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A Historical Perspective: Changes in Grassland Breeding Bird Densities Within Major Habitats in North Dakota Between 1967 and 1992-1993

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A HISTORICAL PERSPECTIVE: CHANGES IN GRASSLAND BREEDING BIRD DENSITIES WITHIN MAJOR HABITATS IN NORTH DAKOTA BETWEEN 1967 AND 1992-1993

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Abstract: Population declines of many grassland-nesting birds are now widely recognized. Fundamental to understanding these declines is knowing if they are caused by changes in the availability of suitable habitats or changes in the densities of birds within those habitats. We address that issue with information from systematic surveys of breeding birds throughout North Dakota in 1967, 1992, and 1993. We compared the availability of 8 major habitat types, and the densities of 24 species of grassland birds in each habitat type, for 128 randomly selected quarter-sections (64.7 ha or 160 ac) that were surveyed in each of those years. Between 1967 and 1992-1993, the area of cropland, planted cover, woody vegetation, and other habitats increased in the 128 quarter-sections, whereas the area of grassland, hayland, and wetland habitats declined. Our results are mixed concerning patterns of population change within habitats, which primarily reflect the disparate habitat requirements of individual species. Some species increased in density in 1 habitat between the 2 periods (e.g., horned lark [*Eremophila alpestris*] in grassland), whereas others declined in that same habitat (e.g., western meadowlark [*Sturnella neglecta*]). Other species (e.g., lark bunting [*Calamospiza melanocorys*]) declined in densities in 1 habitat but increased in another. Some species declined (e.g., Baird's sparrow [*Ammodramus bairdii*]) or increased (e.g., northern harrier [*Circus cyaneus*]) in 1 or more habitats but their statewide populations were stable between the 2 periods; whereas other species were relatively stable within habitats but their statewide populations increased (e.g., upland sandpiper [*Bartramia longicauda*]) or declined (e.g., Le Conte's sparrow [*Ammodramus leconteii*]). Nonetheless, our results provide evidence that populations of some species have declined on their breeding grounds in North Dakota. The disparate habitat requirements of grassland birds emphasize the importance of large-scale conservation efforts for grassland birds, especially those efforts that can provide a complex mixture of vegetation or habitat types.

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Recent analyses of data from the North American Breeding Bird Survey (BBS) revealed several striking patterns concerning grassland bird populations in North America (Droege and Sauer 1994, Knopf 1994, Peterjohn and Sauer 1999, McCracken 2005). First, most grassland bird species had negative population trends. Second, grassland birds had steeper and more consistent

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population declines at the continental level than did other avian groups. Third, these patterns were especially pronounced in the prairie regions of North America, where grassland birds are most common (Droege and Sauer 1994).

Sparked by concerns over recent population trends, considerable attention has been directed toward grassland birds and attempting to identify causes of their population declines (e.g., Herkert and Vickery 1999, Brennan and Kuvlesky 2005, McCracken 2005). Although the factors responsible for population declines of most grassland bird species are largely unknown, many hypotheses have been advanced that focus on habitat. Widespread destruction, fragmentation, and degradation of grassland habitats in North America have been severe (Knopf 1988, 1994; Samson and Knopf 1994), and are considered prominent factors contributing to historic and recent population declines of grassland birds (Vickery et al. 1999, McCracken 2005). There also is compelling evidence that loss or degradation of wetlands and managed grassland habitats (Knopf 1994, Herkert et al. 1996, Herkert 1997) and increases in woodland and shrubland habitats (Bernstein et al. 1990, Grant et al. 2004) are negatively impacting some grassland bird populations.

The North American BBS has been effective in documenting patterns of population change in grassland birds, but it does not provide comparable data on population changes within habitats (Sauer 2000, Hutto and Young 2002). Habitat often forms the foundation of conservation efforts for declining and other species. For conservation efforts to be effective, however, more information is needed on where and in what abundance a species occurs in each habitat (Hutto 1998). Although habitat-specific monitoring usually cannot identify the causes of bird population changes, it can identify areas for further evaluation (Hutto 1998). In a review of research and management needs for grassland bird conservation, Herkert and Knopf (1998) underscored the importance of data on habitat use as well as data on population changes within habitats.

One approach to understanding population changes of grassland birds within habitats is to collect recent data and contrast those with earlier data collected in a similar fashion on the same study area(s). A key component of this approach is that the historical survey provides a standard baseline measurement against which population changes can be assessed (see Igl and Johnson [2005] for a discussion of the advantages and disadvantages of this approach). Some studies (Briggs and Criswell 1978, Baird 1990) have used this approach to examine population declines in forested areas in eastern North America. Similar evaluations in grassland habitats are rare, with most focusing on a single site or habitat type or an area that has undergone succession (Herkert and Knopf 1998). For example, Bernstein et al. (1990) repeated the historic breeding bird survey of Kendeigh (1941) in a single grassland block in northwestern Iowa, where they found declines in grassland birds and increases in woodland-edge birds, which the authors attributed to successional changes (i.e., woody encroachment).

In 1967, Stewart and Kantrud (1972) conducted an extensive survey of breeding birds in North Dakota to estimate breeding bird abundances and frequencies of occurrence statewide. During that survey, Stewart and Kantrud collected but did not publish data on breeding bird populations within specific habitats. In 1992 and 1993, a quarter-century after the original survey, we (Igl and Johnson 1997, Igl et al. 1999) repeated the Stewart and Kantrud (1972) survey but did not publish data on breeding bird populations within specific habitats. The availability of these unpublished data provided a unique opportunity to evaluate not only habitat use of grassland birds during the breeding season in North Dakota, but also within-habitat changes in breeding bird densities in multiple habitats over an extensive area between the 2 periods. The objectives of this paper are (1) to identify habitats used by individual species of grassland birds in North Dakota, and (2) to evaluate changes in their densities within habitats (and statewide) between 1967 and 1992-1993.

STUDY AREA AND METHODS

Study area

The study area and methods were described in detail by Stewart and Kantrud (1972) and Igl and Johnson (1997) and are only summarized here. In 1967, Stewart and Kantrud (1972) divided North Dakota into 8 major strata based on biogeo-

graphical, physiographical, and ecological characteristics. From these 8 strata, Stewart and Kantrud (1972) randomly selected 130 quarter-sections (about 64.7 ha or 160 ac) (Fig. 1). The number of sample units (quarter-sections) allocated to each stratum was proportional to the area of the stratum. The stratification used by Stewart and Kantrud (1972) was effective in reducing the estimated variance in population estimates by as much as 15% compared with simple random sampling (Nelms et al. 1994). To facilitate a direct comparison, we (Igl and Johnson 1997, Igl et al. 1999) used the same sample units (i.e., quarter-sections) in 1992 and 1993 as were used by Stewart and Kantrud (1972) in 1967. However, we visited only 128 of the 130 quarter-sections because landowners denied access to the other 2 quarter-sections. Comparisons among years are based on the 128 quarter-sections that were surveyed in all 3 years.

Bird surveys

Surveys of breeding birds were conducted by 2 observers on foot. Each observer surveyed breeding birds on a rectangular half of a quarter-section by following a standardized survey route. This route was 100 m inside of and parallel to the boundary of the rectangle. Deviations up to 100 m from the route often were necessary to adequately survey all habitats. The rectangular halves of each quarter-section were usually surveyed simultaneously, and a distance of 400 m was maintained between observers. Both observers compared field notes at the end of covering each sample unit to prevent duplications in the counts of wide-ranging birds, such as vultures, hawks and crows. We minimized observer bias in 1992 and 1993 by using the same 2 observers in both years.

We avoided surveying during precipitation or strong winds (>24 km/hr). We conducted surveys of birds in open habitats between 0.5 hr after sunrise and 0.5 hr before sunset. Quarter-sections containing extensive woodland habitats usually were surveyed on relatively calm (<8 km/hr), sunny days between 0.5 hr after sunrise and 10:00 hr. Species were identified by sight or sound. Counts of breeding birds were based on numbers of breeding pairs recorded during peak breeding periods. For most species, nearly all pairs were observed as segregated pairs or as territorial males. The surveys of breeding birds extended from 24 April to 19 July in 1967, from 27 April to 18 July in 1992, and from 24 April to 21 July 1993. The overall absolute difference between the 1967 surveys and the 1992 and 1993 surveys averaged 3.3 days and 1.7 days, respectively. We (Igl and Johnson 1997) categorized each species into a general breeding habitat based on personal obser-

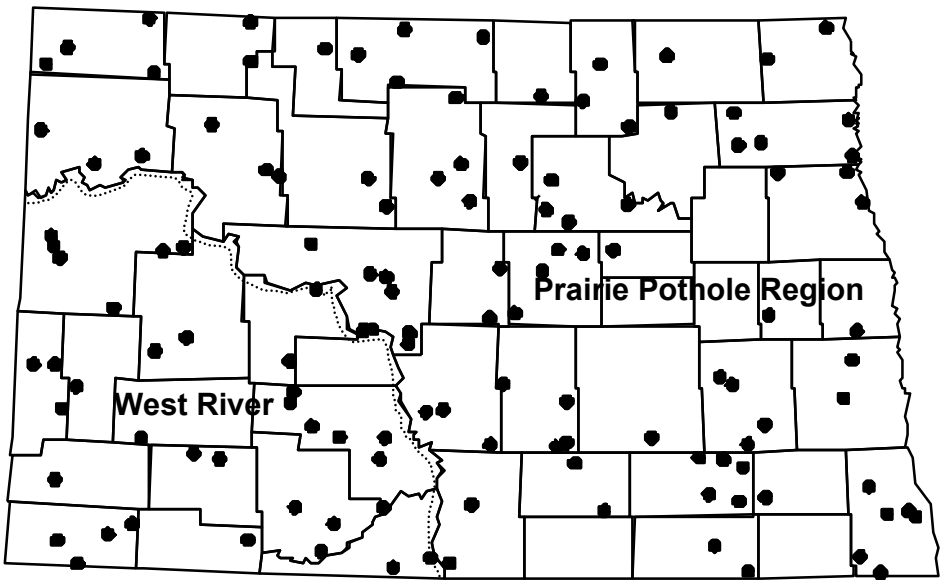

Fig. 1. Distribution of 128 legal quarter-sections in North Dakota where bird surveys were conducted during 1967 and 1992-1993. The dashed line separates the Prairie Pothole Region from the area south and west of the Missouri River (i.e., West River).

vations and the literature (Ehrlich et al. 1988, Peterjohn and Sauer 1993). Twenty-four species were classified as grassland birds.

Habitat classification

Breeding pairs were recorded within the habitats in which they occurred. Stewart and Kantrud (1972; Kantrud, unpublished data) also recorded birds by habitat, but they did not use a predetermined habitat classification system during their field work in 1967. In 1992, before entering the field, we developed a simple habitat classification system that was compatible with Stewart and Kantrud's field notes (Kantrud, unpublished data) from 1967, and that also would form a framework into which categories of more detailed land-use and -cover types could be fitted. The resulting habitat classification system used in this study was a hierarchical classification system that provided a snapshot of land use (purpose of human activity on land) and cover (vegetation and artificial constructions covering the land) at the time of bird surveys on individual quarter-sections. The more general first level was developed or modified from the Northern Prairie Wildlife Research Center Nest File Habitat Classification System (see Cowardin et al. 1988). Although our original classification system included 105 possible combinations of land-use and -cover types, we combined these land-use and -cover types into 8 primary habitats: Cropland, Grassland, Hayland, Planted Cover, Wetland, Woody Vegetation, Right-of-way, and Other Habitats (Table 1). To evaluate overall changes in these 8 habitats on the quarter-sections, we digitized land use and cover for 1967, 1992, and 1993 by drawing vectors over scaled rasters of scanned aerial photographs using Map and Image Processing System software (Micro-Images, Inc. 1992). (Use of trade names in this paper does not imply endorsement for use by the federal government or the U.S. Geological Survey.) This delineation process was facilitated by field notes and habitat mapping of each study area in 1967, 1992, and 1993.

We calculated densities (pairs/100 ha) of breeding birds by species and habitat, but only if a habitat occurred within a quarter-section in all 3 years (Table 2). For each species and habitat type, we compared the average of the 1992 and 1993 densities to the density in 1967. This was done with a paired *t* test, in which observations were weighted by the total area of that habitat type in a quarter-section. Densities within habitats were considered different between 1967 and 1992-1993

Table 1. Habitat classification used during bird surveys in North Dakota in 1967 and 1992-1993.

Habitat class	Description
Cropland	Included all land used for the production of annual field crops, land under summer fallow, and land cleared for annual field crops.
Grassland	Included mostly native grasslands, regardless of the condition of the grassland and regardless of the disturbance regime (e.g., grazed mowed, or idle). Also included grasslands planted to introduced species for improved permanent pasture.
Hayland	Included plowed areas that are seeded to alfalfa or mixtures of grasses and legumes for forage production and that are harvested annually.
Planted Cover	Included land formerly used for agricultural production but is currently idle or semi-idle under federal land retirement programs for erosion control or for wildlife cover. Vegetation often included mixtures of grasses and legumes.
Wetland	Included all areas classified as wetlands by Stewart and Kantrud (1971), including intermittent and permanent stream courses and temporary, seasonal, semipermanent, and permanent wetland basins.
Woody Vegetation	Included all native and artificially stocked tree and shrub stands.
Right-of-way	Included all areas between a road surface or railway bed and the adjacent fenceline or habitat border.
Other Habitats	Included all odd areas that could not be classified into the other habitat groups, including human-made structures and residences and unvegetated rock outcrops and clay buttes.

Table 2. Area in ha (ac) of major habitats and percentage change between 1967 and 1992-1993 (averaged) for 128 quarter-sections in North Dakota. Modified from Igl and Johnson (1997).

Habitat	1967	1992-1993	Percent change	Number of quarter-sections [a]
Cropland	3870 (9563)	4103 (10139)	+5.7	86
Grassland	2142 (5293)	2088 (5159)	-2.5	69
Hayland	458 (1132)	220 (544)	-52.2	10
Planted Cover	403 (996)	564 (1394)	+28.6	7
Wetland	736 (1819)	537 (1327)	-27.1	81
Woody Vegetation	268 (662)	320 (791)	+16.3	74
Right-of-way	173 (427)	174 (430)	0.0	105
Other Habitats	219 (541)	264 (652)	+35.5	103

[a] The number of quarter-sections that contained a particular habitat in all three years. Densities of breeding birds were compared within a quarter-section using paired *t* tests (Fig. 2), but only if a habitat was present within that quarter section in all three years.

if $P \leq 0.10$. We chose a higher *P*-value to reduce the likelihood of a type II error (i.e., failing to detect a change in density within a habitat when a change existed). A paired *t* test with small sample sizes may not have sufficient power to detect a significant departure from zero. By classifying habitats at the time of the bird survey and by using only habitats that were present in a quarter-section in all 3 years to calculate densities, we could focus on changes in bird densities in a habitat that were essentially unrelated to major successional changes or to land-use changes within a single quarter-section.

Statewide Population Trends

Elsewhere, we published statewide population estimates and frequencies of occurrence and evaluated changes in statewide breeding bird populations between 1967 and 1992-1993 (see Stewart and Kantrud 1972, Igl and Johnson 1997, Igl et al. 1999). Because statewide population changes provide different but complementary information with the changes in densities within habitats, we include statewide population changes from this study (1967 vs. 1992-1993, Igl and Johnson 1997) and the BBS in Fig. 2. We obtained trends in abundance from the BBS for North Dakota during the period, 1967-1993 (Sauer et al. 1995). BBS trends are based on statistical methods described by Geissler and Sauer (1990). In North Dakota, the BBS began in 1967, the same year that Stewart and Kantrud (1972) conducted their survey.

RESULTS AND DISCUSSION

We classified 24 species as grassland-breeding birds based on published literature (Igl and Johnson 1997; Fig. 2). These 24 species accounted for 15% of the 161 observed species and 41-51% of the statewide population estimate for breeding birds (24.1-27.4 million breeding pairs) (Igl and Johnson 1997, Igl et al. 1999). Overall, the statewide population estimate for grassland-breeding birds declined by 15.5% between 1967 (12.1 million breeding pairs) and 1992-1993 (10.2 million breeding pairs) (Igl and Johnson 1997). Grassland birds were found in all 8 habitats in all 3 years (Fig. 2). Three species were restricted to a single habitat, but most species were recorded in multiple habitats. Individual species exhibited a variety of patterns of habitat use and changes in densities within habitats between 1967 and 1992-1993. However, a more detailed overview of these patterns is essential to provide a framework for understanding population changes within habitats for individual grassland bird species in North Dakota between the 2 periods. To that end, we have combined the results and discussion portions of this paper into a single section that contains the following sub-sections: 1) Species accounts (in taxonomic order) and 2) Habitat changes in North

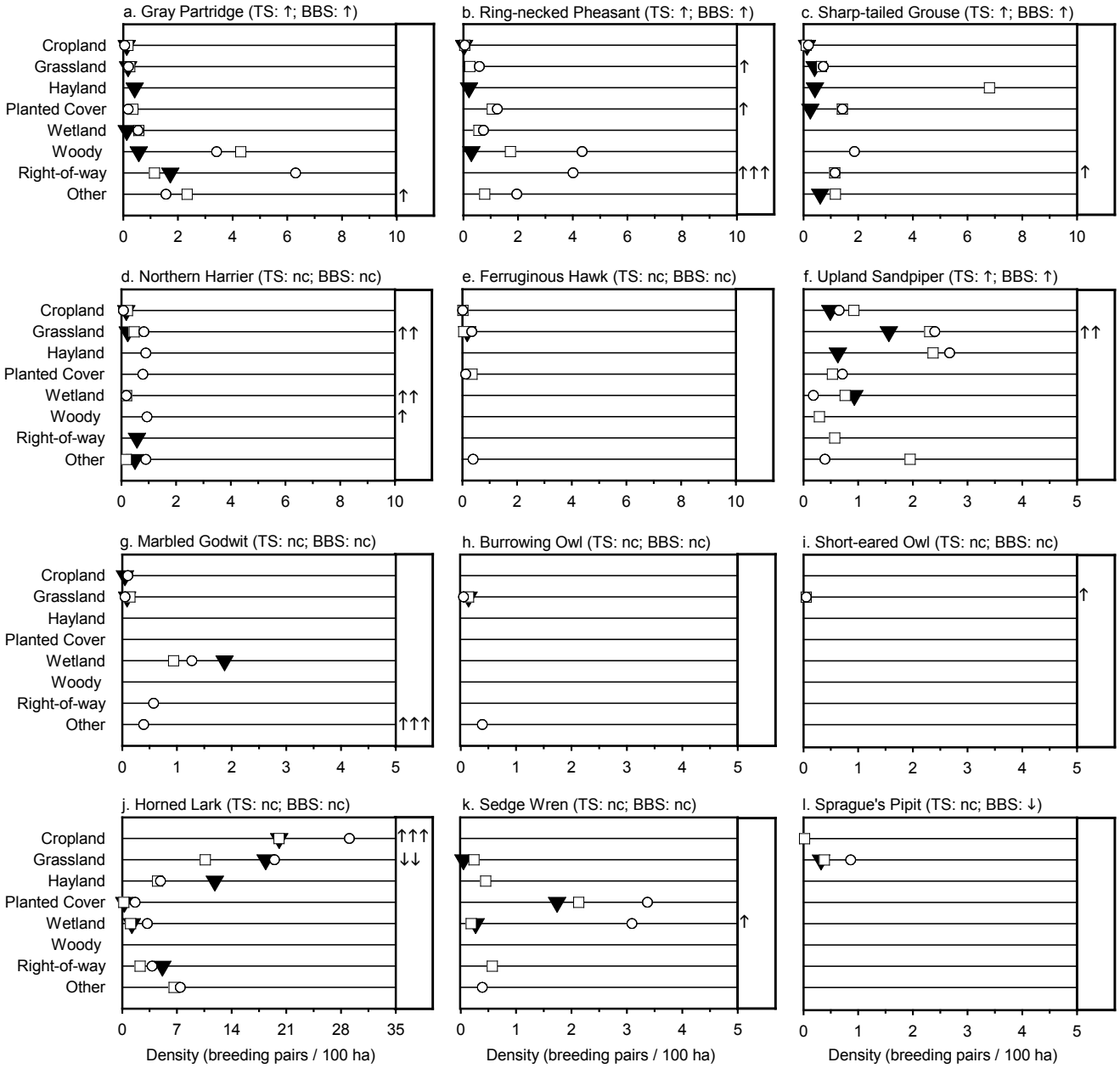

Fig. 2. Habitat associations and within habitat changes in densities of grassland birds. Statewide population trends are indicated in parentheses after the species names; a single arrow pointing up or down indicates a significant population increase or decrease, respectively, between 1967 and 1992 1993 in North Dakota in This Study (TS; Igl and Johnson 1997) or between 1967 and 1993 on the Breeding Bird Survey (BBS; Sauer et al. 1995). "Nc" indicates that there was no change in the statewide population between the 2 survey periods; "na" indicates that data were not available or were insufficient to calculate a BBS population trend for that species. Within each figure, average densities are indicated by habitat and year: a solid triangle indicates densities for 1967, an open square for 1992, and an open circle for 1993. If the species was not observed in a habitat in a given year (i.e., density equals zero), its density is not shown for that year. Changes in densities within habitats between 1967 and 1992-1993 are indicated at the right of each graph: ↓ (decreasing) at $P \leq 0.10$, ↓↓ at $P \leq 0.05$, and ↓↓↓ at $P \leq 0.01$; ↑ (increasing) at $P \leq 0.10$, ↑↑ at $P \leq 0.05$, and ↑↑↑ at $P \leq 0.01$. Non-significant changes are not shown.

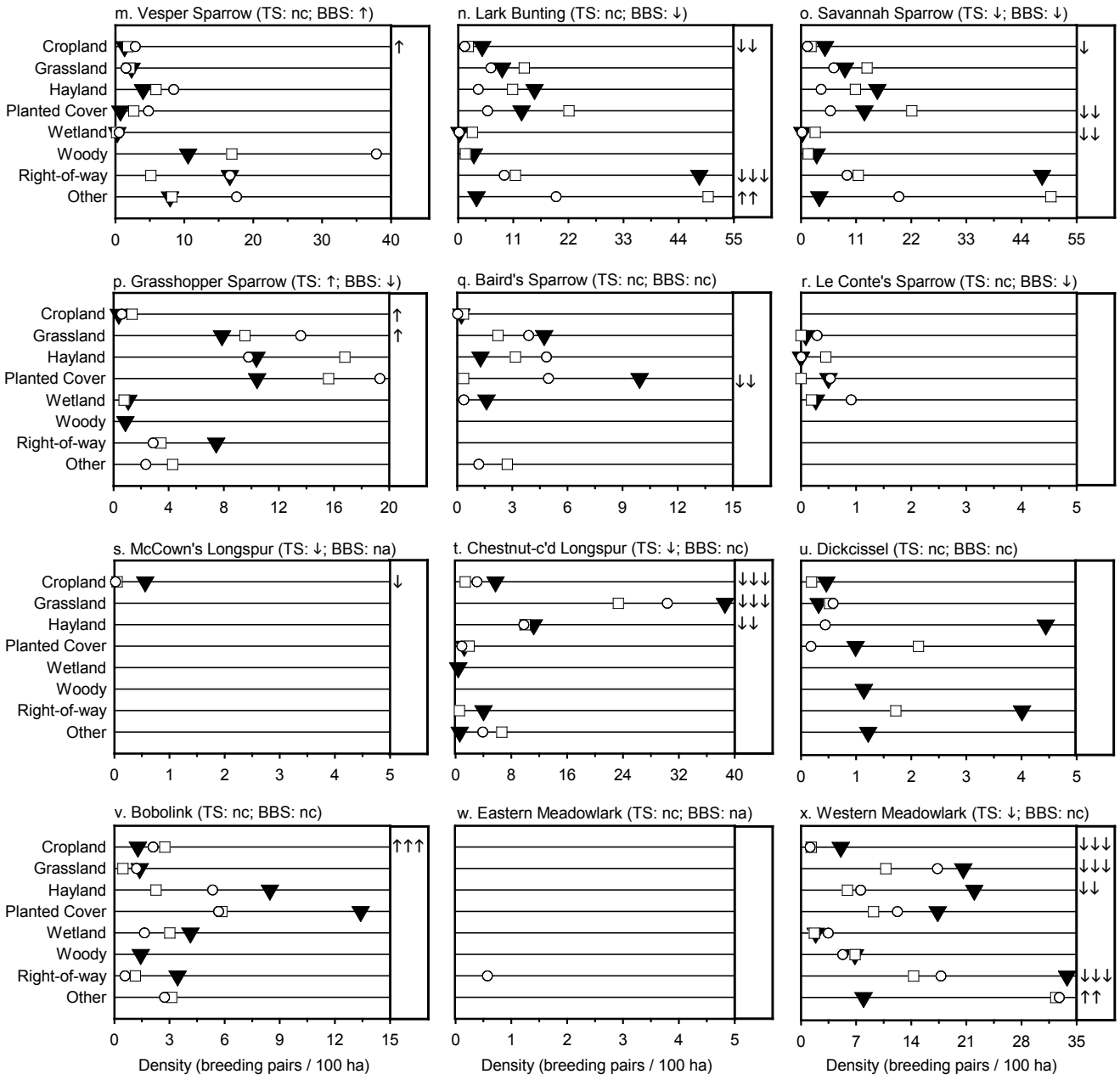

Fig. 2. (Continued)

Dakota. Population changes within habitats (Fig. 2) should be viewed in the context of habitat availability (Table 2).

Species Accounts

Gray Partridge (*Perdix perdix*).–Gray partridge occurred at low densities in all habitats, with highest densities in Woody Vegetation, Right-of-way, and Other Habitats (Fig. 2a). Partridge densities increased between 1967 and 1992-1993 in Other Habitats. Statewide partridge populations increased between 1967 and 1992-1993 in this study (Igl and Johnson 1997) and the BBS (Sauer et al. 1995). The gray partridge is native to Europe and Asia and was introduced into North America in the late 1700s (Johnson and Knue 1989). The species was first observed in North Dakota in 1923 and now occurs throughout the state. Gray partridge tend to thrive in areas of intensive agriculture as long as adequate nesting cover is available during the breeding season, and protective wooded cover and food are available

during the winter. Stewart (1975) characterized the gray partridge in North Dakota as a bird of agricultural croplands and adjoining edge habitats.

Ring-necked Pheasant (*Phasianus colchicus*).–The ring-necked pheasant occurred at low densities in all habitats in this study, with highest densities in Woody Vegetation, Right-of-way, and Other Habitats (Fig. 2b). Pheasant densities increased in Grassland, Planted Cover, and Right-of-way between the 2 survey periods. Statewide pheasant populations increased between 1967 and 1992-1993 in this study (Igl and Johnson 1997) and the BBS (Sauer et al. 1995). The ring-necked pheasant was introduced from Asia into North America in the early 1700s (Johnson and Knue 1989). In North Dakota, the first stocking of ring-necked pheasant occurred in 1910; the species is now distributed throughout the state. As with the gray partridge, pheasants flourish in areas of intensive agriculture where there is adequate nesting cover during the breeding season and protective woody cover and food during the winter. Stewart (1975) stated that pheasants typically breed in agricultural areas and adjoining edge habitats in North Dakota.

Sharp-tailed Grouse (*Tympanuchus phasianellus*).–Sharp-tailed grouse occurred in all habitats except Wetland (Fig. 2c). Densities were low in all occupied habitats, but densities increased between 1967 and 1992-1993 in Right-of-way. Sharp-tailed grouse populations in North Dakota increased between 1967 and 1992-1993 in this study (Igl and Johnson 1997) and the BBS (Sauer et al. 1995). The sharp-tailed grouse is widely distributed throughout most of North Dakota (Stewart 1975), although the species is becoming less common or rare in the eastern portion of the state, which is more intensively farmed (Johnson and Knue 1989). Sharp-tailed grouse are characteristic of mixed-grass prairie and other grasslands, especially those areas that have patches of shrubs or scattered trees or that are located near the margins of wooded areas (Stewart 1975). Though our surveys of breeding birds did not detect sharp-tailed grouse in Wetlands, these habitats often are used for cover during winter and at night during summer (Gratson 1988).

Northern Harrier (*Circus cyaneus*).–Northern harriers occurred in low densities in all 8 habitats (Fig. 2d). Although statewide populations were evaluated as being stable between 1967 and 1992-1993 in this study (Igl and Johnson 1997) and from the BBS (Sauer et al. 1995), densities within Grassland, Wetland, and Woody Vegetation increased between 1967 and 1992-1993. The northern harrier is widely distributed throughout North Dakota (Stewart 1975). Its breeding populations often fluctuate from year to year in relation to prey availability (Grant et al. 1991). The species typically breeds in open habitats, including wetlands, wet meadows, and upland grasslands, especially those dominated by tall, dense vegetation growth (Stewart 1975, Kantrud and Higgins 1992).

Ferruginous Hawk (*Buteo regalis*).–Ferruginous hawks were observed in Grassland, Cropland, Planted Cover, and Other Habitats (Fig 2e). Densities within habitats did not differ between 1967 and 1992-1993, although we found a nearly significant increase ($P = 0.105$) in Planted Cover. Ferruginous hawk populations in North Dakota were stable between 1967 and 1992-1993 in this study (Igl and Johnson 1997) and the BBS (Sauer et al. 1995). Ferruginous hawks breed throughout North Dakota, most commonly in western North Dakota, where there is generally more grassland habitat (Stewart 1975). Ferruginous hawks are closely associated with open habitats, especially native grasslands (Stewart 1975, Gilmer and Stewart 1983) and prairie dog (*Cynomys* spp.) towns (Cook et al. 2003). Other studies have found that the species tends to avoid heavily forested areas (Bechard and Schmutz 1995), cropland areas (Gaines 1985), areas near human dwellings (Gaines 1985), and areas near water sources (Bechard et al. 1990).

Upland Sandpiper (*Bartramia longicauda*).–Upland sandpipers occurred in low numbers in all habitats, with highest densities occurring in Grassland and Hayland (Fig. 2f). Densities within Grassland habitat increased between 1967 and 1992-1993. We found a nearly significant increase ($P = 0.133$) in Other Habitats. In North Dakota, upland sandpiper populations increased between

1967 and 1992-1993 in this study (Igl and Johnson 1997) and the BBS (Sauer et al. 1995). Upland sandpipers breed throughout North Dakota (Stewart 1975), especially in mixed-grass prairie and wet-meadow habitats, as well as other habitats with similar vegetation structure (Stewart 1975). Upland sandpipers often avoid areas with extensive woody vegetation (Sample 1989).

Marbled Godwit (*Limosa fedoa*).–The marbled godwit was observed in 5 of the 8 habitat types, most commonly in Wetlands (Fig. 2g). Godwit densities within Cropland, Grassland, Wetland, and Right-of-way did not differ between 1967 and 1992-1993, but densities increased in Other Habitats. Statewide populations of marbled godwits were stable between 1967 and 1992-1993 in this study (Igl and Johnson 1997) and the BBS (Sauer et al. 1995). The breeding range of the marbled godwit in North Dakota generally is restricted to the Prairie Pothole Region, which contains more wetland habitat. Marbled godwits use short, sparsely to moderately vegetated grassland areas in uplands for nesting and foraging, and wetlands for foraging (Stewart 1975, Ryan et al. 1984). The species generally avoids areas that are intensively cultivated, and godwits show less preference for hay fields and idle grasslands with non-native vegetation (Ryan et al. 1984).

Burrowing Owl (*Athene cunicularia*).–Burrowing owls occurred at low densities and in only 2 habitats, Grassland and Other Habitats (Fig. 2h). Densities within these habitats did not differ between the 2 periods. Because of the species' clumped or semi-colonial distribution, this species may not be well represented by our survey methodology (Igl et al. 1999) or that of the BBS (Robbins et al. 1986). Burrowing owl populations in North Dakota were stable between 1967 and 1992-1993 in this study (Igl and Johnson 1997) and the BBS (Sauer et al. 1995). The burrowing owl was among the breeding birds typical of the mixed-grass prairie of North Dakota before settlement (Murphy et al. 2001). The species once nested throughout the state, but its range has contracted westward in recent decades; burrowing owls are now uncommon or absent in the eastern half of North Dakota. In its current breeding range, the species is found most often in association with colonial burrowing mammals (e.g., black-tailed prairie dogs [*Cynomys ludovicianus*], Richardson's ground squirrel [*Spermophilus richarsoni*]) (Stewart 1975).

Short-eared Owl (*Asio flammeus*).–The short-eared owl was observed only during 1992 and 1993 and only in Grassland, where they increased in density between 1967 and 1992-1993 (Fig. 2i). Populations of short-eared owls were stable in North Dakota between the 2 census periods in this study (Igl and Johnson 1997) and the BBS (Sauer et al. 1995). Short-eared owls breed throughout North Dakota, but breeding populations often fluctuate annually in relation to prey availability (Stewart 1975). The species occurs in open areas, especially large expanses of grassland, but also including wet-meadow zones of wetlands.

Horned Lark (*Eremophila alpestris*).–Horned larks were observed in 7 of the 8 habitats in this study, with highest densities occurring in Cropland followed by Grassland and Hayland (Fig. 2j). This species was not observed in Woody Vegetation. Horned lark densities increased in Cropland but declined in Grassland between 1967 and 1992-1993. We found a nearly significant decline in Hayland ($P = 0.130$). Statewide, horned lark populations were stable between 1967 and 1992-1993 in this study (Igl and Johnson 1997) and the BBS (Sauer et al. 1995). Horned larks are found throughout North Dakota (Stewart 1975) and occurred on 85% or more of our study sites each year (Igl and Johnson 1997). Horned larks are characteristic of open areas with sparse or short herbaceous vegetation, such as cropland and heavily grazed grassland (Stewart 1975). The species tends to avoid areas with extensive woody vegetation, although it will tolerate the presence of some woody cover (Sample 1989).

Sedge Wren (*Cistothorus platensis*).–Sedge wrens were observed in 6 of the 8 habitats, most commonly Wetland and Planted Cover (Fig 2k). The species increased in density between 1967 and 1992-1993 in Wetland. There was no change in sedge wren population abundance in North Dakota between 1967 and 1992-1993 in this study (Igl and

Johnson 1997) or the BBS (Sauer et al. 1995). However, sedge wrens often exhibit erratic intra-seasonal movements during the breeding season (Bedell 1996), which may confound population trend estimates (Peterjohn and Sauer 1999). In North Dakota, sedge wrens occur primarily in the Prairie Pothole Region (Stewart 1975). The species is most characteristic of upland or mesic habitats with tall, dense herbaceous vegetation, including wetland margins and retired cropland fields (Stewart 1975, Sample 1989). Sedge wrens tend to avoid cropland (Johnson and Igl 1995) and dense stands of woody vegetation (Sample 1989).

Sprague's Pipit (*Anthus spragueii*).–Sprague's pipits occurred at low densities in 2 habitats, Cropland and Grassland (Fig. 2l). Although statewide populations of Sprague's pipits did not change between 1967 and 1992-1993 in this study (Igl and Johnson 1997), the BBS detected a population decline for this species for the same interval (Sauer et al. 1995). Sprague's pipits breed primarily in the western two-thirds of North Dakota, especially in areas with extensive grassland habitat. The species is associated closely with idle or lightly grazed native mixed-grass prairie but occasionally will breed in non-native grasslands and cropland (Stewart 1975, Sutter and Brigham 1998, Davis and Duncan 1999). This species usually avoids hay fields (Owens and Myres 1973, Davis et al. 1999) and areas with extensive woody vegetation (Madden 1996).

Vesper Sparrow (*Pooecetes gramineus*).--Vesper sparrows occurred in all 8 habitats in this study, with highest densities occurring in Woody Vegetation, Right-of-way, and Other Habitats and lowest densities occurring in Wetland (Fig. 2m). Vesper Sparrow densities increased in Cropland between the survey periods. Between 1967 and 1992-1993, vesper sparrow populations in North Dakota were stable in this study (Igl and Johnson 1997) but increased on the BBS (Sauer et al. 1995). Vesper sparrows are distributed widely throughout North Dakota (Stewart 1975) and were present on about 50% of the study sites in each year of this study (Igl and Johnson 1997). The species is most characteristic of field and prairie edge habitats that adjoin open grasslands or cropland (Stewart 1975, Sutter et al. 2000); vesper sparrows generally avoid wetland habitats (Sample 1989).

Lark Bunting (*Calamospiza melanocorys*).–Lark buntings were recorded in all 8 habitats during this study, with highest densities occurring in Right-of-way, Other Habitats, Planted Cover, Hayland, and Grassland (Fig. 2n). Between 1967 and 1992-1993, lark bunting densities declined in Cropland and Right-of-way and increased in Other Habitats. In North Dakota, lark bunting populations were stable between 1967 and 1992-1993 in this study (Igl and Johnson 1997) but declined on the BBS during the same period (Sauer et al. 1995). As with the dickcissel, the lark bunting's distribution and abundance fluctuate dramatically within the state from year to year (Hibbard 1965), apparently in response to precipitation patterns and habitat conditions elsewhere in its breeding range (Tout 1902). Peterjohn and Sauer (1999) suggested that nomadic movements of the lark bunting may obscure this species' long-term trends. North Dakota is on the eastern edge of the species' range. Although the lark bunting has been observed throughout North Dakota, it is most common in the western two-thirds of the state, especially the West River area (Fig. 1) (Stewart 1975).

Savannah Sparrow (*Passerculus sandwichensis*).–Savannah sparrows were found in all 8 habitats, occurring at highest densities in Hayland, Planted Cover, and Wetland habitats, and at lowest densities in Cropland and Woody Vegetation (Fig. 2o). Savannah sparrow densities declined in Cropland, Planted Cover, and Wetland habitats. We found a nearly significant increase in Woody Vegetation ($P = 0.125$) and a nearly significant decline in Right-of-way ($P = 0.130$) between 1967 and 1992-1993. Both the BBS and our study indicated that Savannah sparrow populations declined in North Dakota between 1967 and 1992-1993 (Sauer et al. 1995, Igl and Johnson 1997). During the breeding season, Savannah sparrows are distributed throughout North Dakota, most commonly in the Prairie Pothole Region. The species occupies a variety of upland and mesic habitats, including wetland margins, grasslands, and agricultural fields (Stewart 1975). Savannah

sparrows tend to avoid areas with extensive tree cover (Wiens 1969, Sample 1989) and may show an aversion to cultivated areas (Wiens 1969).

Grasshopper Sparrow (*Ammodramus savannarum*).–In this study, grasshopper sparrows occurred in all habitats, most notably Grassland, Hayland, and Planted Cover (Fig. 2p). Between 1967 and 1992-1993, grasshopper sparrow densities increased in Cropland and Grassland. We found a nearly significant increase in Other Habitats (P = 0.110) and a nearly significant decline in Right-of-way (P = 0.131). Statewide populations of the grasshopper sparrow increased in this study (Igl and Johnson 1997) but declined on the BBS (Sauer et al. 1995). The grasshopper sparrow was the only species that exhibited a population change in this study opposite from that of the BBS between 1967 and 1992-1993. Grasshopper sparrows breed throughout North Dakota (Stewart 1975). This species generally prefers moderately open grasslands with some patchy bare ground interspersed among clumps of vegetation (Sample 1989, Vickery 1996). Grasshopper sparrow densities are generally higher in areas with a low coverage of woody vegetation (Arnold and Higgins 1986); the species is known to avoid edges (Wiens 1969, Delisle and Savidge 1996, Helzer 1996). Although the species typically breeds in xeric sites (Sample 1989), grasshopper sparrows use drier, sparser sites in lush, tall grasslands and thicker, brushier sites with short, sparse vegetation in arid regions (Vickery 1996). As with other *Ammodramus* sparrows, grasshopper sparrows are sensitive to precipitation and moisture conditions (Wiens 1974).

Baird's Sparrow (*Ammodramus bairdii*).–Baird's sparrows were found in 6 of the 8 habitats in this study, with highest densities occurring in Grassland, Hayland, and Planted Cover (Fig. 2q). Densities of Baird's Sparrows declined in Planted Cover between 1967 and 1992-1993. We found a nearly significant decline (P = 0.114) in Grassland. Baird's sparrow populations in North Dakota were stable between 1967 and 1992-1993 in this study (Igl and Johnson 1997) and the BBS (Sauer et al. 1995). Like the Sprague's pipit, the Baird's sparrow breeds primarily in the western two-thirds of North Dakota, especially in areas with extensive grassland habitat (Stewart 1975). During the breeding season, Baird's sparrows frequent idle or lightly to moderately grazed grasslands, especially native grasslands (Stewart 1975, but see Davis et al. 1999 and Davis and Duncan 1999). Baird's sparrows tend to avoid areas that have been intensively grazed (Stewart 1975), contain extensive woody vegetation (Madden 1996, Arnold and Higgins 1986), or occur near roads (Davis et al. 1996, Sutter et al. 2000). In more arid regions, the species may use taller grasslands bordering wetlands (Peterjohn and Sauer 1999). The species is relatively intolerant of cultivation (Owens and Myres 1973) but will nest in weedy fields (Stewart 1975). The Baird's sparrow is generally more common in northern portions of its breeding range when areas in the southern portions of its range are experiencing drought, and is less common in the north when areas in the southern portion of its range are experiencing wet conditions (Kantrud and Faanes 1979).

Le Conte's Sparrow (*Ammodramus leconteii*).–This species was observed in 4 of the 8 habitats, including Grassland, Hayland, Planted Cover, and Wetland (Fig. 2r). Densities in all habitats were low and did not differ between the 2 survey periods. Le Conte's sparrow populations in North Dakota were stable between 1967 and 1992-1993 in this study (Igl and Johnson 1997) but declined on the BBS during the same interval (Sauer et al. 1995). In North Dakota, Le Conte's sparrows breed primarily in the Prairie Pothole Region (Stewart 1975). During the breeding season, this species generally prefers moister grassland habitats than either Baird's or grasshopper sparrows (Igl and Johnson 1995, 1999). Le Conte's sparrows show an affinity for tall, dense vegetation in wet meadows and wetland margins, as well as similar vegetation structure in upland habitats (e.g., native prairie, pasture, hayland, and retired cropland). The species generally avoids most areas with woody vegetation (Madden 1996).

McCown's Longspur (*Calcarius mccownii*).–The McCown's longspur was observed only in Cropland, where densities declined between 1967 and 1992-1993 (Fig. 2s). McCown's longspur

populations in North Dakota declined between 1967 and 1992-1993 in this study (Igl and Johnson 1997) but did not change on the BBS (Sauer et al. 1995). McCown's longspurs historically bred in the western half of North Dakota, but the species experienced a dramatic range contraction in the state between 1905 and 1930 (Stewart 1975). Since that period, the species' range has continued to contract, and the species is now restricted to a few counties on the western edge of the state. McCown's longspurs breed in open, xeric habitats with sparse vegetation, including shortgrass prairie or structurally similar habitats, such as intensively grazed mixed-grass prairie (Stewart 1975, With 1994). The species occasionally will nest in agricultural areas, including small-grain stubble fields and newly cultivated areas (Stewart 1975).

Chestnut-collared Longspur (*Calcarius ornatus*).–Chestnut-collared longspurs were observed in 7 of the 8 habitats in this study, with higher densities in Grassland than in the other 6 habitats (Fig. 2t). This species avoided Woody Vegetation in all years. Between 1967 and 1992-1993, chestnut-collared longspur densities declined in Cropland, Grassland, and Hayland habitats. We also found a nearly significant decline ($P = 0.108$) in Right-of-way. Chestnut-collared longspur populations declined in North Dakota between 1967 and 1992-1993 in this study (Igl and Johnson 1997) but did not change on the BBS (Sauer et al. 1995). Chestnut-collared longspurs breed throughout North Dakota, but largely in the western two-thirds of the state (Stewart 1975). The species breeds in arid, short- to mixed-grass prairie that has been recently grazed or mowed (Owens and Myres 1973). The species also nests in pastures with introduced grasses, but generally prefers native grasslands (Davis et al. 1999, Davis and Duncan 1999), where it has been shown to have higher reproductive success (Lloyd and Martin 2005). As with the McCown's longspur, chestnut-collared longspurs will nest in agricultural areas, including small-grain stubble fields and newly cultivated areas with early plant growth (Stewart 1975), but generally avoids areas near roads (Sutter et al. 2000), areas with extensive coverage of woody vegetation (Arnold and Higgins 1986), and areas with tall, dense vegetation (e.g., Conservation Reserve Program fields; Johnson and Igl 1995).

Dickcissel (*Spiza americana*).–Dickcissels occurred at relatively low densities in 7 of the 8 habitats in this study (Fig. 2u). This species did not occur in Wetland habitat. Highest densities were recorded in Hayland, Planted Cover, and Right-of-way. Densities within habitats did not differ between the 2 survey periods. Statewide, dickcissel populations were stable between 1967 and 1992-1993 in this study (Igl and Johnson 1997) and the BBS (Sauer et al. 1995). Dickcissels have been observed throughout much of North Dakota (Stewart 1975), however, the species' breeding distribution and abundance within the state fluctuate erratically from year to year, apparently in response to habitat suitability and precipitation patterns in the southern portion of its breeding range (Roth 1979). North Dakota is on the northern edge of the species' breeding range, and the species is only locally common in most years (Stewart 1975). The species tends to prefer upland habitats with moderate to tall, dense vegetation, often with a forb or low-shrub component (Zimmerman 1971, Sample 1989).

Bobolink (*Dolichonyx oryzivorus*).–In this study, bobolinks occurred in all habitats, with the highest densities occurring in Grassland and Hayland (Fig. 2v). Bobolink densities increased in Cropland between the 2 survey periods. There was no change in bobolink populations in North Dakota between 1967 and 1992-1993 in this study (Igl and Johnson 1997) or the BBS (Sauer et al. 1995). Bobolinks breed throughout North Dakota, but most commonly in the eastern half of the state (Stewart 1975). Historically, bobolinks nested in tall- and mixed-grass prairie as well as wet-meadow zones of wetlands, but they now commonly occur in managed grasslands, such as hayland, retired cropland, and other fields composed of a mixture of grasses and broad-leaved forbs (Stewart 1975, Sample 1989). The species also will nest in annual cropland with well-developed vegetation growth (Stewart 1975). Bobolinks usually avoid areas with woody vegeta-

tion and, to a lesser extent, roads (Sample 1989, Helzer 1996, Fletcher and Koford 2003, Bollinger and Gavin 2004).

Eastern Meadowlark (*Sturnella magna*).–We observed an eastern meadowlark only once in 1993 in a road Right-of-way (Fig. 2w). The eastern meadowlark breeds in adjacent Minnesota (Janssen 1987), but is not a confirmed breeding species in North Dakota. The species has been recorded sporadically in North Dakota during the breeding season (Svingen and Martin 2003). Within its typical breeding range, the species often occurs in areas with some woody vegetation (Sample 1989), but it generally avoids areas with extensive woody cover (Sample 1989, Lanyon 1995). In areas of sympatry with western meadowlarks (*Sturnella neglecta*), eastern meadowlarks usually select more poorly drained grasslands of moist lowland areas.

Western Meadowlark (*Sturnella neglecta*).–Western meadowlarks were observed in all 8 habitats in this study; lowest densities occurred in Cropland, Wetland, and Woody Vegetation (Fig. 2x). Between 1967 and 1992-1993, western meadowlark densities increased in Other Habitats but declined in Cropland, Grassland, Hayland, and Right-of-way. Western meadowlark populations in North Dakota declined between 1967 and 1992-1993 in this study (Igl and Johnson 1997), but populations did not change according to the BBS (Sauer et al. 1995). The western meadowlark is a common breeding bird throughout North Dakota (Stewart 1975) and occurred on 77-95% of the study sites in this study (Igl and Johnson 1997). Western meadowlarks inhabit a variety of open habitats including native grasslands, pastures, hay and alfalfa (*Medicago sativa*) fields, cultivated fields, and weedy borders of croplands, roadsides, orchards, and other open areas (Stewart 1975, Sample 1989, Lanyon 1994). The species tends to avoid areas with extensive woody vegetation (Sample 1989). Rotenberry and Knick (1995) and Sutter et al. (2000) found that western meadowlark abundance was higher near roads than away from roads, which they attributed to this species' use of fences as song perches.

Habitat Changes in North Dakota

The landscape of North Dakota has changed greatly since the westward settlement of the United States by Europeans and other immigrants. Klopatek et al. (1979) estimated that less than 30% of North Dakota's land area remained in natural or semi-natural vegetation in 1967, when Stewart and Kantrud (1972) conducted their bird survey. In particular, the once extensive mixed-grass prairie in North Dakota has been reduced to less than 30% of its original area (Samson and Knopf 1994) and has been converted largely to cropland (Klopatek et al. 1979). Although loss of native grassland to cultivation is widely believed to be responsible for the widespread and consistent declines in grassland bird populations from the mid-1960s to the 1990s (e.g., Vickery et al. 1999), our data indicate only small changes in areas of Grassland (-2%) and Cropland (+3%) between 1967 and 1992-1993 (Table 2). These relatively small changes emphasize that most of the conversion of grassland in North Dakota (and elsewhere in the midcontinent [Maizel et al. 1998]) occurred before the initiation of large-scale, systematic, monitoring programs (e.g., North American BBS in 1967) for breeding birds. Nonetheless, given the amount of Cropland in our study areas (about 50%; Table 2) and North Dakota as a whole (62%, U.S. Department of Commerce 1994), any loss in grassland habitat to cropland should not be trivialized. Moreover, present-day cropland in the northern Great Plains is more intensively managed than in the past (e.g., Bethke and Nudds 1995). Browder (1998) found that most grassland birds were negatively associated with cropland in North Dakota. Most of the 24 species in our study occurred at higher densities in grassland than in cropland, providing perspicuous evidence that as grasslands were cleared for agriculture, populations of many grassland species declined. Moreover, as the area of grassland has declined, remaining tracts of grassland likely have become smaller or more isolated. Several studies (Herkert 1994, Vickery et al. 1994, Johnson and Igl 2001) have found that many species of grassland birds are area-sensitive, requiring far larger areas of contiguous grassland habitat than their territory sizes would suggest.

Hayland declined in area by 52% in our study areas between the 2 survey periods (Table 2). This decline in area is nearly double that reported for all of North Dakota (27%) between 1964 and 1992 (U.S. Department of Commerce 1994), but is consistent with declines in hayland in other portions of the midcontinent (Herkert et al. 1996, Herkert 1997). Herkert et al. (1996) suggested that loss of secondary managed grasslands, such as hayland and improved permanent pasture, may have contributed to grassland bird declines in the midcontinent. In recent years, earlier and more frequent mowing has reduced the suitability of hayland as nesting habitat for grassland breeding birds (Bollinger et al. 1990, Frawley and Best 1991). Seventeen of the 24 (71%) species in this study used Hayland (Fig. 2).

Planted Cover increased in area by 28% between 1967 and 1992-1993 (Table 2), which reflected smaller areas of cropland retired under the Cropland Adjustment Program (CAP) of the 1965 Farm Bill than the Conservation Reserve Program (CRP) of the 1985 Farm Bill. Johnson and Igl (1995) and others (e.g., Reynolds et al. 1994) have suggested that long-term, cropland retirement programs, such as the CRP, may provide a vehicle to reverse population declines of some grassland birds (e.g., lark bunting, grasshopper sparrow), especially those that prefer tall, dense herbaceous vegetation. Vegetation composition likely was similar between CAP fields in 1967 and CRP fields in 1992-1993. However, vegetation cover was probably recently planted or poorly established at the time Stewart and Kantrud surveyed CAP fields in 1967 compared to the older and more established CRP fields surveyed in 1992-1993. Thus, the changes in bird densities between 1967 and 1992-1993 might reflect transient (i.e., early development, plant establishment) effects. In this study, 18 of the 24 (75%) grassland species were recorded in Planted Cover.

The total area of Wetlands in our study areas declined 27% between 1967 and 1992-1993 (Table 2). Since settlement, North Dakota has lost an estimated 49% of its original wetland basin area, primarily as a result of agricultural conversion (Dahl 1990). Although some grassland species tend to avoid wetlands (e.g., vesper sparrow: this study, Sample 1989), many grassland birds frequently use the wet-meadow zone or the periphery of wetlands during the breeding season (Herkert et al. 1996). Wetlands also may be important breeding habitat for some grassland species in arid regions (Peterjohn and Sauer 1999) or during dry periods (Hubbard 1982). Use of wetlands by some grassland birds likely reflects similarity in grassland-like vegetation structure that occurs in both wetlands and grasslands (Igl and Johnson 1999). Fourteen of the 24 (58%) species in this study used Wetlands (Fig. 2).

Although the extent of Woody Vegetation in our study areas was relatively small compared to some other habitats, Woody Vegetation increased 16% between 1967 and 1992-1993 (Table 2). Grassland species vary in their use, tolerance, and avoidance of woody vegetation: some species use it as nest substrate (e.g., dickcissel), some species use it for song perches (e.g., vesper sparrow), some use it for cover (e.g., ring-necked pheasant), some tolerate small to moderate amounts of it (e.g., Savannah sparrow), and others avoid it altogether (e.g., Le Conte's sparrow). In this study, only half of the 24 species used Woody Vegetation, and one-quarter of these species were observed in this habitat in only 1 of the 3 years. Obviously, species that are intolerant of woody vegetation would be affected adversely by an increase in woody vegetation. Most of the 24 species that exhibited population declines in this study or the BBS tend to avoid areas with extensive coverage of woody vegetation (Fig. 2). Grant et al. (2004) found that the probability of occurrence decreased markedly for 11 of 15 grassland bird species as the percentage of woodland, tall shrub, or brush cover increased in the landscape in north-central North Dakota. An increase in woody vegetation also may influence productivity of grassland birds breeding in adjacent habitats. Winter et al. (2000) found that grassland bird nests near woody vegetation had lower nest success than those farther from woody vegetation. Bollinger and Gavin (2004) similarly found that nest success in Bobolinks was lower near woody edges and that the species avoided nesting near woody edges

The area of Right-of-way was relatively small in this study and changed little between 1967 and 1992-1993 (Table 2). A few grassland species (e.g., Baird's sparrow, bobolink) are known to

avoid areas near roadways (Sutter et al. 2000, Bollinger and Gavin 2004). Seventeen of the 24 (71%) grassland species used this habitat during the breeding season.

Other Habitats increased in area by 35% between 1967 and 1992-1993 (Table 2). About 30% of Other Habitats consisted of unvegetated portions of clay buttes and rock outcroppings, and the remaining area consisted largely of human structures and residences. Nineteen of the 24 species in this study used Other Habitats. Browder (1998) found that no grassland birds were positively associated with Other Habitats in North Dakota.

MANAGEMENT IMPLICATIONS

The primary objective of most long-term monitoring efforts is to detect changes in bird populations over time. Historical surveys have played an important role in evaluating changes in bird population in North America (reviewed in Igl and Johnson [2005]). One caveat to repeating historical surveys is that the data cover only 2 or more points in time during a long period, whereas bird populations show tremendous short-term variability. We address these concerns elsewhere (Igl and Johnson 2005), but it is important to remember that all methods of sampling bird populations have shortcomings and constraints and that historical surveys are constrained by the study design and methodology of the original survey. Moreover, repeating historical surveys should be viewed as a supplement to, rather than a substitute for, long-term, large-scale surveys, such as the North American Breeding Bird Survey (Igl and Johnson 2005). Some species (e.g., marbled godwit) or regions (e.g., midcontinent) are poorly sampled by long-term monitoring efforts, and very little historical information exists on large-scale changes of breeding bird populations in North America beyond that provided by the BBS (Peterjohn et al. 1995). Thus, historical surveys can provide a valuable source of baseline data on breeding bird populations in such areas. Indeed, the comparable population changes from this study and the BBS provided corroborating evidence of declining grassland bird populations and strengthened the assessment of population trends from the BBS.

We found grassland birds in all 8 habitats, including woody vegetation. Given the disparate habitat requirements of each grassland bird species, there appears to be no consistent pattern of population change for all grassland bird species. In this study, some species (e.g., Sprague's pipit) were restricted primarily to 1 habitat, whereas others (e.g., Savannah sparrow) were more generalized in their habitat selection. Some species increased in density in 1 habitat between 1967 and 1992-1993 (e.g., horned lark in grassland), whereas others declined in that same habitat (e.g., western meadowlark). Other species (e.g., lark bunting) declined in densities in 1 habitat but increased in another. Some species declined (e.g., Baird's sparrow) or increased (e.g., northern harrier) in 1 or more habitats but their statewide populations were stable between the 2 periods; whereas other species were relatively stable within habitats but their statewide populations increased (e.g., upland sandpiper) or declined (e.g., Le Conte's sparrow).

We did not find strong evidence of a widespread decline in grassland bird densities within a specific habitat (Fig. 2), although overall statewide populations of grassland birds declined by 15.5% between 1967 and 1992-1993. Certainly, loss or changes in the areal coverage of grassland habitat has influenced grassland breeding bird populations in the past and present, but changes in areal coverage of the 8 habitats cannot explain all of the changes in grassland bird densities in specific habitats, especially in the 2 recent years. Nonetheless, our results provide strong evidence that populations of some species declined on their breeding grounds in North Dakota between 1967 and 1992-1993. For example, lark bunting, Savannah sparrow, chestnut-collared longspur, and western meadowlark showed statewide population declines on the BBS and/or in this study between 1967 and 1992-1993 (Fig. 2). All 4 species also exhibited significant declines in densities in multiple habitats between the 2 survey periods, which indicates that populations of these species might be influenced by factor(s) beyond the local scale or specific habitats.

Determining the factor(s) that influenced the observed changes in grassland bird densities within specific habitats is complicated. The absence of information on habitat quality among years makes

it difficult to evaluate the effects of changes within habitats on grassland bird densities between the 2 periods. It is tempting to assume that all changes in grassland bird densities in a particular habitat resulted from factors occurring within that particular habitat. It is unlikely, however, that there is a single cause for all of the patterns of density changes observed within habitats in this study, even for a single species. Graber and Graber (1963) argued that it was a mistake to assume that all species showing population changes were responding to the same factors. To that end, grassland bird populations are influenced by numerous factors during the breeding, wintering, and migration seasons (Igl and Ballard 1999). Among other factors, these include destruction, degradation, and fragmentation of grassland habitats; intensification of agricultural practices; exposure to pesticides; earlier and more frequent mowing of hayfields; reforestation of farmland and encroachment of woody vegetation; and short- and long-term changes in climate (e.g., Brennan and Kuvlesky 2005, McCracken 2005).

In some cases, the factor(s) that were responsible for the increase in a species' density in a particular habitat might have been the same factor(s) responsible for the decline of another species within that same habitat. For example, horned larks and vesper sparrows likely have benefited from the intensification of agricultural practices in the northern Great Plains in recent years, whereas Savannah sparrows and western meadowlarks likely have been negatively impacted by those same practices (Fig. 2). In other cases, the factor(s) that are responsible for the changes in a species' density in 1 habitat may be unrelated to the conditions or changes within that same habitat. For example, grassland bird populations in 1 habitat in North Dakota might be regulated or influenced by factors occurring elsewhere (e.g., dickcissel and lark bunting, see above). Grassland birds exhibit behavioral flexibility and opportunism in their habitat selection on the breeding grounds. They tend to disperse over longer distances and seem to be more capable of responding to sudden changes in distribution and quality of their habitat than species breeding in more stable habitats, such as woodlands. Grassland bird populations can be extremely variable from year to year; some species may be rare or absent in 1 year and then abundant in the following year (e.g., Le Conte's sparrow: Igl and Johnson 1995, 1999). Numerous studies have documented dramatic shifts in grassland bird distribution and abundance (Wiens 1974; Cody 1985; Johnson and Grier 1988; Igl and Johnson 1995, 1999).

McCracken (2005) argued that there appears to be no single management approach or conservation solution that will benefit the entire suite of grassland bird species. Each grassland species has distinct habitat requirements, which emphasizes the importance of large-scale conservation efforts (e.g., Conservation Reserve Program) for grassland birds that can provide a complex mixture of vegetation or habitat types and disturbances (fire, grazing, etc.). Moreover, directing conservation strategies at the local level or within a specific habitat may have limited success if grassland bird populations within a habitat are limited or influenced by events occurring beyond the local scale or within another habitat (Donovan et al. 1996).

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