BREEDING AND NATAL DISPERSAL IN THE LOGGERHEAD SHRIKE

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Abstract.—Breeding and natal dispersal of Loggerhead Shrikes in southeastern Alberta (n = 27) and southwestern Manitoba (n = 73) were analyzed for differences due to sex and age. Return rates in the year following banding were 3 of 249 (1.2%) and 27 of 3716 (0.85%) for juveniles and 31 of 96 (32%) and 22 of 140 (16%) for adults in southeastern Alberta from 1992–1993 and southwestern Manitoba from 1987–1994, respectively. Adult males returned more frequently than females. Both study areas experienced high re-occupation of previous year's territories, largely by new adults. Breeding success was not a significant predictor of return. Differences in distance moved between encounters for adults versus nestlings was significant for intervals of 1 yr and ≥ 1 yr in both study areas. Juveniles and adults dispersed a mean distance of 14.7 km and 2.7 km from previous encounter sites, respectively. Ninety-five percent of returning adults can be expected to be within 4.7 km of their previous year's nest site. Our results provide insights into assumptions incorporated in models of Loggerhead Shrike population dynamics. To take advantage of relatively low breeding dispersal we recommend that re-introductions be attempted with birds >1-yr old for which breeding has been facilitated in the release area.

ANIDAJE Y DISPERSIÓN NATAL EN LANIUS LUDOVICIANUS

Sinopsis.—La reproducción y dispersión natal de Lanius ludovicianus en el sur de Alberta (n = 27) y al sur de Manitoba (n = 73) se analizaron para hallar diferencias asociadas al sexo y a la edad. Las tasas de retorno en el año posterior al anillamiento fueron de 3 en 249 (1.2%) y de 27 en 3716 (0.85%) para los juveniles y de 31 en 96 (32%) y de 22 en 140 (16%) para adultos al sur de Alberta entre 1992 y 1993 y al sur de Manitoba entre 1987 y 1994 respectivamente. Los machos adultos retornaron más frecuentemente que las hembras. Ambas áreas de estudio experimentaron una alta reocupación de los territorios del año previo, mayomente por nuevos adultos. El éxito reproductivo no predijo significativamente los retornos. Diferencias en la distancia movida entre encuentros en los adultos contra los pichones fué significativa en intervalos de 1 año y ≥ 1 año en ambas áreas de estudio. Los juveniles y los adultos se dispersaron una distancia promedio de 14.7 km y de 2.7 km de los lugares de encuentro, respectivamente. Puede esperarse que un 95% de los adultos retornando se hallen a 4.7 km o menos del lugar de anidaje del año previo. Nuestros resultados aclaran aseveraciones incorporadas en modelos de dinamica poblacional de Lanius ludovicianus. Para aprovechar una dispersión reproductiva sumamente baja, recomendamos que las reintroducciones se intenten con aves mayores de 1 año de edad para las cuales la reproducción se ha facilitado en el área de liberación.

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Colonization of new breeding sites and gene flow among populations of migratory birds is effected primarily by juveniles. Yearling birds are more likely to move than older birds which, once they have nested in a given location, seem to become tied to it through habituation, site fidelity, and dominance (Greenwood 1980). Natal dispersal refers to the movement from an individual's birth site to the place where it first reproduces. Breeding dispersal is the movement of adults between successive breeding sites. The tendency of adults to return to the previous year's territory is termed breeding-site fidelity (Greenwood and Harvey 1982). A common pattern in birds is the fidelity of adults to their breeding site while few first year individuals return to their natal site. In most species, males tend to be more faithful to their previous year's territory than females (Greenwood and Harvey 1982).

Early workers concluded that Loggerhead Shrikes (*Lanius ludovicia*nus) were faithful to territories. Miller (1931), Bent (1950), Porter et al. (1975), and Kridelbaugh (1983) all reported shrikes using the same territory year after year—up to 10 yr in some cases. Campbell (1975) called site fidelity a well-known phenomenon in Loggerhead Shrikes based on observations of unmarked shrikes in Ontario occupying the same territory from one year to the next. Haas and Sloane (1989) cast doubt on the level of breeding site fidelity attributable to Loggerhead Shrikes based on movements of banded adults in North Dakota and Florida.

During field studies of the Loggerhead Shrike in southeastern Alberta and southwestern Manitoba from 1987–1994, we analyzed re-encounter rates of banded adults and nestlings to quantify breeding-site fidelity, breeding dispersal, and natal dispersal. Such information is useful in understanding population dynamics, designing reintroduction programs, and managing the species. Studies of breeding passerines often involve study areas too small to allow observation of long-distance dispersal (Haas 1995). Our study areas were large enough to allow reasonable quantification of long-distance dispersal (up to 80 km) and multi-year observations allowed for larger sample sizes of adult and juvenile dispersal than have been reported previously.

STUDY AREA AND METHODS

This study was carried out in two disjunct areas, one in southeastern Alberta and one in southwestern Manitoba, both at the northern limit of the Loggerhead Shrike's range in North America. The southeastern Alberta study was an isolated $36\text{-km} \times 1\text{-km}$ strip of habitat along the CP Rail/Hwy#555 right-of-way between the abandoned Atlee townsite (50°50'N, 111°00'W) and the town of Cavendish (50°48'N, 110°28'W). The Manitoba study area encompassed much of the southwestern portion of the province from the extreme southwest corner (49°00'N, 101°20'W) north and east to Brandon (49°50'N, 100°00'W). Both study areas support the densest known breeding populations of Loggerhead Shrikes in their provinces (pers. obs.).

The southeastern Alberta study area falls within the Dry Mixed Grass

Ecoregion (Strong 1992). Loggerhead Shrikes in this area nest in shrubby areas (mainly thorny buffaloberry [*Shepherdia argentea*]) interspersed with patches of grass and forbs. This habitat is concentrated near railway/highway rights-of-way. Breeding densities of shrikes up to approximately 2 pairs/km² have been recorded (Smith 1991, pers. obs.). Shrub growth is promoted in low-lying ditches because of collection of snowmelt and rainwater as well as the absence of cattle grazing which minimizes shrub mortality from rubbing and trampling.

In southwestern Manitoba over 90% of the shrikes occur in a narrow strip of grassland and associated shelterbelt and aspen parkland habitat from the extreme southwest corner to Pipestone (49°35'N, 100°55'W). Breeding densities of shrikes range from 0.1–0.4 pairs/km². Nesting substrate in pasturelands consists of scattered willows, while in agricultural areas nests are built in shelterbelts or dense willow bands surrounding temporary wetlands (De Smet 1992, De Smet and Conrad 1991, pers. obs.).

The distribution of nesting shrikes in southwestern Manitoba was assessed from 1987–1994 by conducting intensive searches in areas that had high shrike nesting densities in previous years. Searches involved slowly driving all roads and trails in these areas on several occasions between late April and July looking for shrikes and stopping occasionally to scan good habitat or previous nesting territories. All shrikes were checked for bands with binoculars. Nests were located for over half of the nesting pairs in the study area and 60–70% of the nesting population was checked for bands. Banded adults were generally caught using a Potter trap baited with lab mice. Some shrikes that had been caught in previous years proved difficult to catch; band numbers on some of these trap-wary birds were read using binoculars or at close range at their nests with the naked eve.

In southeastern Alberta, both nestling and adult shrikes were banded opportunistically in and around the study area from 1987–1991. During 1992 all known nestlings (n = 239) and 96 of 132 (73%) adults present within the study area were banded. The study area was intensively surveyed in 1993 to ascertain re-use of 1992 territories and to determine whether shrikes present were birds banded in 1992 or previous years. Additionally, all shrike habitat within 4 km on either side of the study area was thoroughly searched for banded shrikes. Search effort in previous years (1988-1992) was lower. Adult shrikes were captured near nest sites during June and July using a variety of trapping techniques: bal-chatri, modified Tordoff trap, Potter traps, and mist nets (Collister and Fisher 1995). Trapping was not conducted during early incubation to reduce risk of abandonment. In both study areas nestlings were banded at 8-12 d of age to ensure that they were large enough to retain the bands, yet young enough to avoid the risk of premature fledging. Each shrike was banded with a unique U.S. Fish & Wildlife Service aluminum band and a colored aluminum or plastic band.

Distance moved was calculated as a straight line distance on 1:50,000 topographic maps from previous to current capture or nest sites. Recap-

tures were grouped into two data sets: birds re-encountered after 1 yr and birds re-encountered after ≥ 1 yr. These data sets were analyzed separately for differences in distance moved by adults and juveniles. Additionally, recaptures were grouped on the basis of whether the shrikes were initially encountered as adults or nestlings. These two groupings were also analyzed for differences in distance moved by each sex.

None of the distance data was normally distributed. Data groupings were compared using chi-square, contingency table, and the non-parametric Mann-Whitney U-test (Norušis 1988). The level of significance was P < 0.05.

RESULTS

Totals of 27 and 73 shrikes were re-encountered on the Alberta and Manitoba study areas, respectively (Tables 1 and 2). Juveniles moved significantly greater distances between encounters than adults for intervals of 1 yr and ≥ 1 yr on both study areas (Table 3). Only 2 of 31 (6.5%) adults in the two study areas dispersed more than 6.1 km from their previous year's nest site even though the study areas were large enough to detect movement over greater distances as evidenced by juvenile reencounters of up to 79.7 km from the natal site. In fact, 10 of 20 (50%) males and 3 of 11 (27%) females were located on the same territory they were originally encountered on.

In southwestern Manitoba, 75% of returning females dispersed more than 2 km compared to only 19% of males. If one male that moved 29 km is excluded, mean male dispersal distance in Manitoba is reduced to 0.85 km (n = 15) compared to 5.0 km for females (n = 4).

Natal dispersal.—Of $\overline{2}49$ nestlings banded during 1992 in southeastern Alberta only 3 (1.2%) were re-encountered within 4 km of the study area during 1993. From 1988–1993, a total of 16 of 582 (2.7%) shrikes was recaptured that had been originally banded as nestlings in the study area. Of these, half were males and half were females. The majority (63%) were re-encountered as 1-yr-olds and only one (6.3%) was greater than 3-yrold. In southwestern Manitoba, of a total of 3176 nestlings banded from 1987–1993, 27 (0.85%) were re-encountered in the study area the year after banding and 74 (2.3%) were re-encountered over the duration of the study. Of these, 34 were males, 18 were females and 22 were not sexed. Most were 1-yr-olds (36%), 2-yr-olds (38%) or 3-yr-olds (20%) when initially re-encountered. Only 5% were more than 3-yr-old, the oldest being a 6-yr-old female.

Breeding dispersal.—Of 96 adults banded in southeastern Alberta during 1992, 18 of 48 (38%) males and 13 of 48 (27%) females were relocated within 4 km of the study area in 1993. The difference between the sexes was not significant ($\chi^2 = 0.79$, df = 1, P > 0.250). Of 140 adults banded or relocated in southwestern Manitoba from 1987–1993, 16 of 71 (23%) males and 6 of 69 (9%) females returned to the study area the following year. The difference between the sexes was significant ($\chi^2 =$ 4.07, df = 1, P < 0.05).

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	i				Dispersal	Dispersal distance (km)				
Grouping	0.0	0.1-0.5	0.1-0.5 0.6-1.0 1.1-2.0	1.1 - 2.0	2.1-3.0	3.1-4.0	4.1-5.0	5.1-10.0	10.1 - 15.0	>15
Adults										
1-yr interval	13	54	Ι	80	0	5	2	2	C	_
All intervals	13	30	2	4	I	5	16	10	÷ —	
Males	10	1	51	60	0	-	ı —	1	- c	
Females	3	7	0	1	Ι	1	-		-	- 0
Nestlings										
1-yr interval	0	I	0	4	2	5	2	×	4	ų
All intervals	0	1	0	9	4	×	0	17	×	23^{a}
Males	0	1	0	5	39	3	1	10	- 10	14
Females	0	0	0	1	1	ъ	I	7	S	×

^a sex was not determined for one bird

TABLE 1. Distribution of dispersal distances of Loggerhead Shrikes in southeastern Alberta (1987–1993) and southwestern Manitoba (1987–1994).

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Grouping	n	Mean	Median	SE	Range	
Alberta						
1-yr interval	19	4.5	3.3	6.3	0.0 - 28.0	
All intervals	27	8.2	4.0	3.00	0.0-70.0	
Adults ^a	11	1.9	0.9	0.71	0.0 - 6.1	
Nestlings ^a	16	12.4	4.1	4.80	0.4 - 70.0	
Manitoba						
1-yr interval	36	8.1	3.9	1.82	0.0 - 40.0	
All intervals	73	12.1	6.1	1.75	0.0 - 79.7	
Adults ^a	20	3.1	0.2	1.54	0.0 - 29.1	
Nestlings ^a	53	15.4	11.4	2.18	1.5 - 79.7	
Alberta and Manitoba						
1-yr interval	55	6.9	3.5	1.30	0.0-40.0	
All intervals	100	11.0	5.1	1.52	0.0 - 79.7	
Adults ^a	31	2.7	0.5	1.02	0.0-29.1	
Nestlings ^a	69	14.7	7.3	2.00	0.4-79.7	

TABLE 2. Dispersal distances (km) of Loggerhead Shrikes in southeastern Alberta (1987–1993) and southwestern Manitoba (1987–1994).

^a all intervals

Territory fidelity.—The Alberta study had similar densities of shrikes in both 1992 (66 pairs) and 1993 (70 pairs). Nevertheless, approximately 60% of the breeding adults in 1993 had not been present the previous year. On the Manitoba study area, 81 of 172 (47%) territories that were occupied by banded adults from 1988–1993 were re-occupied the following year, but only 10 of those (12%) were re-occupied by previous year's adults.

TABLE 3.Significance of differences in dispersal distances (km) of Loggerhead Shrikes in
southeastern Alberta (1987–1993) and southwestern Manitoba (1987–1994).

Grouping	Class 1	n	Median	Class 2	n	Median	U^{a}	Р
Alberta								
1-yr interval	nestling	10	4.1	adult	9	0.5	21	0.049
All intervals	nestling	16	4.1	adult	11	0.9	31	0.005
Adults	male	4	1.2	female	7	0.5	12	0.703
Nestlings	male	8	3.7	female	8	4.8	25	0.461
Manitoba								
1-yr interval	nestling	19	8.1	adult	17	0.0	36	0.001
All intervals	nestling	53	11.4	adult	20	0.2	130	< 0.001
Adults	male	16	0.0	female	4	3.3	18	0.143
Nestlings ^b	male	34	7.1	female	18	11.7	248	0.264
Alberta and Manitoba								
1-yr interval	nestling	29	6.6	adult	26	0.2	105	< 0.001
All intervals	nestling	69	7.3	adult	31	0.5	267	< 0.001
Adults	male	20	0.2	female	11	1.9	82	0.230
Nestlings ^b	male	42	6.7	female	26	8.1	479	0.398

^a Mann-Whitney U-test.

^b sex was not determined on one bird.

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Success as a predictor of breeding site fidelity.—In southwestern Manitoba, 9 of 129 (7.0%) adults that raised young to banding age returned to the same nesting territory the following year, whereas only 1 of 43 (2.3%) adults that failed to raise young to banding age returned. Similar data for southeastern Alberta were not available.

DISCUSSION

Greenwood and Harvey (1992) note that estimates of dispersal from recoveries within limited study areas underestimate effective dispersal, and that this bias is more marked with smaller study areas. Our average dispersal distances support this idea because mean dispersal distances were 20-58% less in the smaller southeastern Alberta study area than in southwestern Manitoba (Table 2). Our results suggest that both male and female Loggerhead Shrikes show some degree of site fidelity between breeding seasons. Returning adults can be expected to be within 4.7 km (mean + 2 SE) of their previous year's nest site. Although females tended to disperse greater distances between re-encounters than males, this difference was not significant in either study area.

Natal dispersal.—Our 1.2% return rate for juveniles in the year following banding was similar to results obtained in other studies of migratory shrike populations. Burton (1990) reported a 1% return rate in Indiana for a partially migratory population, Kridelbaugh (1983) reported a 1.1% (1 of 90) return rate in Missouri, Woods (1994) reported a 2.3% (4 of 171) return rate in Idaho, Haas (1995) reported a 0.8% (2 of 243) return rate in North Dakota, and Brooks and Temple (1990) recorded no returns from 196 nestlings banded in Minnesota. The relatively low proportion (36%) of birds banded as juveniles that returned as 1-yr-olds in southwestern Manitoba suggests that many birds may not return until two years after hatching. Some returning birds may have been missed because the Manitoba study area was not searched as thoroughly as the southeastern Alberta study area. However, search effort should not affect proportions seen during the first year as compared to >1 yr after banding.

Breeding dispersal.—Our return rates for adult males and females in the year following banding are similar to 47% of 15 males and 0% of 15 females in Missouri (Kridelbaugh 1983), 28% of 29 males and 5.3% of 38 females in North Dakota (Haas and Sloane 1989), 55% of males and 19% of females (total of 19 adults banded) in Indiana (Burton 1990), and 43% of 7 males in Minnesota (Brooks and Temple 1990). Our results are consistent with these previous data in suggesting stronger breeding site fidelity in male Loggerhead Shrikes than in females although this difference was less apparent in southeastern Alberta, perhaps due to more intensive surveys.

MANAGEMENT

Two populations of the Loggerhead Shrike are recognized in Canada. The eastern population (*L. l. migrans*) is confined to southern Ontario and southern Quebec and is classified as endangered by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) (Cadman

1990). The western population (*L. l. exubitorides*) of southeastern Alberta, southern Saskatchewan, and southwestern Manitoba is in less immediate danger of extinction and is classified as threatened by COSEWIC (Cadman 1985). The Loggerhead Shrike National Recovery Plan for Canada (Johns et al. 1994) notes that causes for declines in shrike populations are largely unknown and points to survival rates of adults and juveniles as serious information gaps.

Survival, productivity, and dispersal data are important parameters in population models that highlight stages in a species' life cycle where conservation actions may be most critical. Brooks and Temple (1990) developed a stochastic population dynamics model for a population of Loggerhead Shrikes in Minnesota. Our study sheds light on some of the assumptions incorporated into that model. First, Brooks and Temple used territory reoccupancy rates to estimate adult survival. Our results show that shrike territories are more frequently reoccupied by new adults than by the previous year's occupants. Second, Brooks and Temple assumed that surviving male shrikes invariably returned to the previous year's breeding site. Our study demonstrates that returning males often move more than 2 km and movements up to 29 km were recorded. Third, Brooks and Temple assumed that all adult shrikes in their study area bred. However, adults were observed in both southeastern Alberta and southwestern Manitoba for which extended observation and nest searches failed to reveal a mate or nest (pers. obs.). Finally, Brooks and Temple estimated juvenile survivorship based on long-term data available for the Florida Scrub-Jay (Aphelocoma coerulescens) (Woolfenden and Fitzpatrick 1984). It may be more appropriate to estimate juvenile survivorship by applying a correction factor to the 1-3% return rates observed for migrant juvenile shrikes in this and other studies than to estimate juvenile survivorship from a larger, cooperatively breeding and non-migratory passerine.

Although minimal data on dispersal of both juvenile and adult shrikes have led to imprecise survival estimates in the past, low return percentages for both age classes documented by this and other studies suggest that low year-to-year survivorship may be a contributing factor to the decline of the species throughout its North American range. Our results suggest that adult Loggerhead Shrikes exhibit a greater degree of fidelity to their previous breeding site than juveniles do to their natal sites. Males seem to show stronger fidelity to previous breeding sites than females. These findings have potentially important implications for reintroduction programs that are currently being considered for the eastern Canadian population (Johns et al. 1994). To take advantage of greater site tenacity by previous nesters, we recommend that reintroductions be carried out with shrikes > 1-yr-old for which breeding has been facilitated in the release area and consequently have the highest potential to return.

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