AN INVESTIGATION INTO THE DIET

OF THE

BROWN-HEADED COWBIRD

(MOLOTHRUS ATER)

THESIS

Presented to the Graduate Council of

Southwest Texas State University

in Partial Fulfillment of

the Requirements

For the Degree

Master of Science

By

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San Marcos, Texas
December, 1998

ACKNOWLEDGEMENTS

As with any research project, this thesis could not have been completed without the aid of many individuals. I thank The Nature Conservancy and the Fort Hood Natural Resource Division for sponsoring this research with financial and technical support. I thank the entire staff at the Fort Hood field office, in particular, I acknowledge the efforts of Randy Craft, Gil Eckrich, Jim Koloszar, Theresa Koloszar, Terry Cook, Laura Sanchez, John Cornelius, and Mark Goerning.

I am grateful for the support I received from my committee members as well. I appreciate the advice on wildlife research techniques given by Dr. Baccus. Dr. Huffman was more than helpful with the statistics and his knowledge of computers. A special thanks goes to Dr. Tuff, who not only helped design the project, but gave me continual support in every aspect of my life during this project. He proved to be more than just a thesis advisor.

On a more personal note, I thank my parents, John and Edith O'Donoghue, my brother Nathan O'Donoghue, my best friends Michelle Gorham and Colleen Kulesza, my fellow graduate students and new friends, and especially Neil Vannoy for their unconditional and loving support.

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INRODUCTION

In 1992, the Nature Conservancy and the Department of Defense combined efforts to protect and manage two federally listed endangered bird species on the Fort Hood Military Installation in Killeen, Texas. Fort Hood is one of the last refugia for the Black-capped Vireo (*Vireo atricappilus*) and the Golden-cheeked Warbler (*Dendroica chrysoparia*) and is the largest under one management authority (The Nature Conservancy 1997). An integral part of the management strategy is control of the Brown-headed Cowbird (*Molothrus ater*), which has seriously diminished the reproductive success of these two endangered passerines through brood parasitism.

The Brown-headed Cowbird is an obligate brood parasite. Female *M. ater* lay eggs in nests of other bird species, leaving the foster parents with the task of rearing young Brown-headed Cowbirds. Competition between the brood parasite young and the foster nest mates often leads to the demise of the hosts' nestlings because *M. ater* dominate parental resources by having a shorter incubation time and a faster growth rate (Payne 1977). In Central Texas, the Brown-headed Cowbird breeding season begins in late March and continues into early July, coinciding with the breeding seasons of their hosts. Female *M. ater* diligently search out active host nests in which to lay their eggs (Robinson et al. 1995). Each *M. ater* female is capable of laying 30-40 eggs per season, with a success rate of about 6 fledglings (Young 1963).

Over the last 200 years both the range and population of the Brown-headed Cowbird has increased due to landscape fragmentation (Rothstein et al. 1980). Since the early part of this century, Audubon Christmas bird count data indicates an increase in the range of *M. ater*. Prior to 1930 less than 10% of the count circles included Brown-headed Cowbirds, now they are being reported in almost 90% of the counts (Brittingham and Temple 1983). The species prefers forested landscapes containing snags (for females to perch and observe host behavior) surrounded by open, short grass fields in which to feed (Brittingham and Temple, 1996). *M. ater* often feed in association with cattle. It is presumed that Brown-headed Cowbirds originally inhabited the Midwestern United States, following herds of bison (*Bison bison*) across the plains. As the ungulates trampled tall grasses, they exposed seeds and insects, thereby providing suitable foraging conditions for *M. ater* (Friedmann 1929). In time, domestic cattle replaced bison as the dominant grassland ungulate. Land development, agriculture, timber harvest and cattle ranching have fragmented forests and provided ideal breeding and feeding sites for Brown-headed Cowbirds. Corridors between these fragments have resulted in the expansion of the geographic distribution of *M. ater* (Hahn and Hatfield 1995, Mayfield 1965). Currently, *M. ater* populations occur in every state in the continental United States and parts of Southern Canada and Northern Mexico, with the highest concentration in the Mid-West (Robinson et. al 1995).

Over 200 species of birds have been reported to serve as hosts for this brood parasite (Friedmann and Kiff 1985). The expansion of the Brown-headed Cowbird into uninhabited areas has had a detrimental effect on many migratory passerines. The passerines affected most severely are those whose populations are already low due to loss of habitat. Because *M. ater* has broad host specificity, the species always finds enough suitable hosts to keep its population high (Robinson et al. 1995). Between 1950 and 1970, the incidence of parasitism by *M. ater* has increased by 70% (Mayfield 1977). This increase in parasitism has seriously effected populations of threatened and endangered species. For example, Kirtland's Warbler (*Dendroica kirtlandii)* had a 60% population decline between 1961-1971. The Least Bell's Vireo (*Vireo belli pusillus)*, Southwestern Willow Flycatcher (*Empidonax traillii extimus*), Black-capped Vireo, and Golden-cheeked Warbler have experienced similar population declines (Robinson et al. 1993). Many of these birds are new hosts recently exposed to parasitism through the expansion of the distribution of *M. ater*. These species have no defense by which to protect their young. A recent invasion of *M. ater* into Southern California and Puerto Rico has resulted, in part, in the addition of more bird species to the endangered species list (Robinson et al. 1995).

In an attempt to reduce parasitism rates, wildlife managers and conservationists have implemented cowbird control programs throughout the country with impressive results. Trapping and removing cowbirds, especially females, have resulted in almost immediate improvement in host breeding success. For example, the Kirtland's Warbler nesting success increased from 0.8 fledglings per nest to 2.72 since 1972 (Kepler et al. 1996). Black-capped Vireos have benefited from intense Brown-headed Cowbird trapping in Fort Hood with parasitism rates declining from 90.2% in 1987 (Tazik 1988) to 22.2% in 1996 (Weinberg et al. 1998). Shooting female *M. ater* on designated routes in Fort Hood has also contributed to Brown-headed Cowbird control (The Nature Conservancy 1997).

Although trapping cowbirds has increased the breeding success for many endangered passerines, the technique still has some weaknesses. During the breeding season, the number of female cowbirds trapped declines, possibly indicating a trap bias

(Beezley and Rieger 1987). Trapping methods may also have limited impact because cattle are so widespread in many of the control areas, and Brown-headed Cowbirds travel up to 7 km between breeding and feeding sites (Rothstein et al. 1987). This method is also time and labor intensive requiring at least daily inspection of traps. In lieu of these weaknesses, long-term, broad-scale cowbird control programs are being investigated. Broad-scale control requires a complete investigation of the ecology of the Brown-headed Cowbird. One aspect is defining the association of *M. ater* with cattle and using refined cattle management to subsequently manage Brown-headed Cowbird populations. On the Fort Hood Military Installation, removal of cattle from vital locations associated with Black-capped Vireo habitat is being investigated as a possible means of parasite control.

This study was designed to assess the dietary components and feeding ecology of the Brown-headed Cowbird during the breeding season to further clarify the role of cattle in *M. ater* foraging behavior as recommended by the biological opinion established under the U. S. Fish and Wildlife Endangered Species Act and the U. S. Army Corps of Engineers' Construction Research Laboratory. Current theories suggest that the grazing of cattle exposes invertebrates and maintains short-grass habitats, thus, allowing *M. ater* easier access to food and better visibility of predators.

The feeding ecology of the species was investigated through stomach content analysis. Current data on feeding behavior indicate a preference for insects during the breeding season (Morris and Thompson 1998), therefore, emphasis was given to the invertebrate components of the diet.

METHODS

Study Site

Field work was conducted on the Fort Hood military installation in Killeen, Texas in Coryell and Bell Counties (Figure 1). The land area of Fort Hood comprises over 87,000 ha in the Grand Prairie subregion of the Blackland Prairies and the Lampasas Cut Plain subregion of the Edwards Plateau. The dominant vegetation is perennial grassland and oak-juniper woodland. There are currently 37 km^2 of Black-capped Vireo habitat and 139 km^2 of Golden-cheeked Warbler habitat on the facility (Figure 2).

Data Collection

Brown-headed Cowbirds were collected during routine control assignments between 15 March and 15 July in 1997 and 1998. Birds were shot with a .410 gauge shotgun and immediately placed on ice to stop decomposition of the digestive tract and its contents. The date, time, location, and behavior at death were recorded. Behavior at death was recorded as foraging with cattle (FC), perched in a tree near cattle (PT), loitering near a trap (TR) or in nesting habitat (IH). In 1997, 103 birds were collected, 53 were females and 50 were males. In 1998, 206 birds were collected (142 females and 64 males). A total of 309 birds were collected. The birds' digestive tracts were dissected, removed, and stored in 70% ethyl alcohol. Sweep-net samples were taken every other week in 5 different locations containing cattle and/or Brown-headed Cowbirds between 1 March and 31 July in 1997 and 1998. These sites included short grass prairies, and areas surrounding Brown-headed cowbird traps.

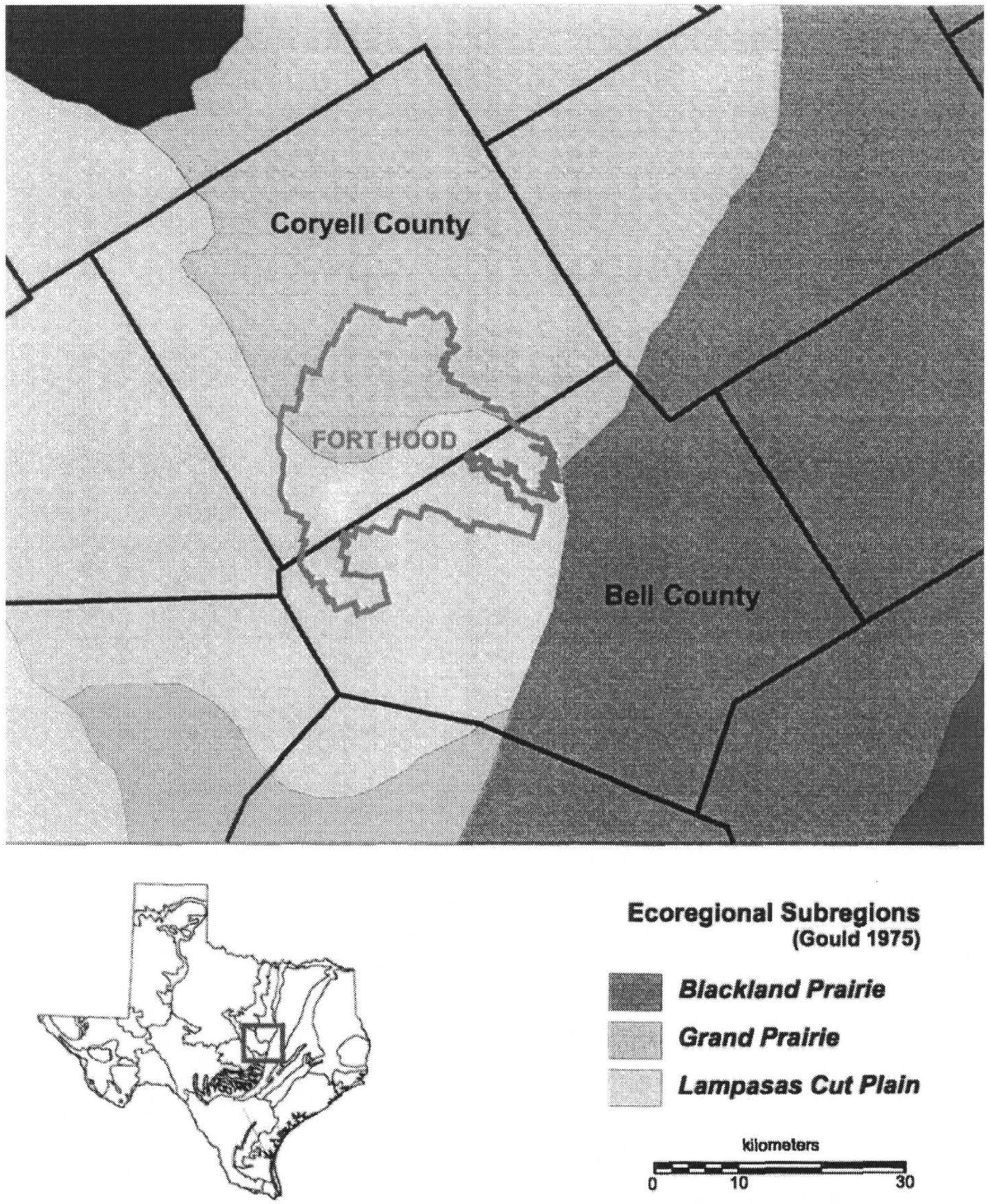

Figure 1. Fort Hood and ecological subregions of Central Texas.

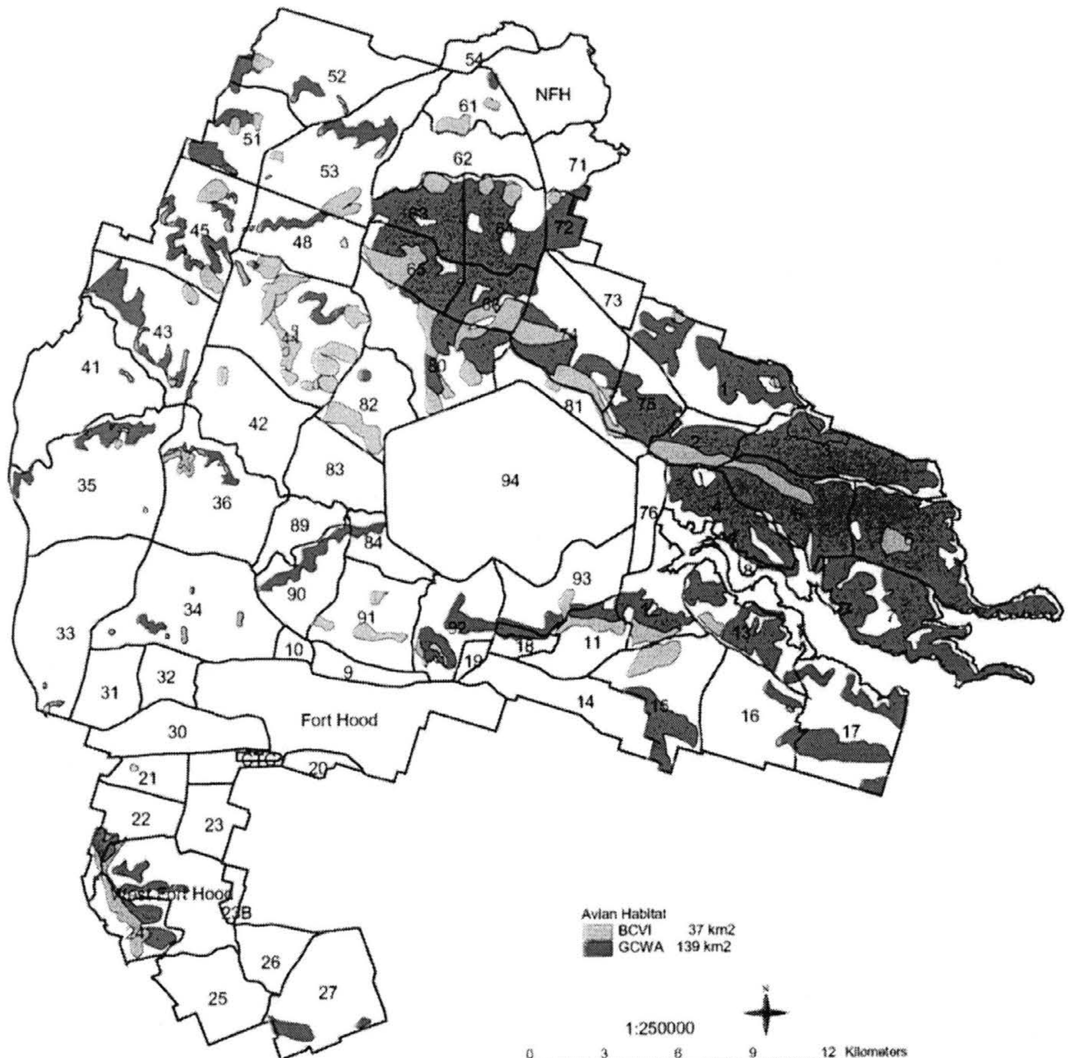

Figure 2. Training areas and endangered species habitat on Fort Hood (The Nature Conservancy 1997).

Sweep-net Sample Analysis

Sweep-net samples were divided into groups according to location. The samples collected around cattle with or without *M. ater* present were cataloged in order to investigate the relative abundance of invertebrates during the Brown-headed Cowbird breeding season. Invertebrates were identified by taxonomic keys to family (Borror et al. 1989, Helfer 1953).

Diet Composition Analysis

A modified point frame method of analysis (Chamrad and Box 1964) was used to calculate percent composition of plant vs. animal fragments in gut content. Samples were washed through a 0.5 mm sieve and emptied into a petri dish with a grid of 50 points. Fragments lying on points were identified as either plant, invertebrate, or other (rocks and feathers). This method assumes a random distribution of fragments in gut contents. Differences in the gut contents of males and females and birds shot foraging with cattle or at a trap were tested for significance by Mann-Whitney analysis. The analysis was run for each year separately to reveal any variation between the two breeding seasons. Data for both years was pooled and analyzed together in order to make general assumptions about *M. ater* feeding ecology. A Kruskal-Wallis analysis was used to determine significance of gut composition differences between birds from different groups.

Animal Fragment Identification

Animal fragments were identified to family or order using taxonomic keys (Borror et. al 1989; Helfer 1953). Arachnida and Mollusca were identified to these taxonomic levels. Fragments were counted regardless of size or stage of decomposition, so body fragments were given equal weight as entire invertebrates.

The feeding strategy of *M. ater* was characterized by calculating a prey-specific abundance (Amundsen et. al 1996), which is the percentage a prey type comprises of all prey items in only those predators in which that specific prey type occurs. Mathematically, it is represented as

$$P_i = (\Sigma S_t / \Sigma S_{ti}) \times 100;$$

where P_i = prey-specific abundance of prey type *i*, S_t = stomach content comprised of prey type *i* numerically and S_{ti} = total stomach content in only those predators with prey type *i* in their stomachs. The prey-specific abundance is then graphed against the frequency of occurrence of the prey type to give a graphical description of the feeding strategy (Figure 3). Prey types occurring in the upper part of the graph are considered specialized food items, meaning prey types that are preferred by the predator; whereas, prey types in the lower part of the graph are considered generalized prey and only eaten occasionally. Concurrently, prey types in the upper right are more important dietary components than those in the lower left which are rare or unimportant. The diagonal from lower left to upper right is a measure of prey abundance in the predator's diet obtained from the product of prey-specific abundance and frequency of occurrence. The diagonal from upper left to lower right represents a measure of niche width. In predator populations with high within phenotype components (High WPC), each individual feeds on a variety of prey types, each shows variation in its own resource use. In populations with high between phenotype components (High BPC), individuals feed on individually

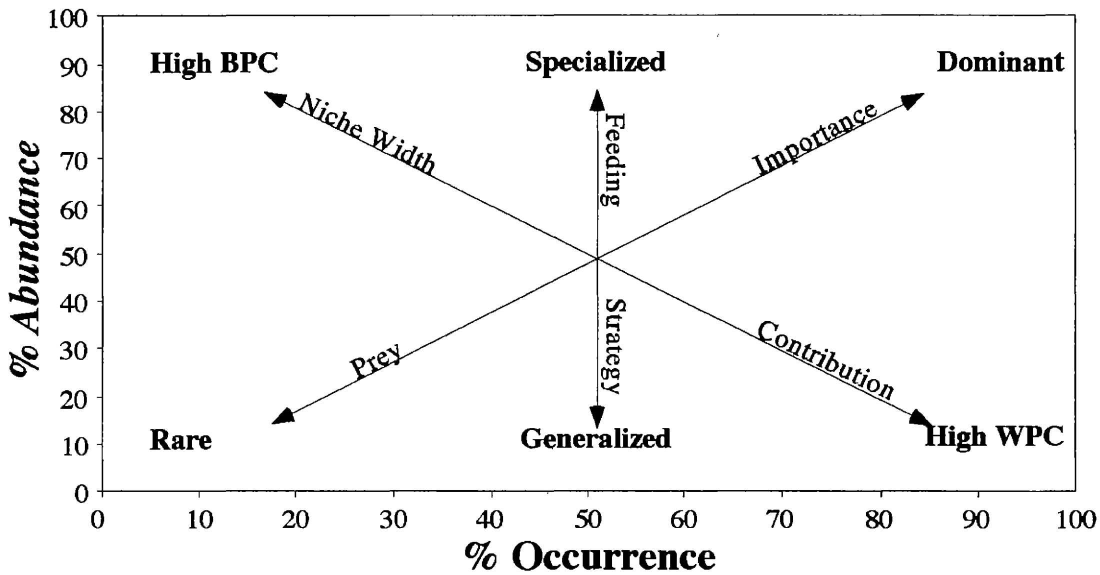

Figure 3. Graphical analysis of hypothetical feeding strategy demonstrating diagonal and vertical axes interpretations of niche width contribution (high between-phenotype component and high within-phenotype component), prey importance, and feeding strategy (Amundsen et al. 1996).

specialized prey types, there is variation in resource use among individuals (Roughgarden 1972).Examining the distribution of all prey types on the graph, as well as the location of specific prey types on the graph allows for overall feeding strategy analysis.

Specimen Housing

All sweep-net specimens and fragments are stored and housed with the Nature Conservancy at the Fort Hood field office. Copies of data logs and data spreadsheets are also on file with the Nature Conservancy.

RESULTS

Diet Composition Analysis

Most of the *M. ater* diet consisted of plant seed material. Other items in the diet consisted of invertebrates (various insects, arachnids, and mollusks) and rocks and feathers (between 0.1 % and 7.1 %). There was considerable variation in diet composition between males and females, between females foraging with cattle and those foraging near traps, and between all categories in 1997 and 1998. Average Brown-headed Cowbird diet composition was 21.9% animal, 75.9% plant, and 2.2% other items. Animal fragments in 1997 comprised only 5.5% of gut contents, while in 1998, 29.6% of fragments were animal (Table 1).

In general, female *M. ater* ate significantly more invertebrates than males: 29.8% and 8.1% respectively, $P(Z_{195,114,33} \geq 6.995) \leq 0.0001$ ($Z_{n1,n2,\#ties}$). Percent composition of invertebrates did not vary in 1997 between males and females: females = 6.7%, males = 4.2%, $P(Z_{53,50,10} \geq 0.815) = 0.4440$. But there was a highly significant difference in 1998: females = 38.2%, males = 10.8, $P(Z_{142,64,32} \geq 6.650) \leq 0.0001$ (Table 2).

Female *M. ater* foraging with cattle consumed more invertebrates than females performing other activities. Gut contents of females foraging with cattle was comprised of 12.0% animal matter in 1997, 42.2 % in 1998, and 38.3 % in both years combined. This is statistically different from the amount of animal matter in the digestive tracts of females foraging at traps, found in nesting habitat, and perched in trees near cattle.

Table 1. Percent composition of invertebrate, plant, and other material found in the digestive tracts of *Molothrus ater* at the Fort Hood Military Installation in Killeen, Texas.

		% Composition		
Year	*n*	Invertebrate	Plant	Other
1997	103	5.5	90.7	3.8
1998	206	29.6	69	1.1
Total	309	21.9	75.9	2.2

Table 2. Percent composition of invertebrate, plant, and other material found in the digestive tracts of male and female *Molothrus ater*.

		% Composition		
Year	*n*	Invertebrate	Plant	Other
Females				
1997	53	6.7	90.2	3.1
1998	142	38.2	60.7	1.1
Total	195	29.8	68.6	1.6
Males				
1997	50	4.2	91.2	4.5
1998	64	10.8	87.1	2.1
Total	114	8.1	88.8	3.1

Probabilities of these results being due to random chance for 1997 were $P(H_{2,3,8} \geq 10.881) = 0.0043$, for 1998 were $P(H_{3,4,29} \geq 24.006) \leq 0.0001$, and for both years combined were $P(H_{3,4,31} \geq 67.039) \leq 0.001$ ($H_{df,\#groups,\#ties}$) (Table 3).

Sweep–net Data Analysis

Sweep-net data for areas grazed by cattle indicated a high relative abundance of two orthopteran families (Table 4). Of the orthopterans approximately 80% were Acrididae (grasshoppers) and 20% were Tettigoniidae (katydids). The coleopterans collected mainly consisted of Chrysomelidae (leaf beetles). The hemipterans were dominated by family Miridae (plant bugs), dipterans by Syrphidae (syrphid flies), and homopterans by Cicadellidae (leaf hoppers). Substantial amounts of arachnids were collected. Considerably fewer invertebrates were collected in 1998 than in 1997 (Figure 4). With the exception of Mollusca, invertebrates collected in the sweep-nets were the same taxa found in the digestive tracts of the birds.

Invertebrate Feeding Strategy Analysis

Since most of the contents were taken from the gizzards of the birds, identification of invertebrate fragments beyond ordinal level proved difficult. Definitive characteristics of Acrididae allowed identification to family, but since this was the only family with distinguishing identifiable characteristics, gut contents were classified to order. The most common invertebrates occurring in digestive tracts were Orthoptera, Coleoptera, Homoptera, Arachnida, Hemiptera, and Diptera. The dominant prey type in the diet of Brown-headed Cowbirds was Orthoptera. This dominance shows a slight specialization for these large invertebrates at Fort Hood. Most other prey items were fed

Table 3. Percent composition of invertebrate, plant, and other material found in the digestive tracts of female *Molothrus ater* collected while foraging with cattle, foraging at a trap, perched in a tree near cattle, or in nesting habitat.

	Year	n	% Composition		
			Invertebrate	Plant	Other
Foraging with Cattle					
	1997	13	12.0	86.0	2.0
	1998	88	42.2	56.6	1.2
	Total	101	38.3	60.4	1.3
Trap					
	1997	33	2.3	95.2	2.5
	1998	16	22.5	75.6	1.9
	Total	49	9.2	88.4	2.4
Nesting Habitat					
	1997	7	16.3	76.6	7.1
	1998	12	12.8	86.5	0.7
	Total	19	14.2	82.5	3.3
Perched in Tree					
	1998	25	43.4	56.5	0.1

Table 4. Invertebrate composition of sweep-net samples collected between 15 March and 15 July 1997 and 1998 at the Fort Hood Military Installation in Killeen, Texas.

		Year collected		
Invertebrate group:	Family	1997	1998	Total
Arachnida		60	77	137
Blattaria	Blattellidae	0	1	1
Coleoptera	Buprestidae	0	1	1
	Chrysomelidae	49	8	57
	Cleridae	0	1	1
	Curculionidae	0	1	1
	Elateridae	1	2	3
	Total	50	13	63
Diptera	Culicidae	1	1	2
	Empididae	2	0	2
	Muscidae	10	0	10
	Syrphidae	39	2	41
	Tipulidae	3	0	3
	Total	55	3	58
Ephemeroptera	Baetidae	1	0	1
	Ephemeridae	1	0	1
	Total	2	0	2

Table 4 cont.

Hemiptera	Berytidae	1	0	1
	Lygaeidae	0	4	4
	Miridae	78	34	112
	Pentatomidae	9	1	10
	Total	88	39	127
Homoptera	Cercopidae	3	0	3
	Cicadellidae	64	23	87
	Membracidae	4	3	7
	Total	71	26	97
Hymenoptera	Vespidae	1	0	1
Mantodea	Mantidae	0	1	1
Neuroptera	Chrysopidae	1	0	1
Orthoptera	Acrididae	133	211	344
	Tettigoniidae	28	56	84
	Total	161	267	428
Tricoptera	Leptoceridae	2	1	3

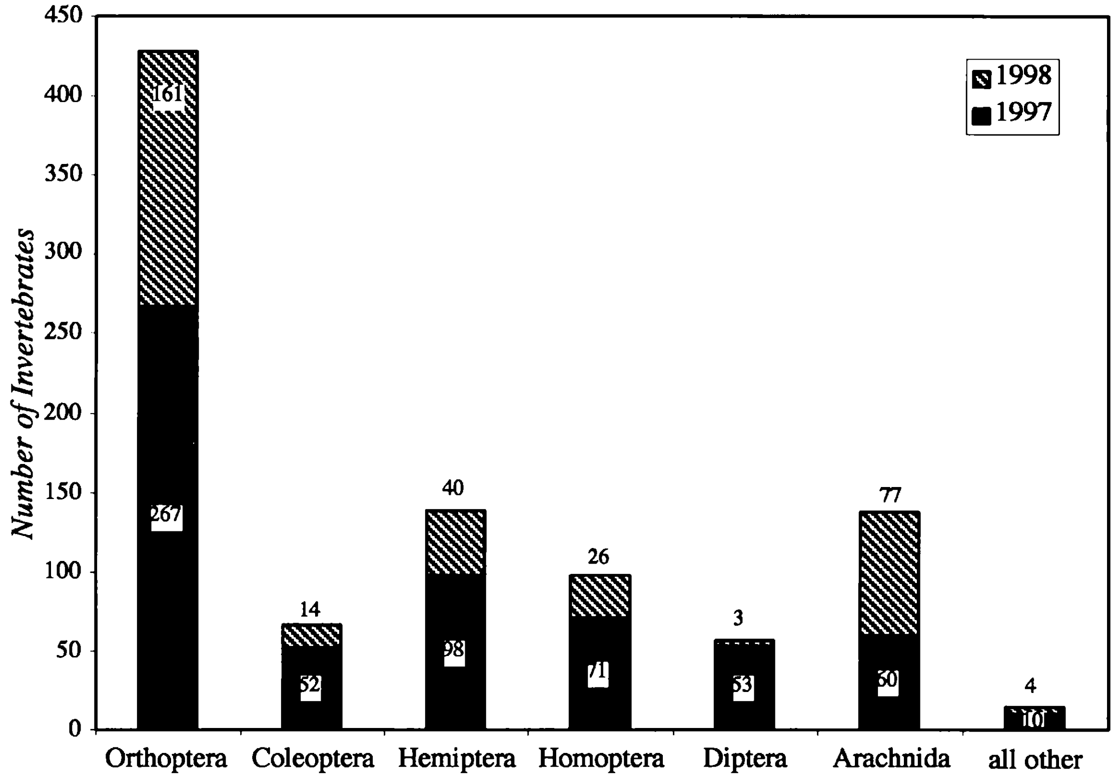

Figure 4. Invertebrate groups comprising sweep-net samples collected between 15 March and 15 July, 1997 and 1998 at the Fort Hood Military Installation in Killeen, Texas.

on indiscriminately and could be considered rare within the birds' diet. Individual birds, as indicated by a high between-phenotype ranking (Figure 5) selectively fed on mollusks.

The feeding strategy of males and females did not vary greatly except for a higher between-phenotype mollusk component in males and a slightly higher importance rating for Coleoptera in females (Figure 6). The feeding strategies of females foraging with cattle were compared to females at traps. Again, most prey types were rare and not specifically selected. Both groups of females ate orthopterans, but females collected at traps ate coleoptrans more often than those collected while foraging with cattle. Mollusks were never utilized by trap birds, and were selectively preyed upon by individual birds (Figure 7). Birds in nesting habitat and perched in trees were excluded since these behaviors are not associated with feeding.

Some females foraging with cattle were collected with developing eggs in their oviduct in 1998. Feeding strategies of these birds were compared to that of other females foraging with cattle in 1998 without developing eggs (Figure 8). The strategies did not vary greatly except for a slightly higher specialization on Coleoptera and higher between-phenotype rating of mollusks in females without developing eggs.

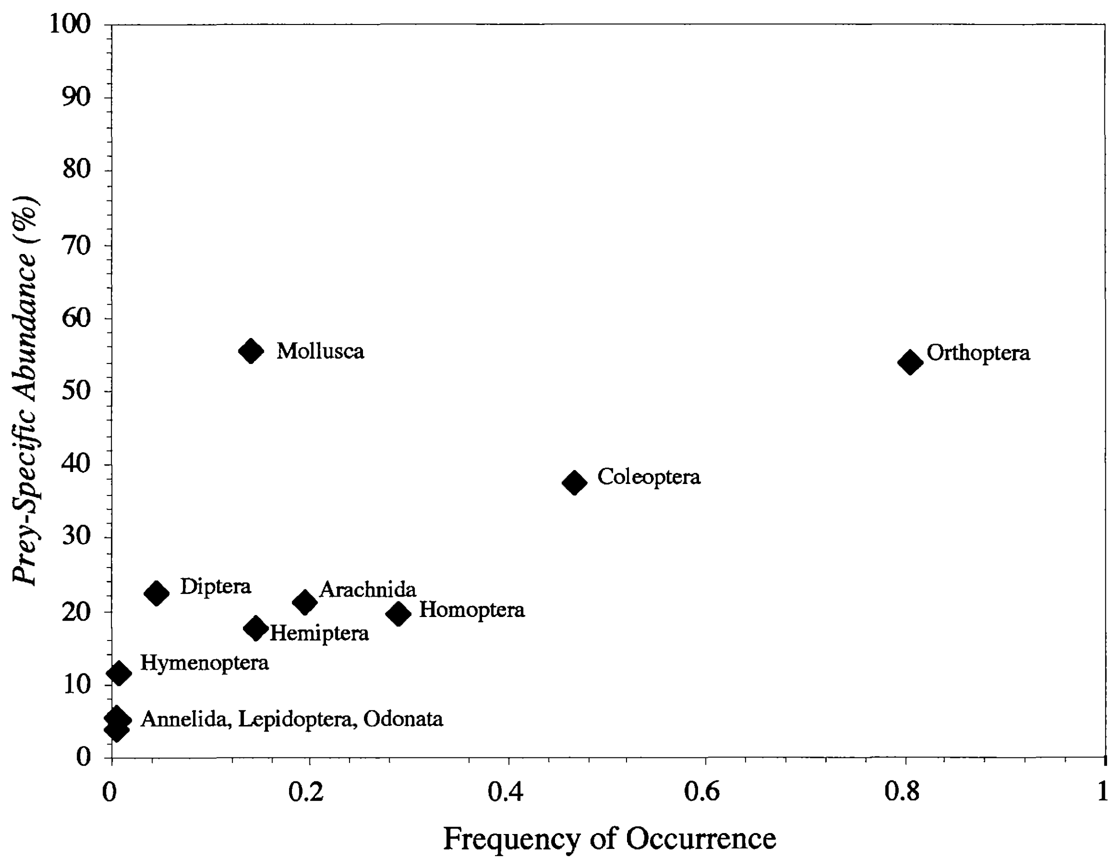

Figure 5. *Molothrus ater* prey-specific abundance. This is a representation of the feeding strategy of all cowbirds collected between 15 March and 15 July, 1997 and 1998 at the Fort Hood Military Installation in Killeen, Texas.

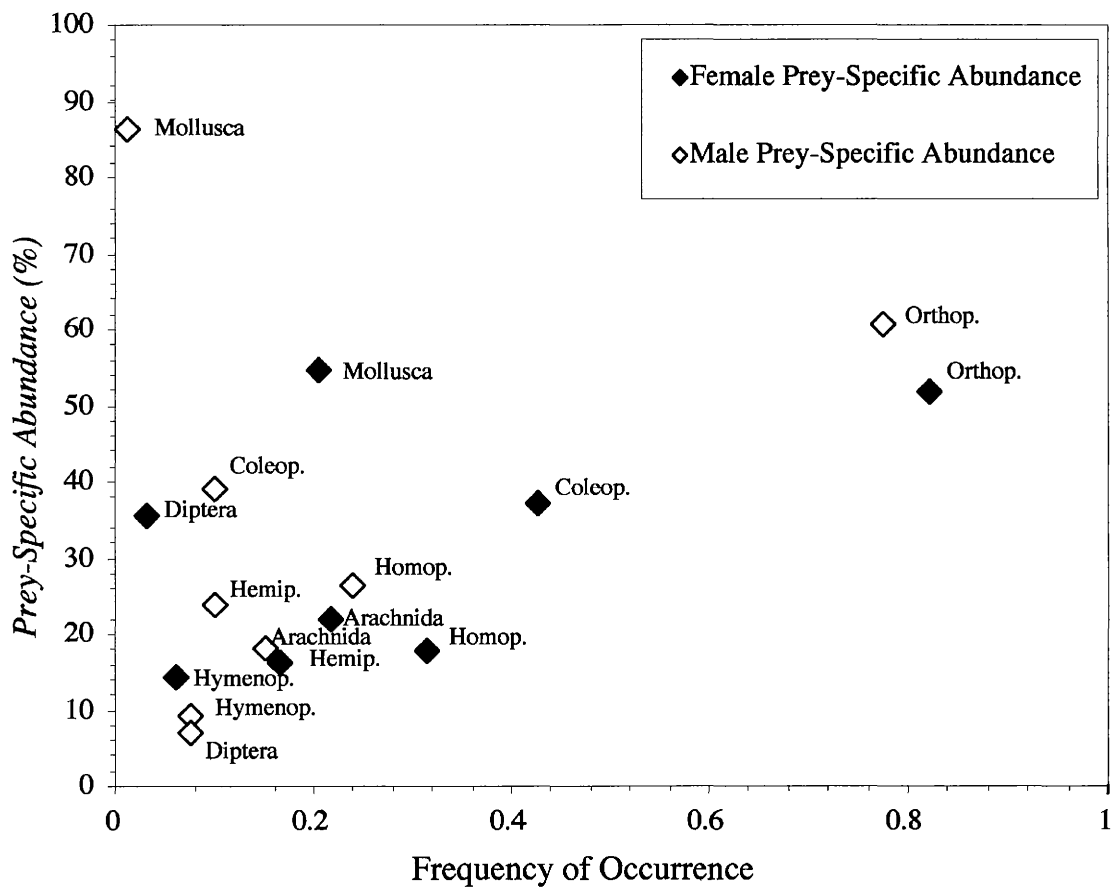

Figure 6. Prey-specific abundance of male and female *Molothrus ater*.

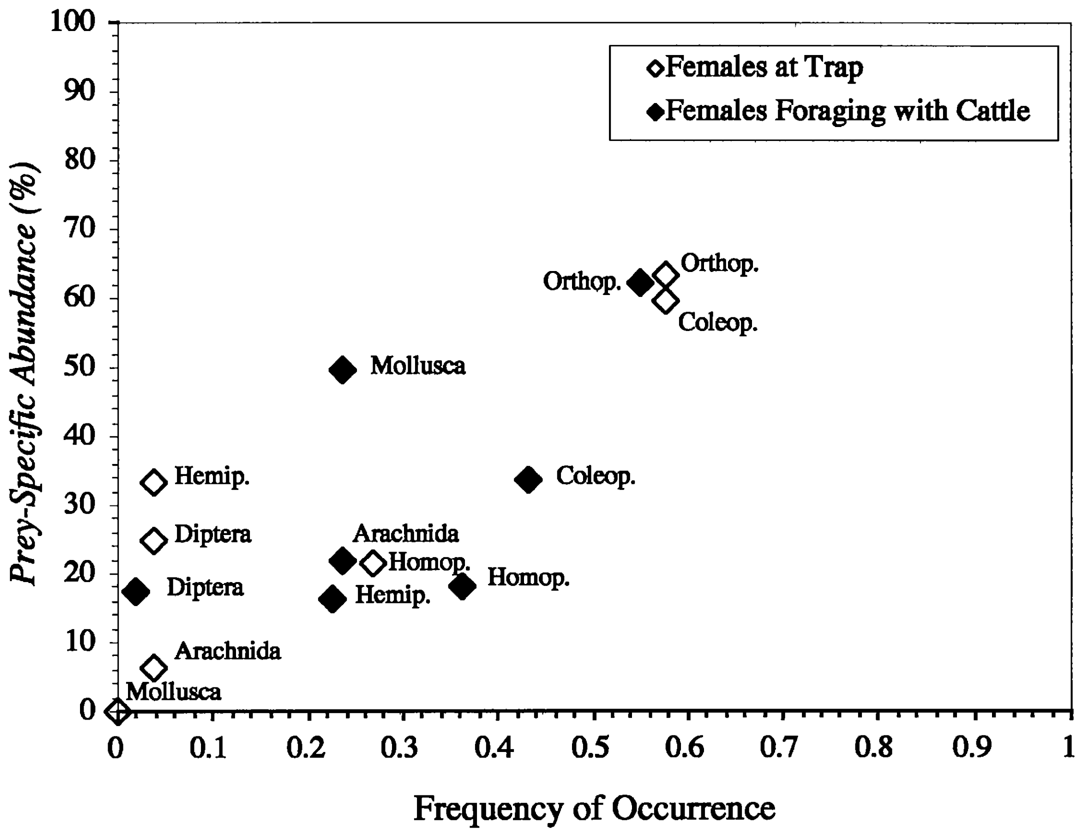

Figure 7. Prey-specific abundance of female *Molothrus ater* foraging with cattle and at traps.

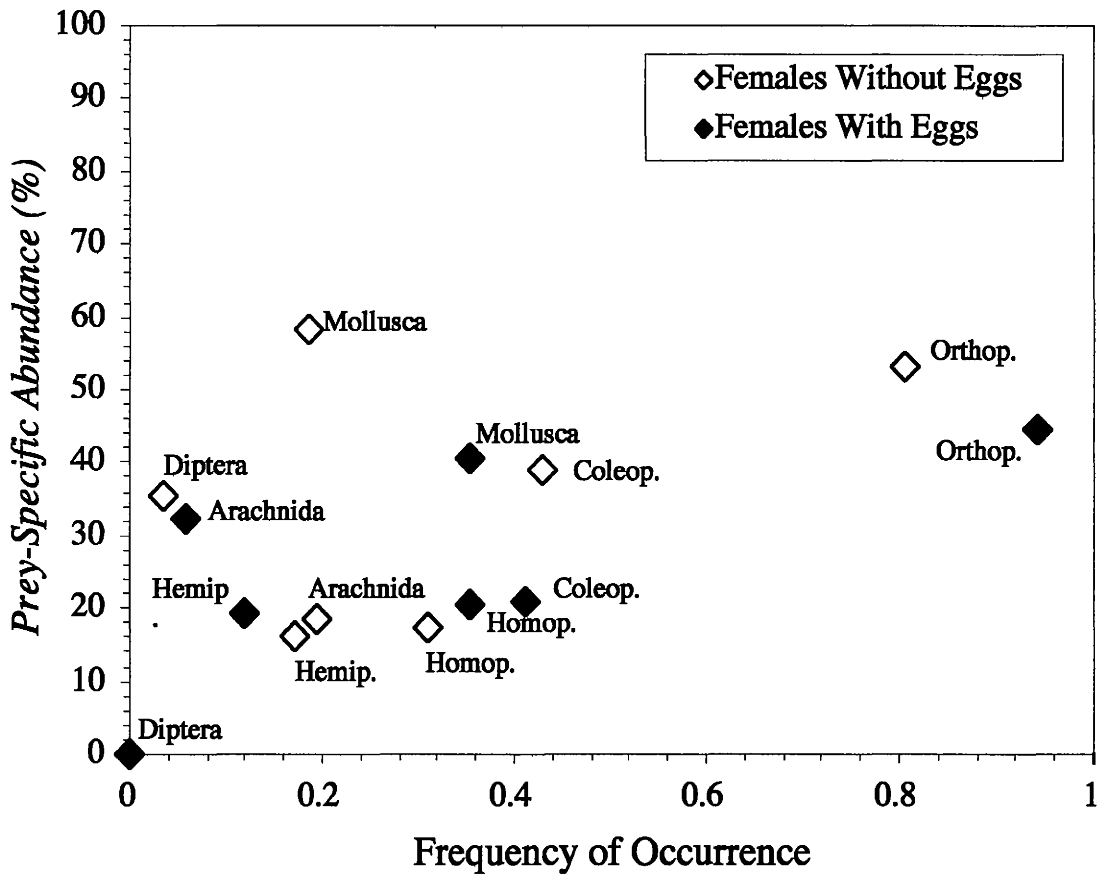

Figure 8. Prey-specific abundance of female *Molothrus ater* collected with and without oviductal eggs.

DISCUSSION

Biases Associated with Diet Analyses

Drawing conclusions from partially digested food fragments can be tenuous, but merely sampling the prey potential is not sufficient to identify a bird's feeding ecology. Analyzing gut contents can be an important contribution to the understanding of the ecology of the Brown-headed Cowbird, and certainly a window into their feeding preferences. Although this information can be useful in an ecological investigation, few researchers are willing to do such an analysis. This is often due to the fear of inadequacy in identifying fragments, and spending an exuberant amount of time on unpublishable data (Rosenberg and Cooper 1990).

There are several techniques that can be used in a diet analysis, such as fragment identification from fecal pellets, crop contents and stomach contents, forced regurgitation, flushing the digestive tract, using ligatures, and direct observation. But all of these techniques only represent a subset of total dietary input and makes the study highly susceptible to bias (Brown and Ewins 1996). For example, in a study conducted on regurgitated pellets of the Ring-billed Gull (*Larus delavarensis),* Brown and Ewins (1996) concluded that "pellets are an over-representation of indigestible hard parts of some food types while chick provisions may be biased towards highly nutritional foods and temporally abundant foods".

Analysis of stomach contents also pose special biases. Post-mortem digestion is not uncommon, and collected birds must be given immediate attention to reduce the likelihood of continued food digestion. The fullness of birds' stomachs can also cause bias. There can be extreme variation in the amount of content depending on the activity of the bird prior to collection. This is also true for crop contents. Analysis of crop contents is thought to be the least biased method of diet investigation provided the bird has a large well developed esophagus, which is generally not the case with smaller passerines (Rosenberg and Cooper 1990).

Gizzard content analyses exaggerate the importance of seeds and hard-bodied invertebrates. Swanson and Bartonek (1970) found that in Blue-winged Teal (*Anus discors)*, as the time between feeding and sampling increased, the degree of bias associated with analysis also increased. They found that soft food items were digested almost immediately while hard food items remained in the gizzard for several days. In addition to the grinding action of the gizzard, hard food particles act as abrasives, further speeding the digestion of soft particles, and increasing the likelihood of a bias toward hard particles.

Aside from the biases in diet analysis techniques, the digestion rates of food items can also pose special problems even before the bird is collected. Soft-bodied insects can be easily under-reported, exaggerating the importance of hard seeds and heavily scleritized insects. Certain important prey items may actually be missed in the analysis due to rapid digestion. Since each bird species has varying degrees of digestion rates, it would behoove investigators to identify the digestion rate of the particular bird with which they are working. Reports from digestive rate studies from passerines vary from 2.5 hours for hard material to less than 5 minutes for soft material (Rosenberg and Cooper 1990). Exact rates of digestion for the Brown-headed Cowbird are unknown.

Action was taken to reduce the extent of bias in this particular study. The behavior of the birds was observed prior to collection, and only those birds engaged in actual foraging behavior were used to study feeding strategy. This process helped reduce bias in stomach fullness, by ensuring some stomach content. Also, content was analyzed as a percent of total composition and not as total weight or volume. Immediately after collecting, birds were put on ice to slow or stop post-mortem digestion. This method, though, was not efficient and created inconsistency between the two years of collection. Analysis of the gut contents of birds collected in 1997 showed a significant bias toward seed particles, which composed 90.7 % of the overall diet. Increased quality control during collection in 1998 decreased plant composition to 69.0 % (Table 1). In a similar study in Ontario, Ankey and Scott (1980) discovered that nearly 65 % of female cowbirds had gut contents comprised only of invertebrates. In this study, only 4.6 % of females had gut contents that were 100 % invertebrates. This difference can be a spacial variation between birds in central Texas and southwestern Ontario, but more realistically, it could be a variation in post-mortem quality control. The Ontario birds were put on dry ice while those in Fort Hood were put on regular ice. Ideally, gut contents should have been extracted and put in 70 % ethyl alcohol immediately after collection, or a solution of formalin should have been injected into the stomachs. Formalin preserves gut material for more accurate identification, especially soft-bodied invertebrates such as caterpillars and aphids (Rosenberg and Cooper 1990). The design of this study was such that neither of these two ideal techniques was possible. Brown-headed Cowbirds were shot as part of a routine control program; collecting and preserving specimens in either manner would not have been feasible.

The entire digestive tract was examined in the analysis. Very few birds had contents in their crops or stomachs. Consequently, most of the material analyzed came from gizzards. This favored the enumeration of items that were the most difficult to digest. For example, while sweep-net samples indicated a high abundance of aphids, no aphids were in samples of the digestive system. Three females collected in 1998 had Lepidoptera larvae in their beaks or crops, and one female was collected with an earthworm in her beak. In the feeding strategy analysis, both of these items were considered rare, but it is likely that these soft-bodied invertebrates were under-represented by technique bias.

Rosenberg and Cooper (1990) consider that 10 or fewer stomachs were sufficient for assessing diets of a particular species at a specific site, within a specific time period. This study used 309 birds, thereby decreasing the chance for technique associated biases. Analyzing gut contents of many birds increased the chance of including rare and quickly digested items.

Although many biases are associated with this type of analysis, making assumptions about dietary habits based on indirect measures such as prey base potential (potential prey available in a predator's habitat), morphology, and even behavior can often times be misleading. Merely documenting the prey base for a particular bird species does not allow for a clear understanding of its ecology, prey usage, or feeding strategy. For example, Rosenberg and Cooper (1990) cite many empirical studies that have found discrepancies between inferred diet data (mainly consisting of foraging observations) and direct examination of dietary components. Gut content analysis in combination with behavioral and morphological characteristics can give investigators a clearer understanding of the ecology of the species.

Feeding Ecology of Brown-headed Cowbirds at Fort Hood

Female Brown-headed Cowbirds begin to increase invertebrate consumption just prior to the breeding season (Ankney and Scott 1980). This is a response to the increased nutritional demands of egg production. Utilization of animal protein continues throughout the breeding season concurrent with egg production. Male consumption of invertebrates also increases, but not to the extent of females. Ankney and Scott (1980) investigated the dietary changes in Brown-headed Cowbirds in Ontario between pre-breeding, breeding, and post-breeding, and they found that the diet of pre- and post-breeding males and females were similar. Both sexes increased their intake of invertebrates during the breeding season. Female consumption of invertebrates was markedly higher, and it was thought that males increased animal consumption primarily as a secondary result of their social feeding habits. They concluded that comparing male and female diets could be useful to assess whether the increase in female consumption of invertebrates was a selective behavior or due to an increase in invertebrate availability.

Brown-headed Cowbirds at Fort Hood showed patterns similar to those in Ontario. Females had a significantly higher invertebrate composition than males even though males were often found feeding with females (Figure 9). In 1997 the percentage of females collected that were actively foraging with cattle equaled that of males foraging with cattle. In 1998 a higher percentage of females were collected feeding with cattle compared to males with cattle, but males still showed a preference to social feeding with

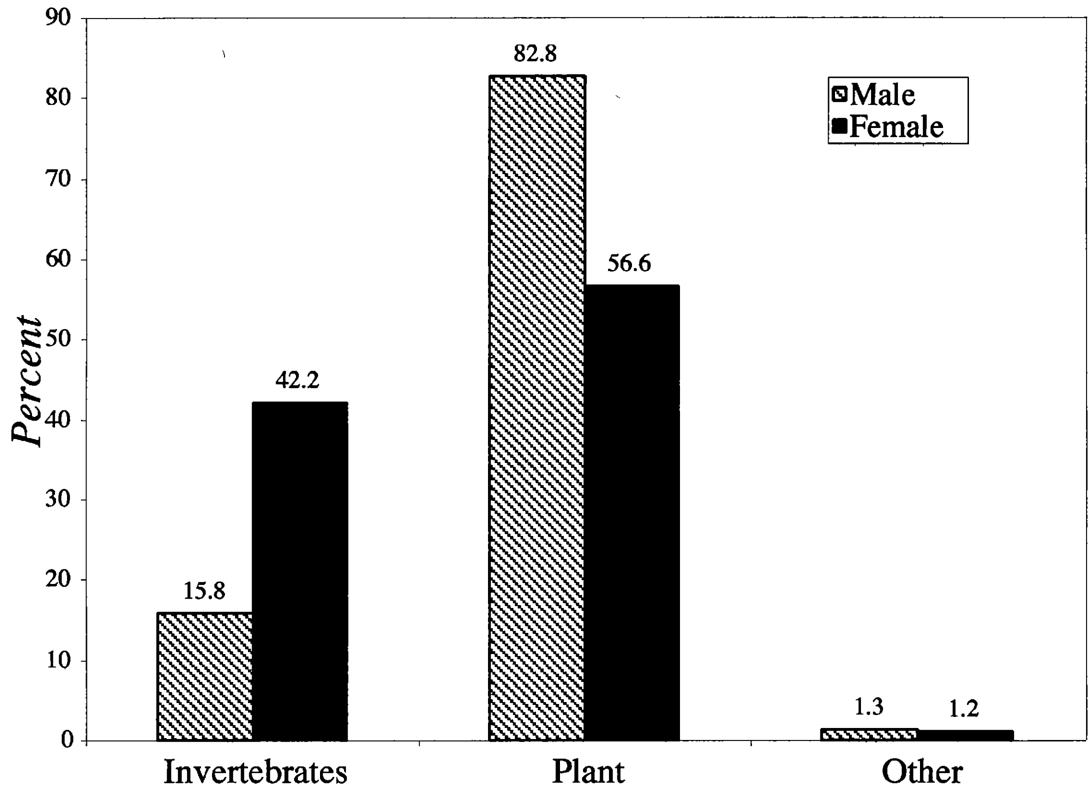

Figure 9. Percent gut composition of invertebrates, plant materials, and other materials for male and female *Molothrus ater* foraging with cattle in 1998.

females around cattle (Figure 10). This suggests that females selectively feed on invertebrates during the breeding season.

In a recent study of Brown-headed Cowbird foraging behavior, Morris and Thompson (1998) investigated the influence of habitat on feeding behavior. They concluded that the species prefers areas of short-grazed grass due to higher food availability. Areas with tall grazed grass were second in preference as feeding sites compared to short ungrazed and tall ungrazed areas. In central Texas, grasshoppers (Acrididae, Table 4) dominate these optimal feeding sites. There are many conflicting studies relating invertebrate composition to cattle grazing. Morris and Thompson (1998) found a slightly higher, but not a statistically higher, invertebrate abundance in grazed pastures compared to ungrazed pastures. Quinn and Walgenbach (1990) reported higher grasshopper populations in grazed sites due to differences in plant community structure. Other studies indicate a reduction in grasshopper diversity concurrent with increased ungulate populations in grazed habitats (Holmes et al. 1979). Finally, it is thought that fluctuations in composition and abundance of grasshopper species are related to seasonal responses and location. It is also documented that any large land disturbance such as grazing, farming, or development can trigger population explosions of certain grasshopper species (Capinera and Sechrist 1982, Jepson-Innes and Bock 1989). Whether or not cattle grazing actually increases grasshopper populations or alters grasshopper community composition, these studies indicate an abundance of larger size invertebrates in grazed grasslands. The dietary composition of females collected foraging around cattle had a significantly higher invertebrate component than that of females collected in other locations ($P < 0.0001$, Table 3). This indicates that females actively seek out grazed

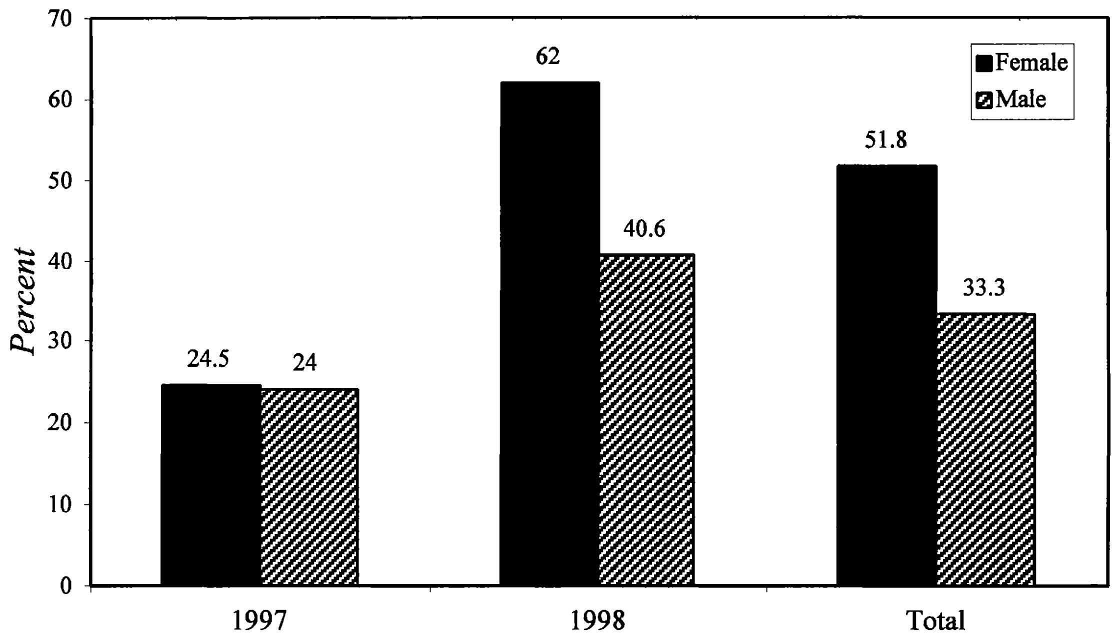

Figure 10. Percent of male and female *Molothrus ater* collected foraging with cattle between 15 March and 15 July, 1997 and 1998 at the Fort Hood Military Installation in Killeen, Texas.

grasslands during the breeding season to obtain invertebrates for their increasing nutritional demands.

To further clarify the ecology of the Brown-headed Cowbird and to investigate whether particular food items are selected, an analysis of their feeding strategy was conducted by measuring the prey-specific abundance. Each diagonal and axis of the diagrammatic representation of feeding strategy (Figure 3) allows for distinct interpretations of feeding strategies, and together allow for clear indication of overall feeding strategies (Amundsen et al. 1996).

In Figure 3, the diagonal axis from bottom left to top right is an indication of prey importance. In all *M. ater*, whether male or female, foraging with cattle or at a trap, or with developing eggs in the oviduct or not, Orthoptera (primarily Acrididae) dominated the diet (Figures 5 – 8). More than half of the birds in each group contained grasshoppers. Coleopterans were also a significant component in the diet. All other invertebrates were considered rare. The importance of a prey item is represented as a function of prey-specific abundance and frequency of occurrence and not necessarily as a linear increase along the diagonal. Percent abundance can therefore be represented as the area enclosed by connecting data points at right angles (Figure 11). By enclosing the areas on each graph, it is evident that orthopterans make up most of the area on the graph.

The vertical axis indicates whether a prey item is a specialized food item, or if it is occasionally part of the diet. Based on the consumption of invertebrates in this investigation, the Brown-headed Cowbird would not be considered specialists. Orthoptera was usually ranked as the most specialized food item consumed. Overall

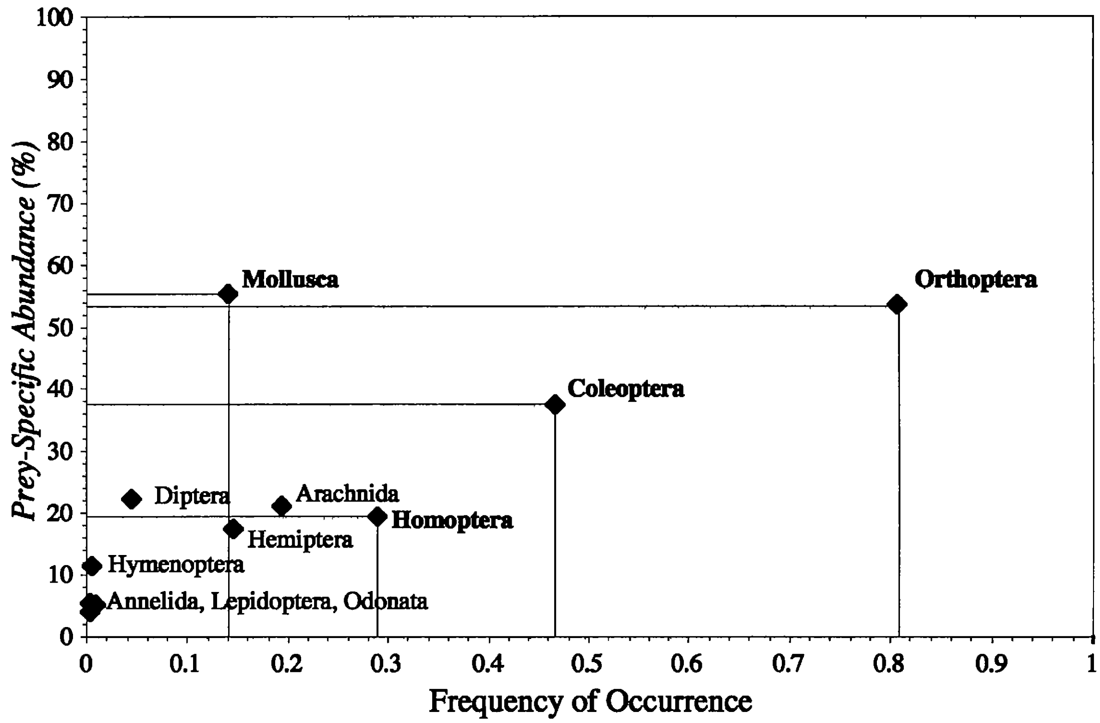

Figure 11. Example of enclosed areas representing percent abundance for food items in the diet of *Molothrus ater*.

cowbirds seem to be generalists, selecting large, conspicuous, and easily obtainable food items such as Orthoptera and Coleoptera. This is evident since most of the food items are represented in the lower left-hand corner of the diagrams (Figs. 5-8). The one exception is Mollusca, which is a specialized prey fed upon by a few females foraging with cattle, and one male found foraging with cattle and females. This feeding strategy is indicative of a population with a broad niche width.

The diagonal extending from upper left down to bottom right allows for further measure of niche width and how a population exploits its resources. When prey items are located in the lower right hand corner, it is an indication of a population with a high within-phenotype component. This means that the population is composed of individuals sharing a diverse phenotype and utilizing a variety of overlapping resources. In this case, individuals would use a wide range of food types occasionally. Prey items located in the upper left corner of the diagram denote a high between-phenotype component. This type of arrangement would be indicative of a population with many specialized individuals each having a unique phenotype. Little or no resource overlap would occur between individuals. The combination of the two components forms the niche width (Roughgarden 1972). The Brown-headed Cowbird population at Fort Hood has a broad niche width indicated by niche width components lying between high WPC and high BPC. There are individuals that show variation in their own resource use, but the population as a whole, utilizes a variety of resources.

The suggestion that the Brown-headed Cowbird population has a broad niche width, generally feeding on the most abundant food items is further supported by the consumption of animals caught in sweep-net samples taken in their foraging habitats.

Grasshoppers were the most abundant food item in the samples (Fig. 4). All food items found in the guts of the *M. ater,* except for mollusks, were captured in sweep-net samples, again suggesting a generalized feeding strategy.

The fact that snails were a specialized food item for females foraging with cattle deems some attention. Aside from requiring a high protein diet during the breeding season, female *M. ater* also require increased amounts of calcium for egg production. Ankney and Scott (1980) found that females supplemented calcium reserves from the medullary bone by consuming mollusk shells. They also suggested that males need a certain amount of calcium for maintenance, but shells were more likely consumed incidentally while foraging with females. Females in this study without developing eggs in their oviduct sought mollusks more selectively than did those with eggs. It has been suggested that the decrease in calcium is a physiological cue to birds to finish a clutch (Ankey and Scott 1980). There is not enough evidence in this study to confirm such a statement.

CONCLUSION

Short, grazed grasslands are the optimum feeding habitat for the Brown-headed Cowbird. Although this study does not provide conclusive evidence as to the reason for their preference, it does shed light on different aspects of their feeding ecology. Brown-headed Cowbirds are likely to feed on any invertebrate species in short grass, evident by the variation of gut contents. As a species, Brown-headed Cowbirds are general feeders, foraging on the most abundant invertebrates (acridid grasshoppers). It is believed, therefore, that the association with cattle is one of convenience. In rural areas the disturbance of grasslands by the movement of cars and tractors attract large numbers of feeding swifts and Cattle Egrets (*Bubulcus ibis)* as well as cowbirds. Cattle provide a similar type of land disturbance great enough to increase the availability of food to Brown-headed Cowbirds, while at the same time allowing them to watch for predators. This also makes sense given the historical ecology of cowbirds following herds of bison. Short-grass also provides easy access to mollusks that live on or near the ground.

The implication that *M. ater* benefit from human activity lends a strong argument for Brown-headed Cowbird management. Large-scale, landscape management requires the reduction of feeding sites. Cowbirds are known to travel up to 7 km between breeding, feeding and roosting sites (Rothstein *et al.* 1984), and on Fort Hood Brown-headed Cowbirds travel 2-7 km between breeding and feeding sites (The Nature Conservancy 1997). Large-scale management therefore requires large tracts of land with few feeding opportunities. This means allowing grass to grow to full height and reducing disturbance in endangered species habitat. Robinson et al. (1993) also suggested eliminating short-grass islands and disturbance sites or minimizing their size if they cannot be avoided. They also recommended avoiding snags and fence rows adjacent and within tall-grass habitats.

Further studies on this population should include analyzing birds during the non-breeding season. Investigating the change in feeding ecology may aid in establishing cattle management practices. Introducing formalin immediately into the stomachs of collected birds may also aid in the identification of invertebrates to a lower taxonomic level. Quick preservation of stomach content will also allow soft-bodied invertebrates to be included in the analysis.

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