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Indirect effects of the pyrethroid insecticide deltamethrin on reproductive success of chestnut-collared longspurs

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An experiment was conducted to determine whether spraying with a broad-spectrum pyrethroid insecticide in grassland habitat for the control of grasshoppers could affect nesting songbirds through the removel of insect food resources. Three 81 ha plots were sprayed at the recommended rate of Decis 5F (6.25 g deltamethrin ha^{-1}). Paired control plots remained unsprayed. The density of (Acrididae) grasshoppers was monitored throughout the spring and summer. The nests of chestnut-collared longspurs (*Calcarius ornatus*) were monitored to determine the nest and nestling survival rates, size at fledging and food habits. Attributes of parental foraging were quantified. Food selection by parents and consumption by nestlings were measured using oesophageal ligatures. Grasshoppers accounted for >85% of the biomass of the nestling diet to spraying and this proportion increased throughout the season in unsprayed plots. Applications of Decis 5F initially reduced the grasshopper density by 93%. After spraying, parent birds switched to other arthropod taxa less affected by insecticide application; the overall biomass fed to nestlings was not significantly reduced although the acridid proportion declined to <30%. The weight and skeletal size of the nestlings at fledging was unaffected. Parent birds in sprayed plots flew no further to feed their nestlings at a similar rate to that of birds in the control plots. The clutch size and nestling survival were similar between the sprayed and unsprayed plots after Decis 5F application, but egg success was lower in the sprayed plots compared to the control plots (67 versus 87%, $p < 0.05$).

Keywords: deltamethrin; songbirds; indirect effects; reproductive success.

Introduction

Extensive spraying of insecticides for the control of grasshoppers (Orthoptera: Acrididae) occurs in the prairie provinces during outbreak years and may negatively affect the wildlife health and habitat quality. Because the prairies are intensively farmed, public and privately owned grazing land represents an important remnant breeding habitat for grassland songbirds. The managers of these grazing lands are under pressure to take action to control grasshopper infestations on their property in an effort to reduce insect damage on pasture vegetation or haylands and also in response to the concerns of farmers producing crops on adjacent land. The grasshopper densities exceeded the levels considered capable of causing significant reductions in grazing capacity and crop yields (the economic threshold is eight to 13 grasshoppers per m^2; Johnson and Olfert, 1994) on 4–19% of grasslands surveyed annually in Alberta between 1984 and 1995. Thus, a substantial proportion of quality wildlife habitat is at risk of exposure to grasshopper control insecticides.

Although the organophosphorus (OP) and carbamate (CA) insecticides typically used may be directly toxic to birds, more important effects on populations may be caused by the depletion of arthropod populations, the principal prey of many species during the breeding season. Pyrethroid insecticides are considered to be a safer method of insect pest control relative to the OPs and CAs, because their avian and mammalian toxicities are low. For example, the LD_{50} values (mg per kg body weight) in mallards are 4640 for deltamethrin versus 0.48 for carbofuran, a CA (Hudson *et al.*, 1984; Elliot *et al.*, 1978). The flowable formulation of deltamethrin, marketed by AgrEvo Canada, Inc. (Regina, SK, Canada) as Decis 5F, has been recommended for grasshopper control on the prairies since 1987, because it is more effective than the older emulsifiable concentrate (EC) formulation (Johnson and Hill, 1986a, b; Johnson *et al.*, 1986). During the

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grasshopper outbreak years of 1985 and 1986, Decis EC was the second most commonly used grasshopper insecticide in Alberta and accounted for 22% (168 000 ha) and 15% (104 000 ha) of the total area sprayed in that province for the 2 years, respectively (Dolinski and Johnson, 1992). Although direct toxicity of deltamethrin to birds is not a concern, it is known to be highly toxic to aquatic invertebrates (Ernst *et al*., 1989; Morrill and Neal, 1990) and is therefore marketed with warnings to avoid wetlands during application. Deltamethrin is also highly toxic to terrestrial invertebrates and its efficacy in the control of grasshopper populations makes it a popular choice for this application. The aerial application of Decis 5F at rates below the current rate recommended for grasshopper control ($6.25\ g\,a.i.\,ha^{-1}$) resulted in grasshopper kills ranging from 91 to 98% (Reichardt *et al*., 1986). Its effects on non-target arthropods are not well documented, but registered uses of Decis include the control of coleopteran, hemipteran, homopteran and lepidopteran pests (Jones, 1991) attesting to its broad-spectrum insect toxicity.

The juveniles of most songbirds rely on invertebrates to provide the protein they require for rapid growth. The nestling diets of most grassland songbirds are composed entirely of terrestrial arthropods; only horned lark nestlings are known to consume any appreciable quantity of seeds (Maher, 1979; Knapton, 1980; Meunier and Bedard, 1984; Petersen and Best, 1986). Even the diets of adult songbirds during the breeding season consist primarily of arthropods, with seeds contributing a mean of only 15% of biomass (Wiens, 1973; Wiens and Rotenberry, 1979). In Saskatchewan, Maher (1979) found grasshoppers to be a preferred food item in nestling diets, with the percentage they contributed to the diet increasing at a greater rate than their availability to foraging parents as the season progressed. The prey diversity was greatest in seven species of grassland songbirds when the grasshopper numbers were lowest ($<1\ m^{-2}$), whereas an increase in grasshopper numbers ($3–5\ m^{-2}$) reduced the prey diversity because all seven species switched to a heavy reliance on grasshoppers (Maher, 1979). This suggests that, even at population levels below economically significant densities, grasshoppers provide a superabundant food source to birds (Wiens and Rotenberry, 1979). Applications of insecticides such as deltamethrin in breeding habitats could not only deplete this superabundant food item, but may reduce populations of other terrestrial arthropods, depleting the entire food supply and affecting the growth and survival of nestling grassland songbirds.

Few studies have assessed the consequences of the indirect effects of agricultural chemicals on wildlife habitat. One notable study involved widespread declines of the gray partridge in agricultural areas of England, which prompted investigations into the role of pesticides (Southwood and Cross, 1969; Rands, 1985). It was determined that invertebrate abundance was severely reduced in sprayed fields, causing increases in foraging time and decreased chick survival (Rands, 1985). Songbird species are probably more susceptible to food shortages during the breeding season than are precocial gamebird species, the chicks of which are mobile immediately after hatch and able to travel extensively in search of food. In contrast, nestling songbirds must be fed by their parents, whose foraging range appears to be quite limited; the feeding territories of clay-coloured sparrows (*Spizella pallida*) and vesper sparrows (*Poocetes gramineus*) are within a 100 m radius of the nest (Knapton, 1980; Adams *et al*., 1994). Grassland songbirds also nest in higher densities than galliformes. The sum of the seven predominant grassland species in southwestern Saskatchewan averaged 109 and 204 breeding pairs per 100 ha in grazed and ungrazed pasture, respectively (Maher, 1979). Thus, spraying a relatively small area of grassland could affect many breeding territories.

The purpose of this study was to assess the potential indirect effects of the pyrethroid grasshopper control insecticide deltamethrin (Decis 5F) on the reproductive success of grassland songbirds through the depletion of the arthropod food resources of their habitat.

Methods

Study site

The study was conducted on the Barnwell Grazing Reserve (49° 48′N, 112° 19′ W, elevation 790 m above sea level) located approximately 20 km east of Lethbridge, Alberta, Canada. The land was moderately-grazed dry mixed grass prairie (Strong, 1991), dominated by blue grama (*Bouteloua gracilis*), needle-and-thread grass (*Stipa comata*) and June grass (*Koeleria cristata*). Our study plots were not grazed during the field season.

Study design

The usable portion of the grazing reserve was divided into three experimental blocks. Within each block we delineated two 81 ha study plots (900 × 900 m) and conducted intensive monitoring within the central 49 ha (700 × 700 m) allowing a 100 m buffer strip on all sides. The plots were separated by a minimum of 500 m, with untreated grassland in between. Plots within a block were randomly assigned as either treated or control. Thus, the study was conducted in a randomized complete block design having three replicate blocks, two treatments and subsampled measurements on the bird and insect variables.

The plots were staked with 1 m, white-painted, wooden stakes at 50 m intervals in a grid pattern and numbered, for orientation and ease of location of the bird nests and arthropod sampling locations. No vehicles were used in the plots for the duration of the experiment.

Pesticide application

After 3 weeks of pre-treatment monitoring, Decis 5F was applied aerially once to each of the three plots (81 ha each) designated as treated, between 25 and 28 June, by a commercial applicator. The insecticide was applied at a rate of 6.25 g.a.i. in 20 l of water per ha, the recommended rate for the control of grasshoppers. The spray deposition was validated using a system of silica gel collection plates, placed on a diagonal line across each sprayed plot (Hill and Inaba, 1987, 1989). Samples of the sprayer tank mix were also taken. Residue analyses were conducted at the Agriculture and Agri-Food Canada Research Centre, Lethbridge, Alberta, using methods similar to those described by Hill and Johnson (1987).

Reproductive success and nestling growth

We searched each of the six plots intensively for nests four times between 18 May and 6 July by dragging a weighted rope (30 m long) on the ground between two people walking approximately 25 m apart. The locations at which female birds were flushed were searched for nests. The nests were marked with two flagged stakes placed 2 m east and west of the nest. We checked the nests on alternate days after discovery, so that the dates of hatch and egg and chick mortality could be determined to within 1 day. The nestling body mass (± 0.1 g) and tarsus length (± 1.0 mm) were determined at 7 or 8 days of age, after which time it was feared that further interference might induce early nest departure. Although undisturbed nestlings might not leave the nest until 8–10 days old (Bent, 1968), we considered the nestlings in the nest to be successfully fledged by the final visit. Comparisons of egg success (number of nestlings hatched/number of eggs laid), nestling success (number of nestlings fledged/number hatched in nests hatching at least one nestling), nest success (number of nestlings fledged/number of eggs laid) and weight at fledging (day 7) were made between the pre-spray and post-spray nests and between treated and control plots. The pre-spray period was 3 weeks in duration and the post-spray period was 10 days.

Nestling diet and parental foraging

Observations of adult foraging and nestling food habits were conducted in seven to ten nests per plot during each of the pre- and post-spray periods. The nestlings were sampled at 7 days of age, between 0630 and 1230 h. Each nestling was fitted with an oesophageal ligature and returned to its nest. The ligatures consisted of plastic-coated, fine, solid copper wire, turned firmly around the nestlings' necks to prevent them from swallowing food, yet not hindering their ability to breathe or beg for food. Immediately prior to the attachment of the ligatures, the nests were observed for a period of 30 min from a distance of approximately 50 m (initial tests indicated that feeding parents ignored observers at that distance). The observations consisted of the number of feedings and the number, directions and distances of foraging flights. These parameters were also measured for the 30 min during which the nestlings were restricted by ligatures. The distances flown by parent birds were estimated by marking the position of the nest and the landing position of each foraging flight on a map of the 50 m field grid. During the ligature period, the nestlings were checked after 15 min if three feedings had occured and food was removed from their throats; otherwise they were undisturbed for 30 min, when food was removed and the ligature wires removed. Prey items were removed from the nestlings' throats using soft-tipped forceps and placed in 70% ethanol for storage. The nestlings were returned to their nests unharmed. The prey items were later identified to species for grasshoppers and to order or family for other insects. The dry weight of each item was obtained to determine the biomass. Nests were sampled once only.

Arthropod monitoring

Each plot had 64 permanent stations at which grasshoppers were counted in permanent 0.25 m^2 quadrants (method described by Johnson (1989)), 128 nearby visual estimates of density were made and 24 sweepnet samples (100 sweeps each) were collected on a weekly basis throughout the field season. The level of grasshopper population reduction resulting from the pesticide application was expressed by Abbot's (1925; as modified by Henderson and Tilton, 1955) formula, mathematically equivalent to one minus the cross-product ratio of a table of before and after treatment counts of insects from all of the treated and untreated plots (Schaalje *et al.*, 1986).

Statistical analysis

Analyses were conducted using the general linear models procedure (PROC GLM) of the SAS Institute, Inc. (1989). The reproductive parameters, fledging weights, diet and foraging parameters were compared between the treated and control groups during the pre-spray and post-spray periods separately, using analyses of variance (ANOVA) with a blocking factor. The treatment and block effects were tested using the treatment $\times$ block interaction mean square as the error term in determining the F statistic. Where there were no significant differences between blocks, the data were pooled and the model mean square error term was used.

Results

Spray deposition

The spray tank analyses indicated that the tank mixes were 80, 73 and 99% of the target rate of 6.25 g a.i ha^{-1}, for blocks 1–3, respectively. Analyses of the spray deposit plates indicated mean deposits of 45, 47 and 45% of the target deposit. These quantities are typical of aerial applications of insecticide.

Grasshopper densities

Prior to spraying, all plots had similar grasshopper densities ($5.82\ m^{-2}$, SE $= 0.19$ and $n = 719$). One week following spraying, the densities were reduced to 6.7% of the control densities and had further declined to 3.6% by week 2. By 4 weeks after spraying, the densities in the treated plots remained at only 8% of those recorded on the control plots, in which they exceeded economic thresholds ($0.98\ m^{-2}$, SE $= 0.14$ and $n = 240$ versus $13.07\ m^{-2}$, SE $= 0.49$ and $n = 239$).

Avian reproduction and growth

Chesnut-collared longspurs were the most abundant songbird species on our study site and they became the focal species of the study. A total of 152 chestnut-collared longspur nests were monitored in the six plots during the pre-spray period (mid-May to late June) and 72 nests were monitored after spraying (July), with 42 in the control plots and 30 in the sprayed plots. The rates of nest survival were similar between the treatments overall, with between 53 and 57% of nests producing fledglings (Table 1). After spraying however, a slightly larger proportion of nests in the treated plots were destroyed by predators during the egg stage than in the control plots (13.3 versus 0%). Of nests in which at least one egg hatched, the egg success was typically greater than 90%, with the exception of nests in treated plots after spraying, when only 83.4% of the eggs hatched (Table 1). In nests that successfully fledged nestlings, between 90.2 and 98.5% of all nestlings fledged.

The reproductive parameters did not differ among blocks. The overall mean clutch size was 4.2 eggs in the pre-spray period and 4.5 eggs during the post-spray period. The hatching success, fledging success and overall nest success did not differ between the treated and control plots during the pre-spray period, but the hatching success was significantly lower in the sprayed plots than in the control plots following spraying (67 versus 87%, Table 2).

Nestling growth was not negatively affected in plots sprayed with deltamethrin. The fledging weights did not differ between the pre-spray and post-spray periods; however, the mean nestling weight, mean tarsus length and minimum tarsus length were all slightly but significantly greater in sprayed plots compared to control plots following spraying (Table 3).

Nestling diet and parental foraging

Foraging observations and examination of the nestling diets were made on 51 nests during the pre-spray period (26 and 25 in the control and sprayed plots, respectively) and on 44 nests during the post-spray period (21 and 23 nests in the control and sprayed plots, respectively). The feeding rate, number of foraging trips and total distance flown by parent birds did not differ between the control and sprayed plots either before or after spraying (Table 4). The 20% post-spray increase in the mean feeding rate (from 9.5 to 11.4 feedings h^{-1}) in the control plots was significant relative to the treated plots where the rates remained close to 10 feedings h^{-1} throughout.

A total of 558 prey items was collected from nestling

Table 1. Fate of nests of chestnut-collared longspurs on control and sprayed plots before and after applying Decis 5F

				Destroyed by predators				
Period	Treatment	*n*	Fledged	Egg stage	Nestling stage	Abandoned	Dead[a]	Unknown
Pre-spray	Unsprayed	66	53.0	12.1	22.7	3.0	9.1	0.0
	Sprayed	86	57.0	10.5	29.1	1.2	1.2	1.2
Post-spray	Unsprayed	42	54.8	0.0	26.2	0.0	0.0	19.1[b]
	Sprayed	30	56.7	13.3	26.7	1.4	3.3	3.3

[a]Chicks were found dead in nests, usually heavily infested with dipteran parasites.
[b]Includes cases where nest markers were accidentally destroyed and the nests could not be relocated and when cattle were released into one plot prior to the completion of some nests at the end of the study.
The values are expressed as a percentage of total nests. *n*, number of nests.

Table 2. Reproductive parameters of chestnut-collared longspurs on control and sprayed plots before and after applying Decis 5F

			Clutch size		Hatching success		Fledging success		Nest success	
Period	Treatment	*n*	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Pre-spray	Unsprayed	59	4.12	0.09	0.75	0.05	0.63	0.06	0.44	0.06
	Sprayed	82	4.30	0.08	0.82	0.04	0.63	0.05	0.52	0.05
Post-spray	Unsprayed	41	4.49	0.09	0.87[a]	0.04	0.54	0.08	0.50	0.07
	Sprayed	25	4.48	0.12	0.67[b]	0.08	0.67	0.09	0.41	0.09

[ab]Means within a period with different superscript letters are significantly different ($p < 0.05$; ANOVA).
n, number of nests.

Table 3. Nest mean and minimum weights (g) and tarsus lengths (mm) of chestnut-collared longspur nestlings at 7 days of age before and after spraying with Decis 5F

			Mean weight per nest (g)		Minimum weight per nest (g)		Mean tarsus per nest (mm)		Minimum tarsus per nest (mm)	
Period	Treatment	*n*	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Pre-spray	Unsprayed	36	14.45	0.30	13.53	0.33	18.14	0.16	17.63	0.18
	Sprayed	44	14.42	0.17	13.25	0.26	18.18	0.14	17.35	0.21
Post-spray	Unsprayed	33	13.65	0.21	12.75	0.24	17.75[a]	0.16	17.12[a]	0.17
	Sprayed	26	14.45	0.26	13.50	0.30	18.54[b]	0.17	17.88[b]	0.20

[ab]Means within a period with different superscript letters are significantly different ($p < 0.05$; ANOVA).
n, number of nests.

Table 4. Mean (SE) foraging characteristics of parent chestnut-collared longspurs before and after spraying with Decis 5F

	Pre-spray		Post-spray		% pre-spray values	
	Unsprayed	Sprayed	Unsprayed	Sprayed	Unsprayed	Sprayed
n	26	25	21	23	–	–
Number of flights	8.7 (0.7)	10.5 (0.8)	10.2 (0.5)	10.2 (1.1)	1.17	0.99
Number of feedings	9.5 (0.7)	10.3 (0.8)	11.4 (0.5)	10.0 (0.9)	1.21[a]	1.04[b]
Distance flown (m)	279.0 (22)	295.0 (27)	319.0 (27)	341.0 (32)	1.28	1.27

[ab]Means within a period with different superscript letters are significantly different ($p < 0.05$; ANOVA).
n, number of nests.

oesophageal samples. Grasshoppers accounted for a large proportion of the diet of nestling longspurs during the pre-spray period (>85% biomass and >75% of total prey items; Table 5). The primary species in the pre-spray samples was the overwintering grasshopper, *Psoloessa delicatula*. After spraying, the grasshoppers remained prominent in the diets of nestlings in the control plots, accounting for 84% of the biomass and 91% of the total prey items (Table 5). The post-spray grasshopper species consumed by nestlings were primarily *Melanoplus sanguinipes, Melanoplus gladstoni* and *Melanoplus infantilis*. In contrast, in the sprayed plots, the biomass of grasshoppers in the nestling diets dropped to 27% of the total, although the proportion of total prey items dropped to only 49%, reflecting the abundance of small size classes of hatching grasshoppers available shortly after spraying. The overall arthropod biomass fed to the nestlings was not significantly reduced by spraying with Decis. The proportion of lepidopteran larva in the nestling diet increased, however, to more than twice that of the pre-spray period (34 versus 13.5%) and was 14 times greater than that in the control nests in the post-spray period (2.4%).

Table 5. Mean biomass, proportion of total biomass and proportion of total prey items of acridid (grasshopper) and non-acridid prey in the diet of nestling chestnut-collared longspurs in plots sprayed and unsprayed with Decis 5F

	Pre-spray		Post-spray	
	Unsprayed	Sprayed	Unsprayed	Sprayed
Biomass (mg)/% of total				
Acrididae	106/93	137/87	93/84[a]	40/27[b]
Non-acrididae	8/7	22/13	18/16[a]	106/73[b]
Total	114	159	111	146
Items (% of total)				
Acrididae	84	78	91	46
Non-acrididae	16	22	9	54

[ab]Means within a spray period with different superscript letters are significantly different ($p < 0.01$; ANOVA).

Discussion

By the time of spraying, the grasshopper densities approached or exceeded threshold levels of $8–13\,m^{-2}$ that would normally elicit insecticidal pest control; later in the season, the densities exceeded those levels in the unsprayed plots. Applications of deltamethrin at recommended rates caused immediate and lasting reductions of grasshoppers; the densities on the sprayed plots remained below 10% of the controls for 4 weeks following application. Control was somewhat more persistent than that achieved in a previous experimental application at the same rate where, although 95–97% control was initially attained, the densities increased to 12–16% of the controls by day 15 (Reichardt *et al*., 1986).

Despite removal of the acridid population, there were minimal impacts on the reproduction of chestnut-collared longspurs. Although there was a slight reduction in hatching success in the sprayed plots, the net productivity per nest was similar due to a slightly higher fledging rate. In our study, the principal cause of egg nestling mortality was nest predation; there were no indications of nestling starvation. The overall nest predation rates of 26–40% were slightly lower than typical for grassland songbirds. O'Grady *et al*. (1996) found rates of predation ranging from 39 to 59% for chestnut-collared longspurs in Alberta and the predation rates of McCown's longspurs (*Calcarius mccownii*) were approximately 50% in each of Colorado (With, 1994), Wyoming (Greer and Anderson, 1989) and Saskatchewan (Felske, 1971). As with these studies, the predation in our longspur population was higher during the nestling stage than during incubation, probably due to increased activity with nestling feeding.

Observer disturbance of nests causing an increase in predation is often a concern in nest monitoring studies (reviewed by Gotmark, 1992). The relatively low rates of predation in our study indicate that this was not a problem. O'Grady *et al*. (1996) found the rates of longspur nest predation actually decreased with increasing frequency of researcher visits up to a maximum of every 2 days and suggested predators were actively avoiding human contact.

A few nests initially located during the egg-laying stage were abandoned, while three more were abandoned following a violent hail storm. Another unusual cause of non-predation nest failure was severe parasitism of the nestlings by parastitic blowfly larva (Diptera: Calliphoridae). In five nests, entire broods were found dead or moribund, infested with these parasites.

Very few individual eggs or nestlings died in nests that were otherwise successful. This finding corroborates that of With (1990), who reported almost 100% survival of McCown's longspur nestlings within successful nests. However, eggs in otherwise successful nests in plots sprayed with Decis 5F suffered 16.5% mortality, twice the rate of those in unsprayed plots during the same period. In addition, the rate of overall nest failure during incubation was higher than in the control plots. The possibility of embryotoxicity is unlikely; California quail (*Coturnix japonica*) eggs immersed in a Decis EC tank mix showed no effects on the hatchability or chick viability (Martin, 1990). It is possible that the physical disturbance of aerial overspraying caused the females (the sole incubator) to spend a prolonged period of time away from the nest, providing greater predation opportunities. Richardson's ground squirrels (*Spermophilus richardsoni*), American crows (*Corvus brachyrhynchos*), ring-billed gulls (*Larus delawarensis*) and Franklin's gulls (*Larus pipixcan*) were suspected egg predators and could have been responsible for both total and partial predation. Nevertheless, increased predation did not occur in nests with nestlings at the time of spraying. A few individual nestlings died due to blowfly parasitism in nests where less heavily infested siblings survived to fledge.

As with many temperate zone breeders, chestnut-collared longspurs are known to attempt to raise two broods and to renest persistently (Bent, 1968). An overall lower productivity per territory resulting from reduced renesting efforts was the primary reproductive impact upon black-throated blue warblers (*Dendroica caerulescens*) in deciduous forests sprayed with the lepidoptera insecticide *Bacillus thuringiensis* (Rodenhouse and Holmes, 1992). We were unable to assess this aspect of longspur productivity because we did not have a marked population and the territories were too close together to be able to ascribe renesting attempts to specific pairs with certainty. As longspurs commence breeding in May, many second nesting and renesting attempts were likely already in progress by the late-June insecticide application.

The nestlings in the sprayed plots exhibited no reductions in fledging weight or skeletal growth; they were, in fact, slightly larger than those in the unsprayed plots. This lack of effect upon nestling growth is in contrast to some other studies assessing food limitation. Blue tit (*Parus caeruleus*) nestlings in a plot sprayed with cypermethrin ($75\,g\,a.i.\,ha^{-1}$) had decreased survivorship and their fledging weight was reduced by 1–2 g (Pascual and Peris, 1992). The lepidopteran target species and other lepidopterans as well as most other arthropods were severely reduced at this spray rate. Cypermethrin applied at a much lower rate ($3.75\,g\,a.i.\,ha^{-1}$), however, reduced the target species to a lesser degree without affecting other arthropods or the fledging weight. Western kingbird (*Tyrannus verticalis*) nestlings had higher growth rates in high- versus low-prey density sites, where the variation in prey densities was over two orders of magnitude (Blancher and Robertson, 1987). In an island population of song sparrows (*Melospiza vocifera*) breeding at very high densities, the nestling weight increased when supplemental food was provided (Arcese and Smith, 1988). Adams *et al*. (1994), however, found no reduction in the fledging weight of vesper sparrows in grassland territories in which the grasshopper densities had been experimentally reduced by approximately 66% using insecticidal bran bait. Grassland ecosystems are often considered to have a superabundant arthropod food resource for birds, making inter- and intraspecific competition insignificant (Wiens, 1974; Wiens and Rotenberry, 1979). This suggestion is supported by the findings of Greer and Anderson (1989) that the fledging success in McCown's longspurs was unrelated to prey density and that territorial and non-territorial areas had no difference in prey density. There was very little evidence of competition between seven species of grassland songbirds, as the diets of the nestlings consisted of similar taxa and size classes (Maher, 1979).

Despite the almost complete elimination of their apparently preferred acridid prey, the longspurs in our study were able to switch to other available arthropod prey. Maher (1979) found that grasshoppers accounted for only 30–39% of the diet of chestnut-collared longspur nestlings in Saskatchewan in May and June, this proportion increasing to 64% in July as the acridid populations increased. Lepidopteran larvae and cicadellid homopterans (leafhoppers) were much more prevalent in the diet than in our study. The early season dominance of grasshoppers in the nestling diets observed in our study reflected the presence of a population of *P. delicatula*, a non-pest grasshopper species that overwinters in the nymphal rather than the egg stage and is therefore available in May and June (Johnson *et al*., 1995). This life history is uncommon among grasshopper species, most of which overwinter as eggs. This species and other appropriately sized overwintering species were rare during the Saskatchewan study (Maher, 1979), thus grasshoppers were not a plentiful option early in the season. By late June in our study, the acridid species composition was dominated by those of economic importance as pests, including *M. sanguinipes*. The densities of *Melanoplus* species increased as the season progressed, a trend which was reflected in the diet of nestlings from the unsprayed plots, in which the frequency of grasshoppers increased from 85 to 95% in the pre- and post-spray periods.

After application of the insecticide treatments, lepidopteran larvae, primarily cutworms (*Euxoa quadridentata*, Lepidoptera: Noctuidae) increased substantially in the diets of longspurs in the sprayed plots, whereas their frequency in diets declined in the control plots. Maher (1979) and Adams *et al*. (1994) found lepidopteran larvae to decrease seasonally both in nestling diets and environmentally. Cutworms, due to their nocturnal and subterranean habits, are not normally readily available to foraging birds, but their feeding at or near the soil surface (Hardwick, 1970) exposes them to deltamethrin, a product recommended for their control (Jones, 1991). Toxic residues from Decis 5F are available to insects feeding on plants for 8 days after spraying (Hill and Inaba, 1990); thus, moribund cutworms were observed on the soil surface at densities as high as $1.5\ m^{-2}$ for up to 6 days following spraying. They were apparently attractive prey to foraging birds, as evidenced by the large increase in lepidopteran larvae fed to nestlings post-spray relative to unsprayed areas.

The switch to alternative prey when grasshoppers were depleted obviously did not reduce the quality of the nestling diet because the fledging weight was slightly greater in the sprayed plots. Although grassland lepidopteran larvae are slightly lower in protein than acridids (64–68 versus 70–75%, respectively; Robel *et al*., 1995) they contain more than twice as much lipid (17.5 versus 7.5–9.1%, respectively; Robel *et al*., 1995) and their overall energy values are similar. Parent longspurs did not have to fly farther or make more flights to obtain equivalent food resources in the sprayed plots. This suggests that although grasshoppers may have been selected when abundant, other prey that may have been less affected by the insecticide were readily available in their absence. That grasshoppers still represented almost 50% of the food items fed to the nestlings indicates that the longspurs were able to capture grasshoppers that were not apparent during censuses. Many of the grasshoppers fed to the nestlings in the sprayed plots were first instar nymphs (2–3 mm long) hatched on plots after spraying occurred, thus explaining why acridids accounted for a much smaller proportion of the total biomass (27%) than of the total prey items (49%). For example, several nestlings contained clumps of three to five first instar nymphs weighing less than 10 mg each. A single fifth instar individual could weigh well over 100 mg, depending on species. In contrast to our study, Adams *et al*. (1994) found that, although the number of feedings did not decrease and the proportion of grasshoppers offered nestlings remained unchanged, parent vesper sparrows foraged further from the nest in territories in which grasshopper populations had been reduced through insecticide bran bait compared to untreated territories. Vesper sparrows may be less able to switch to alternate prey items and, thus, fly further when necessary to obtain grasshoppers. It is possible that longspurs are unusually versatile foragers, making them more capable of surviving indirect insecticide effects than other grassland species. Maher (1979) reported that the nestling diet of chestnut-collared longspurs exhibited the greatest diversity of the seven grassland songbirds studied (vesper sparrows were not among them). Nevertheless, grasshoppers comprised less then 50% of the total prey items in the diets of all species prior to July (Maher, 1979), suggesting that grassland songbirds generally are relatively versatile foragers and that chestnut-collared longspurs provide an adequate model for this group in assessing the effects of food removal.

The importance of fledging weight to post-fledging survival is unclear and the results of studies are often contradictory (Perrins, 1965; DeSteven, 1980; Ross and

McLaren, 1981; Nur, 1984; Blancher and Robertson, 1987; Krementz *et al*., 1989). The major benefit conferred on heavier fledgings is thought to be the ability to withstand periods of low food availability after gaining independence (Perrins, 1965). Stromborg *et al*. (1988) suggested that the variability in the results of studies of this impact is due to differing and unaccounted for levels of food resources. Certainly, recently independent juveniles are inexperienced foragers and most likely to be unsuccessful when food supplies are low. Juvenile juncos (*Junco phaeonotus*) were observed to spend 90% of the day foraging, whereas adult birds were able to spend less than 75% of their time foraging to maintain broods of nestlings and themselves (Sullivan, 1989). Thus, although the reduction in the densities of insects in the sprayed plots evidently was not a limiting factor for adult longspurs, juvenile songbirds in general may have difficulty surviving due to their lack of foraging experience.

Our study indicated that application of the pyrethroid insecticide deltamethrin at the rate recommended for grasshopper control had a minimal effect on the productivity of chestnut-collared longspurs. However, our study lasted for only 10 days after spraying, during which time moribund cutworm larvae were readily available as an alternate food source for foraging parent birds. Late breeding longspurs and other species of grassland songbirds that are typically later breeders may suffer greater adverse effects of the continued reduction of grasshopper populations in a sprayed habitat. In addition, other non-pyrethroid insecticides that do not cause cutworm larvae to emerge from the soil after intoxication would produce an equal reduction in grasshopper numbers without providing the immediate benefit of increases in lepidopteran prey.

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