

Population increase in Kirtland's warbler and summer range expansion to Wisconsin and Michigan's Upper Peninsula, USA

John R. Probst, Deahn M. Donner, Carol I. Bocetti and Steve Sjogren

Abstract The threatened Kirtland's warbler *Dendroica kirtlandii* breeds in stands of young jack pine *Pinus banksiana* growing on well-drained soils in Michigan, USA. We summarize information documenting the range expansion of Kirtland's warbler due to increased habitat management in the core breeding range in the Lower Peninsula of Michigan during 1990–2000. We collected records and conducted searches for the species in Michigan's Upper Peninsula and Wisconsin over 1978–2000. During that time 25 males were found in Wisconsin and 90 males in the Upper Peninsula. We documented colonization of Michigan's Upper Peninsula by six ringed males from the Lower Peninsula of Michigan. Four ringed birds also moved back to the core breeding range, including two males that made two-way movements between the core breeding range and the Upper Peninsula. Thirty-seven females were observed with males from 1995 to 2000, all in Michigan. Nesting activities were noted for

25 pairs and at least nine nests fledged young. One male ringed as a fledgling returned to breed in two subsequent years. After a 19-year period of population stability, the Kirtland's warbler population increased four-fold during 1990–2000, most likely in response to a tripling in habitat area. This increase in sightings and documented breeding may be related to habitat availability in Michigan's Upper Peninsula and to saturation of habitat in the main breeding range. The increase in extra-limital records during 1995–1999 corresponds to the time when the population went from the minimum to the maximum projected population densities, and a decline in natural wildfire habitat was just offset by new managed habitat for the Kirtland's warbler.

Keywords Carrying capacity, colonization, dispersal, *Dendroica kirtlandii*, jack pine, Michigan, population expansion, Wisconsin, USA.

Introduction

Kirtland's warbler *Dendroica kirtlandii* is categorized as Endangered by the USA Endangered Species Act (Endangered Species Program, 2003), and as Vulnerable on the IUCN Red List (IUCN, 2002) under criteria D2, i.e. population very small or restricted (D) and characterized by restriction in its area of occupancy or in number of locations (2). This bird species breeds in large (>40 ha) stands of young (5–23 years old) jack pine *Pinus banksiana* growing on extremely well-drained soils in northern Michigan ecosystems (Kashian *et al.*, 2001). The density

(>3,000 stems ha⁻¹) and patchy distribution of jack pine that comprises suitable habitat regenerates naturally after wildfire (Zou *et al.*, 1992), and can be mimicked imperfectly by plantations and natural regeneration following site preparation with and without seeding, which can have a similar percent cover of trees but at lower densities than produced by wildfires. Plantations created specifically for Kirtland's warbler breeding habitat have more trees than in stands resulting from standard forestry prescriptions or from the natural regeneration that follows tree harvesting (Probst & Weinrich, 1993). Female Kirtland's warblers frequently place their nests on the ground at the edge of thickets and openings in these young jack pine stands (Walkinshaw, 1983; Bocetti, 1994).

As a result of their ecosystem specificity, this neotropical migrant breeds in a limited area in northern Lower Michigan (Probst, 1986, 1991), although it is presumed to have been more widespread in the distant past (Mayfield, 1960, 1988a). A comprehensive census of Kirtland's warbler within the core breeding range was conducted in 1951, 1961, 1971, and annually thereafter (Probst & Weinrich, 1993; Kepler *et al.*, 1996). The 1951 and 1961 counts were 432 and 502 males, respectively. However, when the population dropped

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Received 25 April 2002. Revision requested 16 September 2002. Accepted 9 April 2003.

to 201 in 1971, annual censuses, control of brown-headed cowbird *Molothrus ater*, and increased habitat management were three of the steps taken to stabilize the population. The population was stable over 1971–1986, leading to speculation that the species might be limited on the wintering grounds in the Bahamas (Ryel, 1981a). However, there was evidence that habitat decline from over-maturity of many jack pine stands was offsetting new habitat regenerated from wildfires or management (Probst, 1986). The amount of suitably-aged habitat doubled from 1987 to 1990 due to extensive habitat management and two large wildfires (1975 and 1980), leading to predictions of a substantial population increase (Probst & Weinrich, 1993).

Specimens and sight records of Kirtland's warblers outside the nesting range on the Lower Peninsula of Michigan had been reported (Probst, 1985). There is a single nest record from Ontario in 1944 (Speirs, 1984). Five males were found in Canada during the breeding season between 1977 and 1980 (Ryel, 1981a), two of which had been ringed in the Lower Peninsula of Michigan. A loose cluster of Kirtland's warbler males found in 1916 in Ontario could have been a breeding population, based on the number of birds, but no nests were reported (Harrington, 1939).

Migrants have been recorded across a broad range from Missouri and Minnesota in the west to Massachusetts and Virginia in the east. Over the past 150 years eight specimens and 17 sighting records of Kirtland's warblers in May or June, all migrants presumed off the migration route (Mayfield, 1988b), have been reported in Wisconsin (Tilghman, 1979; J. Trick, pers. comm.). A male was sighted in central Minnesota in 1944 (Hiemenz, 1980) and in northern Minnesota in 1958 and 1964 (Gullion, 1964). Unconfirmed sightings were reported in northern Minnesota in September 1982 and May 1993.

An un-mated male was found at the same location in Marquette County (Fig. 1a) in the Upper Peninsula of Michigan in 1982 and 1983 (Probst, 1985). Since then, the amount of habitat in the Lower Peninsula of Michigan has increased (Probst & Weinrich, 1993), and the Kirtland's warbler population has grown. This population increase and presumed habitat saturation has led to speculation about whether surplus birds may disperse widely or expand their habitat choices or both (Probst, 1986). In response to more available habitat Kirtland's warblers initially limited their habitat selection to naturally regenerated jack pine following wildfires and plantations (Probst & Weinrich, 1993), but as habitat filled in recent years there have been more widespread sightings of this species.

In this paper we provide an update of recent sightings in Wisconsin and the Upper Peninsula of Michigan, and present the first nesting records outside the established

nesting range in the Lower Peninsula of Michigan. We also document the Lower Peninsula origin of some Upper Peninsula colonizing birds, and several movements of ringed birds between the established and new breeding locations. We update trends in both wildfire and managed habitat area, and the increase in Kirtland's warbler population in response to the substantial increase in wildfire and managed plantation habitat in the core breeding range (Probst & Weinrich, 1993). Range expansions are of interest for the understanding of dispersal distances, carrying capacity, habitat limitation, and range-wide population dynamics.

Methods

In the core breeding range comprehensive annual censuses (e.g. Ryel, 1981b) have been conducted from 1971 in all known suitably-aged habitats (5–23 years old) or until occupied habitats are abandoned. Habitat area, age, and location were summarized from data maintained by the Michigan Department of Natural Resources and the United States Department of Agriculture (USDA) Forest Service. Suitable habitat in the Lower Peninsula of Michigan is concentrated in areas of sandy, glacial outwash (Probst, 1991; Probst & Weinrich, 1993), thereby limiting the extent of the areas that have to be covered in habitat inventories and bird censuses. The annual count is almost comprehensive, especially in the core breeding range.

A regional-scale search for extra-limital birds in the Upper Peninsula of Michigan and Wisconsin was facilitated by their known concentration in outwash ecosystems (Fig. 1), which occur primarily on public lands. Management maps and aerial photographs were used to identify potentially suitable habitat, the amount of which was smaller than in the core breeding range, and thus almost all of it could be periodically checked by a small team of searchers. Until 1991, surveys for Kirtland's warbler varied in coverage and intensity across years and locations in Michigan's Upper Peninsula and Wisconsin but suitable habitat was checked annually thereafter. Interest among volunteer searchers increased with the success in finding extra-limital birds.

Major outwash systems in Wisconsin were surveyed comprehensively (Fig. 1a) from 1977–1980 (Tilghman, 1979; Probst, 1985). Major jack pine ecosystems in the Upper Peninsula of Michigan were searched during 1980–1982, as were two north-west Wisconsin wildfire areas in 1988. Discovery of Kirtland's warblers in Wisconsin in 1988 led to comprehensive surveys in Jackson-Juneau and Washburn-Douglas Counties in subsequent years. Kirtland's warblers were discovered in Vilas County in northeast Wisconsin in 1995, followed by USDA Forest

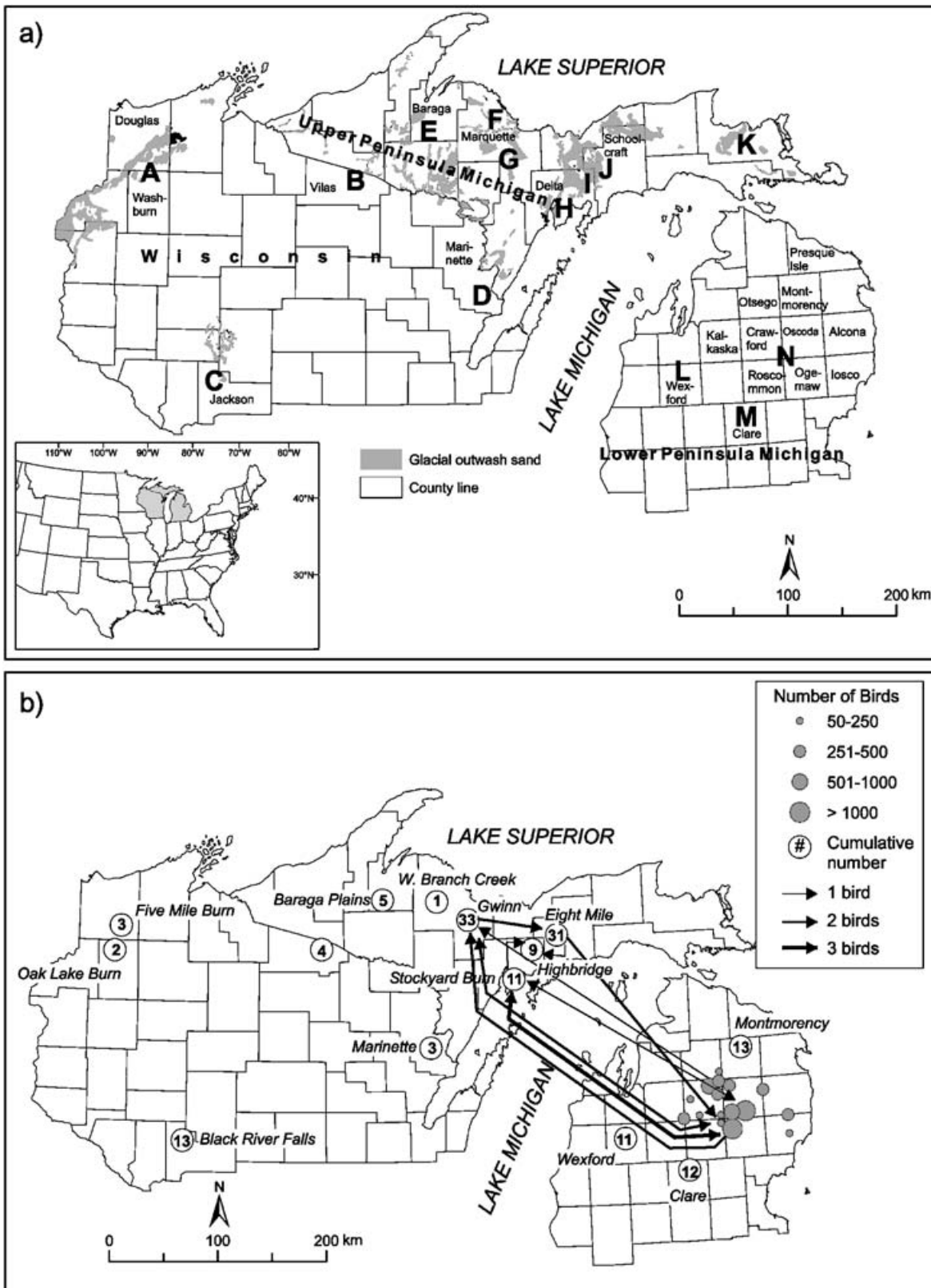


Fig. 1 (a) Areas (A–N, in marked counties) surveyed for Kirtland’s Warblers from 1978 to 2000 in Michigan and Wisconsin; the inset indicates the location of the main figure. (b) Locations and cumulative numbers of male Kirtland’s Warblers found during 1978–2000 in Michigan and Wisconsin. Arrows indicate known movements of ringed birds.

Service, North Central Research Station surveys in 1996–1999. United States Fish and Wildlife Service personnel added Marinette and Oconto Counties in Wisconsin to the survey in 1997 and organized a broader search during 1998–2000.

USDA Forest Service personnel searched the Ottawa and Hiawatha National Forests of the Upper Peninsula of Michigan during 1991–2000, and volunteers searched state and federal lands during 1993–2000 (Fig. 1a). Personnel from the USDA Forest Service and the Michigan Department of Natural Resources searched habitats at least once per year during 1991–2000, and three times per year during 1996–2000 at localities where birds were found previously. Locations were visited multiple times to document dispersal patterns of mated and un-mated warblers. Those visits increased chances of finding females or young.

United States Geological Survey personnel expanded a long-term ringing effort for Kirtland's warblers from the Lower Peninsula of Michigan into the Upper Peninsula during 1996–2000. In both areas warblers were captured using two techniques. Firstly, during the nesting season males were attracted with taped songs and captured in mist nets; incidental captures of females occurred as well. Secondly, a passive capture programme was used in late July to early September in which mist nets were placed in habitats without tape playback; this method netted hatch-year and after-hatch-year warblers. Movements of colour-ringed birds provided information about survivorship, site tenacity within years, and site fidelity between years. In addition, ringed individuals helped document dispersal between habitat patches, or between Michigan's Upper Peninsula and the established breeding range, allowing inferences about the relative importance of dispersal versus local reproduction in maintaining the newly established populations. Nesting occurrence and nest success were determined by observations of adult

warblers, including behaviour such as alarm or food-carrying activities. If possible, nests were checked once to determine nesting stage for future searches of recently fledged young. Fledglings were captured and ringed when possible.

Results

Core breeding range populations and habitat

An aggressive habitat management effort by federal and state agencies has led to an increase in habitat overall, and a decrease in the proportion of male Kirtland's warblers in wildfire habitat, from 76% in 1984 to 18% in 2000 (Fig. 2). The Kirtland's warblers responded to the substantial increase in habitat from 1987 to 1997 by tripling their population, as measured by the 1994 census, and exceeding the population of 532 males in the 1961 decennial census. The population in the core breeding range in the Lower Peninsula of Michigan (Fig. 1b) increased in 10 of 11 years from 1989 to 2000. During 1990–2000 the population has increased from below an estimated average carrying capacity to estimated maximum projected densities or higher (year 2000). By the end of the century the amount of managed and wildlife habitat had stabilized, leading to projections of a stable population based on historical densities (Fig. 3).

Extra-limital records

Kirtland's warblers outside the established breeding range were found in 18 of 23 years between 1978 and 2000 (Table 1). One to 24 males were found in each of the 18 years, with a total of 115 males, although some males were the same birds in different years. For example, searches in the Upper Peninsula of Michigan from 1979 to 1984 located a male in about the same site in a 1968

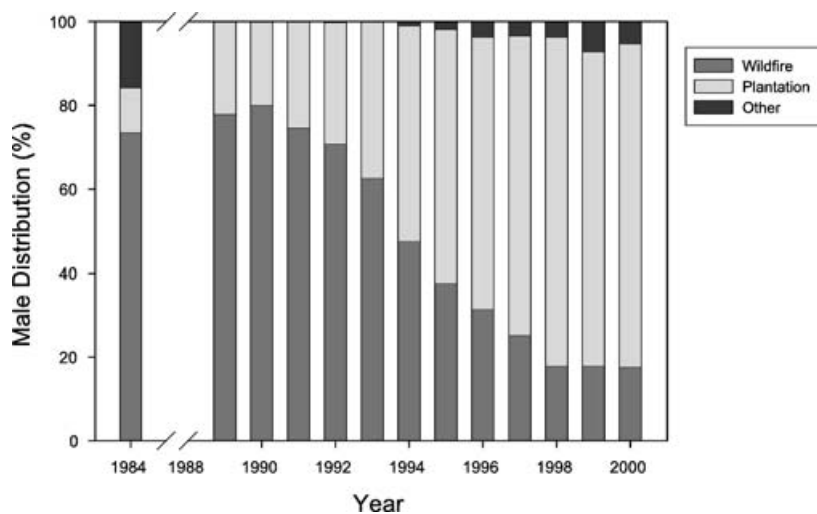
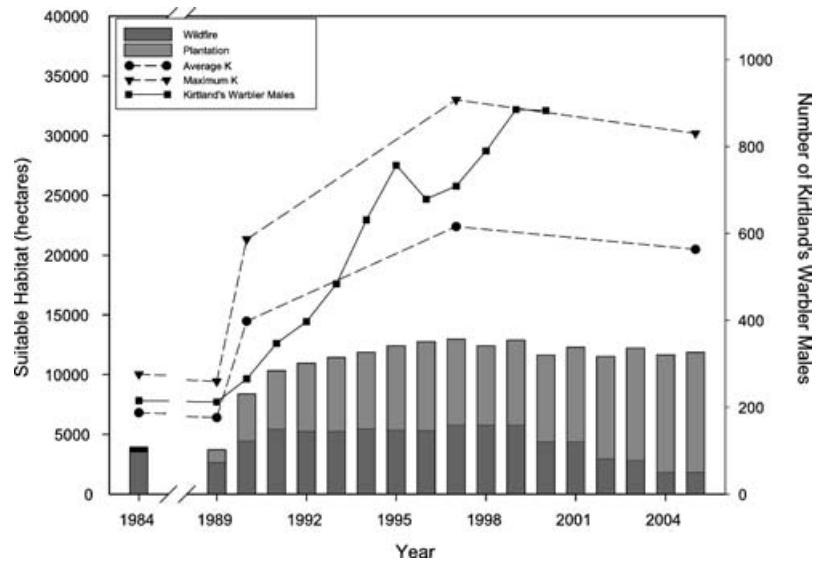


Fig. 2 Proportion of male Kirtland's warblers found in the three major habitat categories within the core breeding range, Lower Michigan, USA, from 1984 to 2000.

Fig. 3 Habitat and population trend of male Kirtland's warblers within the core breeding range, lower Michigan, USA, from 1984 to 2000. Projected average and maximum carrying capacity (K) estimates were based on historical male densities (1.9 males per 40 ha and 2.8 males per 40 ha, respectively) (Probst & Weinrich, 1993).



burn at Gwinn Sand Plains in 1982 and 1983. It is likely that this was the same individual but it was not ringed.

Between 1994 and 2000, 95 males were found at eight areas, only one of which (Gwinn Sand Plains) supported birds before 1993. A sharp increase in extra-limital Kirtland's warbler sightings started in 1995 in the Upper Peninsula, when 9 males and the first female and nesting attempt were recorded. Thereafter, the number of males increased from 15 to 24 during 1996–1999 and the number of females increased to a maximum of 12 in 1999 (Table 2). This corresponds to the period when Kirtland's warblers approached their maximum densities overall after a lag from 1989 to 1993 (Fig. 3), suggesting habitat saturation.

There were 17 records in May or June of Kirtland's warblers in Wisconsin from 1853 to 1978 (J. Trick, pers. comm.), and three during 1978–1979 in the jack pine barrens near Black River Falls, Jackson and Juneau counties, at the southern most range of that ecosystem in the upper Great Lakes region (Fig. 1a). Additionally in 1988 and 1989 one of us (JRP) found two males on each side of the Douglas-Washburn County line near Minong, Wisconsin (Fig. 1b). Nine warblers were found in Black River Falls, Wisconsin, from 1988 to 1995 in five different years (Table 1). Three male warblers were found in Marinette County, Wisconsin in 1997. No warblers were found in potential habitats in north central and northeast Wisconsin until 1996.

Breeding records

From 1995 to 2000, 38 Kirtland's warbler pairs were found at five localities in the Upper Peninsula of Michigan (Table 2). All but one female captured by netting had a brood patch. The first breeding record was a nest

discovered at Baraga Plains in 1995. Another nest was found in 1996 at Gwinn Sand Plains (Fig. 1). Nesting activities were observed at Baraga Plains (1 in 1995), Eight-mile Burn (2 in 1996, 3 in 1997, 3 in 1998, 3 in 1999), Highbridge Area (1 in 1995, 1 in 1997, 1 in 2000), Stockyard Burn (1 in 1995, 1 in 1997), and Gwinn Burn (1 in 1996, 2 in 1998, 6 in 1999), which had re-burned since earlier sighting in 1982 and 1983. Of these, at least five nests failed, and 10 were known to have fledged young (Stockyard, 1 in 1997; Highbridge, 1 in 2000; Gwinn, 1 in 1998, 2 in 1999; Eight Mile Burn, 1 in 1996, 2 in 1997, 2 in 1999). In 1999 few successful nests were documented and young (hatch-year) birds netted were often from an unknown number of adult pairs. One pair was found with fledged young at Eight Mile Burn. Another successful nesting was discovered at Gwinn and hatch-year birds were netted at two locations more than 2 km apart. In 2000 only one of four females was known to have fledged young, at Highbridge in north-east Delta County.

Breeding dispersal

In summary, 25 male warblers were found in Wisconsin and 90 in the Upper Peninsula of Michigan from 1978 to 2000 (Table 1); all 38 females were found in the Upper Peninsula of Michigan (Table 2). Dispersal distances were up to 350 km, assuming that un-ringed birds were originally from the core range in Lower Michigan. At least six ringed birds colonized the Upper from the Lower Peninsula: three from north-west Ogemaw County, one from Mack Lake Burn, Oscoda County, one from Eldorado, Crawford County, and one from Bald Hill Burn, Crawford County (Fig. 1b). In addition, a male that hatched at Eight Mile Burn in 1996 was

Table 1 Number of male Kirtland's Warblers found outside the core breeding range of Lower Michigan from 1978 to 2000.

Region	Area	1978	1979	1980	1982	1983	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000
<i>Upper Peninsula Michigan</i>																			
Baraga Delta	Baraga Plains								1				1	1	1				2
	Rapid River (Stockyard Burn)													2	2	3	3	1	
Marquette	Highbidge													2		1		2	4
	Gwinn (1968 burn)				1	1								1	5	7	5	12	1
	Gwinn Sand Plains															1			
Schoolcraft	W. Branch Creek										1	1	1	2	6	7	9	4	1
	Eight-mile				1	1					1	2	2	8	14	19	17	19	8
<i>Wisconsin</i>																			
Douglas	Five-mile Burn						2	1											
	Black River Falls	2	1	1			5	1	1	1				1					
Marinette	Marinette															3			
	Land O'Lakes														1	2	1		
Washburn	Spooner						1				1								
	(Oak Lake Burn)	2	1	1	1	1	8	2	1	1	1	1	2	9	1	5	1		
<i>Total</i>		2	1	1	1	1	8	2	1	1	1	1	2	9	15	24	18	19	8
<i>Grand total</i>		2	1	1	1	1	8	2	1	1	1	1	2	9	15	24	18	19	8

Table 2 Number of male (above) and female (below, in italics) Kirtland's Warblers in the Upper Peninsula of Michigan and Wisconsin from 1994 to 2000. Number of ringed birds in parentheses.

Area	1994	1995	1996	1997	1998	1999	2000	Total
<i>Upper Peninsula Michigan</i>								
Baraga Plains	1 (0)	1 (0) 1 (0)	1 (0)				2 (0)	5 (0) 1 (0)
Eight-mile Burn	1 (0)	2 (0)	6 (5) 4 (2)	7 (4) 2 (2)	9 (7) 5 (3)	4 (2) 4 (0)	1 (0)	30 (18) 15 (7)
Gwinn Burn		1 (0)	5 (1) 1 (0)	7 (3)	5 (4) 2 (0)	12 (3) 8 (2)	1 (0) 1 (0)	31 (11) 12 (2)
Highbridge		2 (0) 1 (0)		1 (0) 1 (0)		2 (2)	4 (4) 3 (0)	9 (6) 5 (0)
Stockyard Burn		2 (1) 1 (0)	2 (1) 1 (0)	3 (2) 1 (0)	3 (3) 2 (0)	1 (0)		11 (7) 5 (0)
West Branch Creek				1 (0)				1 (0)
<i>Wisconsin</i>								
Jackson/Juneau County	1 (0)							1 (0)
Vilas County			1 (0)	2 (1)	1 (0)			4 (1)
Marinette County				3 (0)				3 (0)
<i>Total</i>	3 (0)	8 (1) 3 (0)	15 (7) 6 (2)	24 (10) 4 (2)	18 (14) 9 (3)	19 (7) 12 (2)	8 (4) 4 (0)	95 (43) 38 (9)

observed in northern Crawford County in 1997, but it returned to its natal location in 1998. One of the four birds colonizing the Upper Peninsula in 1996 and previously observed in the Lower Peninsula (at Mack Lake Burn in 1995) returned to Mack Lake Burn in the same breeding season. In 1999 two more males from the core breeding range were found in Gwinn and 4 males moved from one Upper Peninsula location to another (Fig. 1b). Finally, a male ringed as a juvenile at Eight Mile Burn in 1996 returned to breed successfully in 1997, about 3 km south of its hatching site. The following year this male was not found at any location searched in the Upper or Lower Peninsula until 22 June, when he was discovered at Eight Mile Burn, apparently un-mated, in mature jack pine trees unburned by the stand regeneration fire. It is possible, but unlikely, that the bird was present earlier in the season. Four birds (3 males and 1 female) ringed in the Upper Peninsula were subsequently found in Lower Michigan (2 in southern Crawford County, 1 in northwest Ogemaw County, and 1 in southwest Oscoda County) (Fig. 1b).

Discussion

Dispersal and population dynamics

The transition of the Kirtland's warbler population from below to above estimated carrying capacity in one decade supports the notion that the population is limited on the breeding grounds (Probst, 1986). If the carrying capacity of the core breeding range can be estimated by habitat area then it becomes less likely that the

population is limited on the wintering grounds (Ryel, 1981a; Haney *et al.*, 1998). These findings also suggest the importance of maintaining unoccupied habitat for this and other species. For example, the consistency of Kirtland's warbler sightings in Wisconsin and the Upper Peninsula of Michigan during 1978–2000 suggests that these birds are not migrants off the presumed migration route (Mayfield, 1988b), but were seeking breeding habitat in an expanding breeding range. The success of these individuals depends on habitat availability in these peripheral areas and the population dynamics in the source populations. Most of the recent sightings of Kirtland's warblers outside the known Lower Peninsula breeding range were recorded between 1995 and 1998, corresponding approximately to the time Kirtland's warblers were predicted to fill existing suitable habitat in the core breeding range as the population gradually increased to over 800 males in 1995–1999 (Fig. 3). We suggest that as the core habitat became saturated, these source populations provided increasing numbers of dispersing individuals to occupy the peripheral sites.

The sightings of Kirtland's warblers in Wisconsin and the Upper Peninsula of Michigan also suggest that long distances and large water bodies are not serious barriers to dispersal. We observed movement between the Upper and Lower Peninsula of Michigan both between and within breeding seasons. Movement at this scale indicates that long-distance dispersal of birds may occur to support 'sinks' where reproduction is below replacement level, as is the case for Wood Thrush and some other species in Illinois, USA (Robinson *et al.*, 1995). It is uncertain whether Upper Peninsula populations were

producing young at replacement levels, but nevertheless our findings suggest that population interactions should be considered at expanded geographic scales.

The future of Kirtland's warbler in Wisconsin and the Upper Peninsula of Michigan is uncertain. The timing and numbers of birds found during 1995–1998 suggest a population increase and overflow from the established breeding range in lower Michigan. The Lower Michigan population is projected to stabilize because no net gain in habitat was projected early in the century (Probst & Weinrich, 1993; Fig. 3). Additionally, the four areas in the Upper Peninsula where male and female warblers have been found regularly are nearing the end of their suitability as habitat, with tree heights near the upper limit of 1.7 to 5.0 m (Probst, 1988). However, regeneration of young pines in Upper Michigan at Baraga Plains, north-east Delta County, and Schoolcraft County attracted colonizers in 1998–2000.

Conservation implications

Clearly there is a need to develop more habitat for Kirtland's warbler for peripheral populations, but there are practical barriers to expensive, single-species land management objectives. Based on historical breeding densities (Probst & Weinrich, 1993), 200–400 ha of high-density jack pine on suitable sites would be required on a sustained basis to support 25 pairs of Kirtland's warblers (Probst, 1985). Assuming 50 years of commercial forest rotation and a 10-year warbler occupancy of a habitat patch, 1,000–2,000 ha would therefore be required to sustain the minimum amount of young pine regeneration for 25 pairs of Kirtland's warblers and associated wildlife. Based on the dispersal data presented here, these lands need not be contiguous. Regardless of whether a self-sustaining peripheral population can be established, any suitable habitat serves as a reservoir, as in 1995–1999, during periods of habitat shortage in the core breeding range even if peripheral populations subsequently decline. For example, we documented a reservoir function of harvested, unplanted habitat from 1971 to 1984, which supported Kirtland's warblers until higher quality habitat became available (Probst & Weinrich, 1993).

Currently, habitat management in the Lower Peninsula of Michigan requires expensive full planting or fill-in planting to regenerate dense stands of jack pine (Probst, 1988) on lands dedicated to warbler management and harvested for fibre (Probst & Weinrich, 1993). However, the cooler climate and greater soil moisture in the Upper Peninsula foster natural regeneration of jack pine on federal, state and county lands not dedicated to warbler management. Where such regeneration is dense enough in tracts of sufficient size to meet the needs of Kirtland's

warbler, the species may still breed without lands dedicated to Kirtland's warbler habitat management. Perhaps the most expedient way to justify regenerating forest stands of sufficient size for this species is to place Kirtland's warbler habitat management within a multi-species management programme with other area-sensitive, openland species such as northern harrier *Circus cyaneus*, sharp-tailed grouse *Tympanuchus phasianellus*, or upland sandpiper *Bartramia longicauda*. By the beginning of the current decade, 700 ha of large (>80 ha) jack pine stands have been harvested and regenerated by the Hiawatha National Forest in the eastern Upper Peninsula of Michigan for timber management and multi-species wildlife, including the Kirtland's warbler. The US Fish and Wildlife Service is planning to develop cooperative agreements to manage 400 ha for similar multiple resource objectives. Active land management for Kirtland's warbler should provide a continued reservoir during habitat shortages in the core breeding range, and perhaps a self-sustaining population over most time periods.

Acknowledgements

We thank R. Aho, M. Berg, G. Corace, K. Doran, J. Edde, S. Lietz, P. Thompson and M. Worland for their contributions of field records, and P. Thompson, M. Berg, J. Fussman, H. McCann, J. Martin, M. Petrucha and R. Urbanek for ringing assistance in the Upper Peninsula of Michigan. Additionally, we thank Phil Huber, Jerry Weinrich and John Nellist for continually assisting in assembling habitat acreages over the past years. Bill Reardon first discovered Kirtland's warblers in north-east Wisconsin in 1995, and Louis Taccolini discovered the first nest outside northern Lower Michigan in 1995. Joel Trick organized a comprehensive search for warblers beginning in 1998. E. Gustafson, S. Robinson, P. Sykes, J. Trick, and an anonymous reviewer provided helpful comments on the manuscript.

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Biographical sketches

John Probst has a primary interest in integrated wildlife research and management, especially range-wide species assessments. His other research interests include sea turtles, forest bird communities, wildlife water impoundments and barrens ecosystems.

Deahn M. Donner's research and management interests that include the effect of land management on species populations, especially herpetofauna. She has also studied freshwater turtle communities.

Carol Bocetti conducts research on Kirtland's warblers and Delmarva Fox Squirrels. Her other interests include the demographic responses of small population to habitat characteristics and changes, computer simulation of population dynamics, and landscape level conservation planning.

Steve Sjogren manages wildlife and integrated resource programmes. He has been a leader in openlands and jack pine ecosystem management for restoration or maintenance of Kirtland's warblers, sharp-tailed grouse, upland sandpipers, rare plants, and other biota.