Adults do not brood young away from the nest.

Behavior Of Fledglings

Fledglings are difficult to find for several days out of the nest. They sit for long periods quietly under ground cover or on low twig in pine thickets, well camouflaged (gray-brown color and heavy markings on breast, much like other *Setophaga* but unlike plain-breasted*Oreothlypis* in this habitat). Fledglings usually allow human approach within an arm's length before flying. At first they can sustain flight for only 2–3 m before tumbling to the ground, but within a week they can maintain altitude for 10–20 m before tiring. In this tail-less stage their flights are direct. When sitting, their eyes are often closed, but at the approach of an adult bird, they give a low chip and sometimes move to meet the adult. Their flights are short, but by the second day they may have moved 100–200 m from the nest. As they grow, they continue to receive food (up to 44 d of age), but by 23 d they appear to be gathering most of their own food (Mayfield 1960).

Tail Length

A convenient field mark for aging fledglings is length of the tail. At nest-leaving (age 9–11 d), young appear tailless. At age 12–13 d, the tail is about 1 cm long; at age 15 d, about 2 cm; at age 16 d, 2.4 cm; by age 23 d, 5.0 cm. White spots in outer rectrices are more prominent than in adults.

Division Of Brood

Adult male and female each take a portion of the brood and feed only their own portion of the family. These units move about separately but remain in loose association, held together by the food-carrying of the adults. If the brood is produced early enough in the season to permit a second nesting, the female will sometimes start her next nest while still feeding young (Mayfield 1960).

Demography and Populations

Measures Of Breeding Activity

Age At First Breeding

Both sexes breed when 1 yr old. Second-year males may be disproportionately unmated (CB), but the exact population-wide estimate of this proportion is unknown. Yearling females lay eggs later in season than older females (Walkinshaw 1983).

Sex Ratio

Ratio of males to females appears to be about even for the entire population (Sykes et al. 1989, Bocetti 1994). Early long-term intensive study of established colonies revealed few unmated males or other imbalance between the sexes (Mayfield 1960, Walkinshaw 1983), but later studies showed sex ratios differ among habitats. Some sites in some years have brought reports of up to 15% unmated males (Probst 1986) and similar numbers of males with two females (see Behavior: sexual behavior). In the early 1990s, 8% of males were unmated and 22% had 2 females (sex ratio 1:1.14) in wildfire stands, but 28% of males were unmated and only 6% had 2 females (sex ratio 1:0.78) in managed plantations (Bocetti 1994). In 2008, Rockwell (2013) reported 8% of males were unmated and 5% of males had 2 females in optimal-aged plantations.

Clutch Size

3–6, mean 4.63, *n* = 67. First nest of the season usually 5 eggs, occasionally 6; replacement nests usually 4 (Mayfield 1960, Walkinshaw 1983). Bocetti (1994) found mean 4.59, *n* = 46 in all habitats combined (because no difference between habitats), and Rockwell (2013) found mean 4.58, *n* = 279 in plantation-regenerated habitat. Rockwell (2013) also found a nest with 7 eggs in one clutch, and a nest with 9 eggs that were laid in 2 clutches (5 and 4) in the same nest (no eggs hatched). Precise statistical calculations were unwarranted because of uncertainty injected into the data by cowbird interference. An observer can never be sure how many eggs have been removed by cowbirds.

Reproductive Success

Productivity varies from year to year, but estimates over early decades (cowbirds present in area) show production of young per pair without interference by cowbirds was about 2.2 fledglings, vs. 0.8 in parasitized nests. These figures incorporate the fact that some females make > 1 nesting attempt in a season, especially to replace destroyed or abandoned nests. (Mayfield 1960, Walkinshaw 1983). This is roughly the same production rate as that of the Prairie Warbler, 2.2 fledglings per territory per year (Nolan 1978).

After cowbird control was institutionalized in 1972, several studies estimated productivity: Shake and Mattson (1975) reported 2.84 young fledged per nest in 1972, on average; Kelly and DeCapita (1982) reported 2.76 young fledged per nest per year from 1972-1981; Bocetti (1994) found 3.59 young fledged per nest attempt in 1990-1992; Rockwell (2013) reported 2.72 fledglings per nest attempt from 2007-2009.

Survival and mortality rates have been calculated in terms of probabilities, which take into consideration the numbers of eggs and young and the time each is exposed to the hazards of existence (Mayfield 1975b, Johnson 1979). Probabilities of survival at successive stages of nesting may be combined as follows: survival of eggs during incubation 0.54, hatching of eggs present at hatching time 0.78, survival of nestlings until fledging 0.76, combined survival of eggs until fledging 0.32.

These calculations are based on data from nests without cowbird interference. Cowbird pressure depresses survival rates at every stage of nesting. Probability a warbler egg will produce a fledgling in a parasitized nest is 0.07. This calculation lumps experience with various levels of cowbird pressure. Actual production is zero in nests that receive 2 or more cowbird eggs (see Breeding: brood parasitism).

Mortality And Disease

Life Span and Survivorship

Survival rate of adults from one June to the next is about 65% (Mayfield 1960, Walkinshaw 1983; C. Bocetti, C. Kepler, and P. Sykes, unpubl. data.). Identical rate reported for Prairie Warblers (Nolan 1978) and similar rates calculated for 6 other species of warblers (Roberts 1971). Number of young needed to compensate for adult losses leads to calculation that about 35% of birds must survive their first year to maintain the population (Ryel 1981a); current estimates for hatch-year survival is 0.45 (C. Bocetti, C. Kepler and P. Sykes, unpubl. data). Survival estimates are available by sex: adult male 0.65, adult female 0.62, hatch-year male 0.46, hatch-year female 0.37 (C. Bocetti, C. Kepler and P. Sykes, unpubl. data). Rockwell et al. (unpublished) estimate annual survivorship of adult males at 0.58, and survivorship for separate periods of the year: oversummer 0.86, migration 0.74, and overwinter 0.90.

Calculated life expectancy of adults from June forward is thus about 2 yr (Mayfield 1960,Walkinshaw 1983). Greatest age on record is 11 yr for male (C. Bocetti, M. Petrucha and P. Thompson, unpubl. data) and 8 yr for female (Mayfield

1960, Walkinshaw 1983).

Winter Mortality

Exact causes unknown. Conditions on the wintering grounds, where each bird spends two-thirds of the year, are important to survival. Through the 1970s, when population and breeding habitat changed little, fluctuations in numbers of males on the breeding ground correlated with local rainfall (r = 0.86, within .05 confidence limits; (Ryel 1981a). Rockwell et al. (unpublished) have shown that levels of March rainfall in the Bahamas positively influences survivorship of male adults in later seasons, presumably because higher rainfall brings a more plentiful food supply, as described by Wunderle et al. (2010). In confirmation, high losses in many species of birds followed a drought in the winter of 1970–71 (Radabaugh 1974). Hurricanes may be hazard in winter and in migration, but they may also create habitat on the wintering ground (Wunderle et al. 2007).

Losses Of Nests And Eggs

In the presence of cowbirds, about one-third of all nests are deserted during the incubation period (Mayfield 1960). In the absence of cowbirds, desertion drops to about 10% (Walkinshaw 1983).

About 15% of eggs and similar numbers of nestlings are destroyed by predators (Walkinshaw 1983). Predators have been tentatively identified by circumstances; only 3 cases have been witnessed: 2 by Blue Jays (*Cyanocitta cristata*) and 1 by a garter snake (*Thamnophis* spp.; Walkinshaw 1983). Suspected nest predators include American Crow (*Corvus brachyrhynchos*), thirteen-lined ground squirrel (*Citellus tridecemlineatus*), and red squirrel (*Tamiasciurus hudsonicus*). Cowbirds also remove eggs and kill nestlings (see Breeding: brood parasitism).

Diseases And Body Parasites

Little information. Evidence of lesions (suggestive of avian pox) observed on feet and bills of a few adult birds during late-summer banding (Bocetti, Kepler, and Sykes, Jr. pers. obs.), but birds were released in otherwise good condition. No histological assessment done. Hippoboscid flies were also observed on a few birds during the same period.

Range

Natal Philopatry

Few data; needs study. First-year birds tend to disperse widely over the breeding range of the species.

Fidelity To Breeding Site And Winter Home Range

Males nearly always return to the “colony” in which they have nested, unless that habitat is destroyed. Unmated strays outside the normal nesting range are less likely to return to territories occupied the previous year, but some do show site tenacity. Females usually return to the same colony but are more likely to shift territories than males. This means that colonizing areas tend to recruit more yearlings than established areas. Populations in well-established areas decline with aging habitat when recruitment by yearlings diminishes (Ryel 1979a; Probst 1988, Bocetti 1994).

When both adults of a pair return, the probability they will mate again is about 50%, but samples are small. Similar to the Prairie Warbler (Nolan 1978), remating may be prevented if the female returns at a late date and finds her male already paired.

Winter records also suggest site fidelity. Wunderle et al. (unpublished) estimated the return rate of all age classes of male Kirtland’s Warblers to locations used the previous year on s. Eleuthera, averaged across sites and years as 50.0% and for females 28.3%, probably an underestimate as Kirtland’s Warblers occur at different sites during the winter and are difficult to detect.

Population Status

Numbers

During the official 2012 census, 2,090 singing males were observed -- an increase from the 1,828 males observed in 2011. Of these, 23 singing males were observed in Wisconsin and 2 in Ontario. Based on the assumption that all males are paired, the breeding population size in 2012 was 4,180 individuals.

Under the direction of the Kirtland’s Warbler Recovery Team, males in the population are monitored annually through a joint effort by the U.S. Forest Service, Michigan Department of Natural Resources, U.S. Fish and wildlife Service, Michigan Department of Veterans and Military Affairs, Michigan Audubon Society, and citizen volunteers. The objective of the monitoring is to count all singing males within the known breeding range in n. Lower Michigan and the eastern and central Upper Peninsula, Wisconsin, and Ontario to get a relative index of the population to help evaluate its response to environmental conditions and management practices (Ryel 1981, Probst and Weinrich 1993, Probst et al. 2005).

Trends

Historically, the first census of the entire population of singing males within Michigan recorded 432 in 1951, and the next census in 1961 recorded 502 singing males. By the 1971 decennial census, the male population had decreased to 201, a 60% decline in population (Mayfield 1972), prompting the Kirtland’s Warbler to become classified as an Endangered Species.

From its lowest levels in 1987 of 167 singing males, the population has increased rapidly. From the early 1970s to 1990, the male population remained stable near 200

males, but grew quickly over the next 2 decades until 2007, when it achieved stability (Probst and Weinrich 1993, Donner et al. 2009).

Population Regulation

Lack of suitable habitat and parasitism by Brown-headed Cowbirds have been key factors influencing breeding rates and numbers.

The initial population decline from 1961 to 1971 was attributed primarily to nest parasitism by the Brown-headed Cowbird, but the quantity of suitable breeding habitat had also decreased in that period (Ryel 1981). Cowbird control by trapping initiated in the early 1970s stabilized the population by the late 1970s and early 1980s (Kelly and DeCapita 1982, Ryel 1981). During this period, there is evidence that the decline of suitably-aged pines in core breeding areas was the primary limiting factor for the population (Probst 1986). Much of the available habitat was aging; coupled with the lack of upcoming, dense jack pine habitat, this kept the population at low levels.

The explosive population increase that began in the late 1980s was in response to large amounts of young pine habitat becoming suitably-aged for occupancy – mostly the result of the 1980 Mack Lake Fire but also some large, dense plantations reaching the right age (Probst and Weinrich 1993, Bocetti 1994, Kepler 1996, Donner et al. 2009). During this period, the Kirtland's population expanded its breeding distribution into the Upper Peninsula of Michigan (Probst et al. 2003, Donner et al. 2009), and most recently, into s.-central Wisconsin (Anich 2011). As the type of suitably-aged habitat changed to plantations, and the amount of such habitat stabilized, the rate of population growth began slowing in early 2000s (Donner et al. 2009). The population has continued increasing with numbers stabilizing near 2,000 males in 2010-2013.

Drought and hurricanes in the Bahama wintering grounds are reported as potential limiting factors (Trautman 1979, Ryel 1981). Recent research shows drought conditions in the wintering grounds often delay arrival and nest initiation on the breeding grounds, with fewer offspring fledged in those years (Rockwell et al. 2012). How the magnitude of changes in the timing of migration in response to changing wintering ground conditions may influence long-term population trends is unknown.

Conservation and Management

Effects Of Human Activity

Disturbance At Nest And Roost Sites

In moderation, human presence and activity near nests does not seem to affect the warblers' behavior or survival (Anderson and Storer 1976. Nests are sometimes located in openings created by trails through forest, causing some people to call it a "roadside bird", but these nests appear to have lower success rates. Banding

activities do not appear to affect individuals (Bocetti 1994, Rockwell 2013). Gross disturbances, such as the approach of a crowd of people, may cause males to leave territories temporarily.

Shooting And Trapping

Deliberate destruction of birds and nests is no longer a problem, although earlier in this century there was concern about collecting birds and eggs on wintering and breeding grounds.

Pesticides And Other Contaminant/Toxics

Not known to have been affected by contaminants.

Degradation Of Breeding And Wintering Habitat

Breeding habitat is now heavily managed, leading to stabilized populations; see above.

Wintering habitat in the Bahamian Archipelago are disturbed sites resulting from deforestation throughout the archipelago followed by abandoned agricultural fields that have converted to scrub (Byrne 1980). Succession of this habitat without some type of disturbance to keep it in scrub reduces the amount and quality of wintering habitat (Wunderle et al. 2010). Grazing by goats is one approach that is being explored currently. Residential and commercial development away from the coastline is resulting in habitat loss (Wunderle et al. 2010). Previously occupied pine habitat is becoming unsuitable due to altered fire regimes (Haney et al. 1998).

Management

Measures Proposed And Taken

Efforts to assure future breeding habitat began in 1957, when 3 areas, each 4 miles square (1,036 ha) were set aside to be managed for Kirtland's Warblers on state forest lands in Ogemaw, Crawford, and Oscoda counties, Michigan (Radtke and Byelich 1963,Mayfield 1963). The intention was to maintain a portion of each tract in trees of different ages so that some would be suitable for the warbler at all times, some would be in preparation and early growth, and some would be allowed to grow to harvestable size for pulpwood. In 1962 U. S. Forest Service followed suit, setting aside a tract of 1,600 ha within the Huron National Forest in se. Oscoda County. The plan envisaged only minor departures from normal forestry practice, with trees proceeding to harvest in about 50 years, while portions were kept in younger age classes. It was expected that this treatment might eventually be extended to other tracts not already designated. Management was to include burning, cutting, and planting as required.

After 60% decline in population between 1961 and 1971, emergency measures were instituted through cooperation of federal, state, and private agencies. These measures included trapping of cowbirds from nesting sites, starting in 1972. Cowbirds were captured in large walk-in traps previously used by government to control blackbirds on agricultural land. Outstanding success resulted. Parasitism dropped immediately to about 3% of warbler nests, virtually eliminating the cowbird problem (Kelly and DeCapita 1982). The numbers of cowbirds caught each year, however, has not declined, and trapping may need to be continued indefinitely.

Preservation efforts were advanced when the Endangered Species Act of 1973 became national law and was supplemented with similar legislation in Michigan in 1974. A Recovery Team, representing the government agencies involved, was appointed by the Secretary of Interior in 1975. Its Recovery Plan's (Byelich 1976, rev. 1985) primary objective was to reestablish a self-sustaining Kirtland's Warbler population throughout its known range at a minimum level of 1,000 pairs. The plan initiated the following steps to reach its goal of reversing the population declines: (1) conduct an annual population census to monitor singing males and the amount and quality of suitable habitat, (2) reduce Brown-headed Cowbirds by trapping in all nesting areas, (3) close breeding areas during the nesting season to protect warblers from human disturbance, (4) develop emergency measures to prevent extinction by studying the feasibility of reintroduction techniques, and (5) expand the available habitat by identifying new habitat management areas (Probst 1986, Kepler 1996, Corace et al. 2010).

In 1981, the USDA Forest Service and the Michigan Department of Natural Resources adopted the habitat management plan that designated 23 management areas that covered nearly 51,700 ha of public lands (Kepler 1996). Another 1,100 ha habitat was established on Michigan Department of Military Affairs lands in 1985, and another 4,400 ha was obtained in 1989 by public agencies (Kepler 1996). Habitat management in these areas called for 12,141 ha of suitably-aged habitat to be regenerated to sustain the 1,000 nesting pairs identified in the Recovery Plan, and initial management guidelines called for maintaining 20% of each management area in each 10-year age class to the 50-year timber rotation (Probst 1988).

The initial habitat management program focused on using seed tree harvest followed by prescribed burning (Probst 1988), but direct seeding and natural regeneneration proved insufficient at getting new pine forest established. Plus, there are few days each year with suitable burning conditions. Management agencies began emphasizing planting and using alternative site preparation methods, such as piling and burning of slash, mechanical scalping, and planting without further site preparation (Kepler 1996). Today, much of the suitable habitat is created using dense plantations interspersed with small openings, variable spacing of plantings, and leaving strips of live trees, snags and down wood to closely mimic wildfire-regenerated habitat (see Habitat; also Corace et al. 2010). Management agencies are shifting from machine planting to Bracke scalping and hand planting to minimize ground disturbance. With the increasing population, additional habitat management plans and actions are being taken for the small breeding groups found in eastern Upper Peninsula of Michigan, and s.-central Wisconsin. These plans also focus on

creating dense jack pine plantations on a rotational-basis to maintain a consistent supply of young habitat.

Habitat management for Kirtland's Warbler has evolved from a single species approach typical of Endangered Species Recovery programs to an adaptive management approach that favors ecosystem recovery. Currently, the habitat management program is allowing public land managers to actively manage large landscapes throughout xeric ecosystems of Michigan that will benefit many species through the restoration of this unique barrens habitat.

Effectiveness Of Measures

Measures taken, especially removal of cowbirds, clearly halted a declining population, but the population remained stable until the late 1980s when large amounts of habitat became suitably-aged after the 1980 Mack Lake Wildfire. The creation of breeding habitat through dense plantations retained large amounts habitat on the landscape once the wildfire-regenerated habitat became too old. Currently, Kirtland's Warblers are primarily breeding in plantation habitat (Donner et al. 2009) created by federal and state agencies. Management is constantly changing to find better ways to create breeding habitat that also helps maintain plant and animal species that rely on these xeric ecosystems. Now that the population appears stable near 2000 pairs, management is exploring ways to incorporate natural disturbances in the jack pine ecosystems of northern Michigan.

The Kirtland's Warbler was designated as a "keystone" species by the National Fish and Wildlife Foundation in 2009. In May 2011 the key managing agencies, Michigan Department of Natural Resources, U. S. Fish and Wildlife Service, and U. S. Forest Service, signed a Memorandum of Understanding to develop a Conservation Plan and foster a public-private partnership for long-term conservation in the face of potential down-listing. The Conservation Plan is in preparation and the non-profit Kirtland's Warbler Alliance has been established and is working with the Recovery Team. This plan will guide future conservation actions through a combination of habitat management, cowbird control, minimizing land-use activities during breeding season, adaptive management (monitoring, research), information and education programs, and pursuing funding opportunities to provide financial support through a long-term trust fund to support Kirtland's Warbler and jack pine management.

Appearance

Kirtland's Warblers have 9 functional primaries, 9 secondaries (including 3 tertials), and 12 rectrices. No geographic variation in appearance (see Systematics: Geographic Variation) or geographic or sex-specific variation in molt strategies reported.

Molts

General

Molt and plumage terminology follows Humphrey and Parkes (1959) as modified by Howell et al. (2003, 2004). Kirtland's Warbler exhibits a Complex Alternate Strategy (cf. Howell et al. 2003, Howell 2010), including complete prebasic molts, a partial preformative molt, and limited prealternate molts in both first and definitive cycles (Mayfield 1960; Sykes et al. 1989; Curson et al. 1994; Dunn and Garrett 1997; Pyle 1997a, 1997b; Fig. 4).

Prejuvenal (First Prebasic) Molt

Complete, primarily May–Jun, in the nest. Feather tracts defined and ensheathed primary remiges visible at 3 d; pin feathers cover body, remiges not yet erupted at 5 d; juvenal plumage emerging at 7 d and well-developed at 8 d (Mayfield 1960). Prejuvenal Molt presumably completed or near-completed by fledging at day 9–11; rectrices require extra days to complete growth; reported about half grown at 16 d.

Preformative Molt

"First Prebasic" or "Prebasic I" Molt of Humphrey and Parkes (1959) and some later authors; see revision by Howell et al. (2003). Partial, primarily Jun–Aug (Fig. 4), on or near natal territory. At 24–28 d molt evident on sides of breast; by 38–43 d body molt complete or near-complete; on some birds by 16 Aug, but not yet complete on others by 10 Sep (Sykes et al. 1989). Includes most or all body feathers and upperwing secondary coverts but no primary coverts, primaries, secondaries, or rectrices (Pyle 1997b).

First And Definitive Prealternate Molts

Limited, primarily Feb–Apr (Fig. 4), on non-breeding grounds (Maynard 1896, Bonhote 1903). Includes body feathers only, probably primarily on head; study needed on extent of molt among all feather tracts. First and

Breeding male Kirtland's Warbler; Mio, MI; 19 June.

Breeding male Kirtland's Warbler; Mio, MI; 25 May.

Breeding male Kirtland’s Warbler; Adams County, WI; 8 June.

Breeding male Kirtland’s Warbler; Huron-Manistee NF, South Branch, MI; 16 June.

Definitive Prealternate Molts similar in timing and extent, as far as known. Reports that Prealternate Molts can begin as early as Oct on non-breeding grounds (Pyle 1997a) require confirmation; limited feather replacement at this time may instead be part of protracted/suspended Preformative and Prebasic Molts (see Definitive Prebasic Molt).

Kirtland's Warbler; Magee Marsh, Oak Harbor, Ohio; 15 May.

Definitive Prebasic Molt

Complete, primarily Jul–Oct (Fig. 4), on or near breeding grounds. Adult males begin molting about time they stop singing (4 Jul–15 Aug), continues about 40 d (Sykes et al. 1989). Evidence of molt reported on migrant in hand in S. Carolina 29 Oct 1903 (Wayne 1904) may have been part of protracted Definitive Prebasic Molt. In field molt first apparent on breast and back, probably at or just after first primaries and tertials dropped. Primaries replaced distally (p1 to p9), secondaries likely replaced proximally from s1 and proximally and distally from the central or innermost tertial (s8 or s9), as typical of passerines. Rectrices lost almost simultaneously; adults can appear almost tailless for about 10 d.

Female Kirtland's Warbler; Adams County, WI; 1 July.

Kirtland's Warbler fledgling; Adams County, WI; 1 July.

Plumages

Following based primarily on detailed plumage descriptions of Ridgway (1902), Roberts (1955), Curson et al. (1994), and Dunn and Garrett (1997); see Goodwin (1982), Sykes et al. (1989), Pyle (1997a), and Probst et al. (2007) for specific criteria related to age and sex determination. Appearances of sexes similar in Juvenal Plumage but differ in subsequent plumages; Definitive Plumages can be assumed at Second Basic and Second Alternate plumages; in some males not reached until Third Alternate Plumage (Probst et al. 2007).

Natal Down

Present primarily May–Jun, in the nest. Down

brown, about 8 mm long on head but shorter on scapular, mid-dorsal, and femoral regions; distinguishable from Brown-headed Cowbird hatchlings, which have white down.

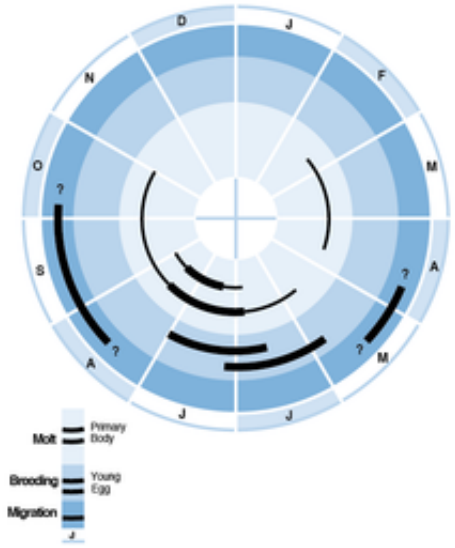

Figure 4. Annual cycle of breeding, molt, and migration of the Kirtland's Warbler.

Juvenal (First Basic) Plumage

Present primarily May–Jul. Somewhat similar to subsequent plumages but paler and duller; upperparts heavily fringed pale brown; forehead. lores, and auriculars without dark, uniform in color with rest of head; underparts primarily buff, often tinged darker brownish on breast and yellowish on flanks and lower underparts. Upperwing median and greater coverts brown with pale buff tips forming wider wing bars than in subsequent plumages. Primaries, primary coverts, secondaries, and rectrices as in Formative Plumage (below). Sexes similar except for average difference in amount of white to outer rectrices (see below).

Formative Plumage

"First Basic" or "Basic I" plumage of Humphrey and Parkes (1959) and later authors; see revision by Howell et al. (2003). Present primarily Aug–Mar.

Male. Body plumage similar to Definitive Basic female but lores and auriculars average darker black.

Female. Similar to Definitive Basic female but duller; upperparts more heavily washed brown and with smaller and less-distinct dark centers to feathers; outer rectrices (r4–r6) with reduced and less-distinct whitish patches, usually confined to r5–r6; underparts average paler yellow and with less distinct and extensive blackish streaking to sides and flanks.

Formative Plumage further distinguished from Definitive Basic Plumage by molt limits between replaced formative upperwing greater coverts contrastingly with older and browner, retained, juvenal primary coverts with little or no grayish edging; retained juvenal outer primaries and rectrices thinner, more pointed, browner, and relatively more worn, the latter averaging smaller and less-distinct white patches to r4–r6, sex for sex (Pyle 1997a).

First Alternate Plumage

Present primarily Mar–Aug.

Male. Similar to Definitive Alternate male but lores and auriculars duller blackish;

crown and back variably tinged brownish; back feathers average smaller dark centers; outer rectrices (r4–r6) with reduced and less-distinct white patches, sometimes absent from r4; underparts average paler yellow, often whitish toward vent, and with less-distinct streaks to sides and flanks. Based on detailed plumage study of known-age birds, body plumage overlapped with Definitive Alternate males in 20-25% of individuals (Probst et al. 2007).

Female. Similar to Formative female and duller than Definitive Alternate female. Criteria to separate First Alternate from Definitive Alternate plumages similar to that described under Formative and Definitive Basic plumages, often becoming more pronounced due to increased degradation rate of retained juvenal feathers compared with replaced formative feathers.

Definitive Basic Plumage

Present primarily Sep–Mar.

Male. Crown, back, rump, and uppertail coverts bluish gray, the feathers fringed brownish when fresh; crown with small black streaks; remainder of upperpart feathers with large and distinct blackish to black centers, obscured by gray and brown feather fringing when fresh. Forehead, lores, and auricular region below eye blackish, blending to dusky and bluish gray through auriculars posteriorly; wide white crescents above and below eye. Rectrices dusky with bluish fringing, widest on central pair (r1), the outer three pairs (r4–r6) with distinct and relatively large white patches, always or almost always present on r4. Upperwing lesser coverts bluish gray with dark centers; median and greater coverts dusky blackish with narrow whitish tips forming indistinct wing bars; remiges and primary coverts dusky blackish with grayish fringing to outer webs, widest on tertials and narrow to absent on primaries. Underparts yellow, washed buff when fresh, brightest on throat and dullest on vent and undertail coverts; sides of breast and flanks with bold and distinct black streaking, partly obscured by buff to pale-yellow feather fringing when fresh.

Female. Similar to Definitive Basic male but duller overall. Crown, back, rump, and uppertail coverts brownish gray, the feathers fringed pale brown when fresh; crown with less distinct streaks; remainder of upperpart feathers with smaller blackish centers obscured by pale brown feather fringing; forehead, lores, and auricular region dusky gray, blending more with remainder of face; outer three rectrices (r4–r6) with reduced white patches, only sometimes present on r4; underparts paler yellow with less distinct dusky streaks to breast and flanks.

In both sexes Definitive Basic Plumage separated from Formative Plumage by having wing and tail feathers uniform in quality and freshness, the primary coverts duskier with broader gray or brownish-gray fringing, not contrasting in feather quality with greater coverts; basic outer primaries and rectrices broader, more truncate, duskier, relatively fresher, and averaging larger white spots to r4–r6, sex for sex (Pyle 1997a).

Definitive Alternate Plumage

Present primarily Mar–Aug.

Male. Similar to Definitive Basic male but plumage brighter and bolder due to combination of molt and wearing of brownish and buff feather fringing. Upperparts brighter bluish gray with bolder and more distinct black streaking; forehead, lores, and auriculars blacker and more distinct; underparts brighter yellow with bolder black streaking to sides and flanks. These criteria average brighter than in First Alternate males (see above) and also average duller in Second than in Third Definitive and older males, based on detailed study of known-age birds (Probst et al. 2007).

Female. Similar to Definitive Basic female but plumage slightly bolder; upperparts tinged bluish; forehead, lores, and auriculars darker; underparts brighter yellow with bolder dusky streaking. See above for criteria to separate First from Definitive Alternate plumages.

Bare Parts

Bill

In hatchlings pinkish-brown with darker tip; in adults blackish in spring, becoming duller brown in fall (Dunn et al. 1997).

Iris

Dark brown

Legs And Feet

In hatchlings pinkish (Curson et al. 1994); blackish in adults.

Measurements

Appendix 2. Some people have believed that yearling males, but not females, can be distinguished from older birds by fine, rather than coarse, spotting on breast. Therefore, such males have been grouped separately in this appendix, although proof is lacking for this indicator. The finding here and elsewhere that adult females are sometimes heavier than males may be an artifact of sample gathering on the nesting ground, where females may show pre-egg-laying gain in weight.

Kirtland's Warblers weighed in field during nesting season have yielded measurements similar to those of this appendix: males 13.7 ± 0.6 g, *n* = 64; females 14.2 ± 1.1 g, *n* = 13 (Mayfield 1960). Males 13.7 ± 1.1 g, *n* = 19; females 13.8 ± 1.1 g, *n* = 32 (Walkinshaw 1983).

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