CONSEQUENCES OF BROOD PARASITISM BY COWBIRDS ON HOUSE FINCHES IN A NEW AREA OF SYMPATRY

by

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ABSTRACT

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I investigated interactions between the brood parasitic Brown-headed Cowbird (*Molothrus ater*) and House Finch (*Carpodacus mexicanus*) host during 1983-1993. House Finches are native to western North America where they are sympatric with cowbirds. Recent introduction of House Finches to eastern North America has resulted in the association of both species there. Frequency of parasitism on House Finches appears to be related to duration of sympatry; the species is seldom parasitized in its native range but is frequently parasitized in its naturalized range. To determine the mechanisms responsible for this difference in host exploitation, I studied the consequences of parasitism on both species in California and in Ontario where cowbirds have very recently encountered the House Finch.

House Finches were heavily parasitized soon after contact with cowbirds but sustained relatively little reproductive loss to cowbird activity. House Finches represent the most common cowbird host in urban habitat and in some non urban environments. Large numbers of House Finches in concert with frequent parasitism suggests that this host may serve an important role in influencing cowbird reproductive success.

Cowbirds were not successfully reared in House Finch nests. This is apparently the result of an inappropriate diet (seeds) fed to cowbird young by their foster parents. Accordingly, the House Finch is an unsuitable host species. Failure of parasitism in House Finch nests indicates that host diet may be important in determining cowbird choice of host.

Parasitism was not detected at Goleta, California. Frequency of cowbird parasitism on House Finches in eastern North America varied with their time in sympatry. Frequency of parasitism was highest in areas of initial contact between the species and nonexistent after 20 years of sympatry. Decrease in parasitism over time suggests cowbird response to an unsuitable host. Differential reproductive success as well as learning by cowbirds may contribute to the observed decrease in parasitism. It is suggested that host discrimination by a generalist parasite resulting in changes in host preference may occur rapidly.

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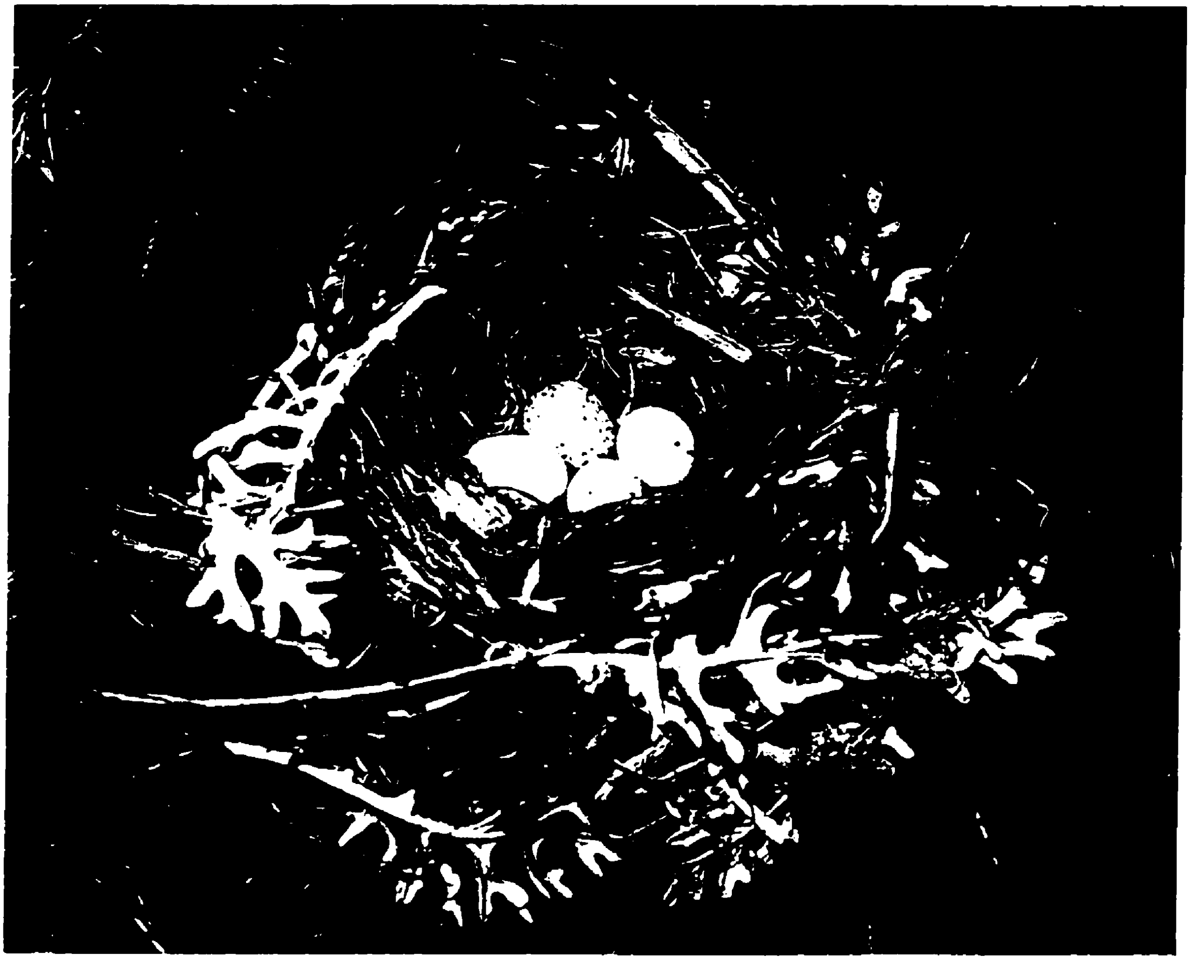

Nest and Eggs of the House Finch (*Carpodacus mexicanus*) with One Egg of the Brown-headed Cowbird (*Molothrus ater*).

Does one visit the cliffs at Pizmo to get the salty sting of the gales, or "to hear old Triton blow his wreathed horn," lo! the House Finch has come before.

W.L. Dawson

1

General Introduction

Avian Brood Parasitism

Interspecific avian brood parasites do not rear their young, but lay their eggs in the nests of other species, referred to as hosts, which provide parental care. Examples of brood parasitism occur in four orders of birds, including a parasitic duck (Anseriformes: Anatidae), cuckoos (Cuculiformes: Cuculidae), honey guides (Piciformes: Indicatoridae), and two passeriform families: weaver finches (Ploceidae), and cowbirds (Emberizidae) (Payne 1977). Some parasitic species act on a single host or a group of related host species, while others are generalists and distribute their parasitism among many different hosts (Friedmann 1929). Most instances of brood parasitism result in a decrease of host reproductive success (Rothstein 1990).

Parasite-Host Coevolution

Avian brood parasitism is an ideal system in which to examine coevolution because parasite-host interactions can be studied independently of other evolutionary processes (Rothstein 1990). Some host species have evolved anti-parasite defences in direct response to parasitism (Rothstein 1975, 1990). In turn, parasites may respond with counter-adaptations that make their parasitism more difficult for hosts to detect. Reciprocal adaptations between parasite and host may escalate and, therefore, result in an evolutionary arms race (Dawkins and Krebs 1979). The evolution of egg mimicry by cuckoos (*Cuculus canorus*) in response to rejection of their eggs by Reed Warblers (*Acrocephalus scirpaceus*) illustrates this process (Brooke and Davies 1988, Davies and Brooke 1988, 1989a, 1989b).

Host Choice

The reproductive success of a brood parasite depends greatly on its choice of host. Some studies have sought to identify patterns of host selection in a generalist brood parasite (Mason 1986, Wiley 1988, Post et al. 1990). Indeed, host choice may be influenced by a variety of factors including the timing of host breeding (Scott 1963, Payne 1973, Wiley and Wiley 1980, Finch 1983), characteristics of host habitat (Lowther and Johnston 1977, Hahn and Hatfield 1995), spatial distribution of nests (Clark and Robertson 1979, Martinez et al. 1996), host size (King 1979, Lowther 1979, Carter 1986, Mason 1986, Wiley 1988), host age (Smith 1981, 1984; Mark and

Stutchbury 1994), host aggression and nest attentiveness (Robertson and Norman 1977, Briskie and Sealy 1989, Hobson and Sealy 1989, Neudorf and Sealy 1992, 1994), egg discrimination by hosts (Rothstein 1975, 1978, 1982, 1990), host diet (Eastzer et al. 1980, Davies and Brooke 1989a, Middleton 1991), parasite competition with host nestmates (Finch 1983, Marvil and Cruz 1989, Soler and Soler 1991, Ortega and Cruz 1992) and duration of sympatry between parasite and host populations (Cruz et al. 1989, Nakamura 1990, Post et al. 1990, Briskie et al. 1992).

Colonizing Populations as Natural Experiments of Parasite-Host Interactions

How parasites select their hosts is poorly understood. This is because most studies of brood parasitism have involved parasite and host populations that have coexisted for a long time (Wiley 1985). Recent experiments on brood parasitism in allopatric and sympatric host populations have provided insights into the coevolutionary relationships between parasites and their hosts (Soler and Møller 1990, Briskie et al. 1992). New insights can be gained by studying parasitism during the initial contact of parasite and host populations, such as when an avian population colonizes an area. New parasite-host associations result from colonization by either parasite or host populations. If the history of such colonization processes is well documented, then interactions between host and parasite species can be chronicled within a known time frame.

Cowbirds and House Finches

The Brown-headed Cowbird (*Molothrus ater*) is a common brood parasite, known to parasitize more than 200 host species (Friedmann 1963, Friedmann et al. 1977, Friedmann and Kiff 1985). It is widely distributed in North America from southern Canada to southern Mexico (Lowther 1993). Recent colonization of eastern North America by the House Finch (*Carpodacus mexicanus*, Elliott and Arbib 1953) has provided indigenous cowbirds with a new host species. Because House Finch colonization has been well documented, the time that cowbirds have been associated with this host can be accurately determined throughout eastern North America. Colonization by House Finches provides a singular opportunity to investigate the biology of brood parasitism in a dynamic host-parasite relationship.

Objectives of the Thesis

This dissertation concerns interactions between Brown-headed Cowbirds and House Finches in North America. The study is based on examination of incidence of parasitism in the eastern colonized range and in the native western population of House Finches. This study addresses several important aspects of parasite-host coevolution in House Finches and cowbirds. In chapter 2, I focus on how frequently House Finches are parasitized by cowbirds, ascertain if parasitism has a significant effect on House Finch reproductive success, and determine if House Finches demonstrate anti-parasite defences. In chapter 3, I investigate what proportion of the host community is represented by House Finches in the colonized eastern range and the availability of House Finches as hosts. In chapter 4, I assess reproductive success of cowbirds in House Finch nests and its potential impact on cowbird host choice. In chapter 5, I investigate whether or not geographic differences in frequency of parasitism reflect variation in host preference, and explore the roles of colonization and duration of sympatry in determining frequency of parasitism.

LITERATURE CITED

Briskie, J.V., and S.G. Sealy. 1989. Changes in nest defense against a brood parasite over the breeding cycle. Ethology 82: 61-67.

Briskie, J.V., S.G. Sealy, and K.A. Hobson. 1992. Behavioral defenses against avian brood parasitism in sympatric and allopatric host populations. Evolution 46: 334-340.

Brooke, M. De L., and N.B. Davies. 1988. Egg mimicry by cuckoos *Cuculus canorus* in relation to discrimination by hosts. Nature 335: 630-632.

Carter, M.D. 1986. The parasitic behavior of the Bronzed Cowbird in south Texas. Condor 88: 11-25.

Clark, K.L., and R.J. Robertson. 1979. Spatial and temporal multi-species nesting aggregations in birds as anti-parasite and anti-predator defences. Behav. Ecol. Sociobiol. 5: 359-371.

Cruz, A., J.W. Wiley, T.K. Nakamura, and W. Post. 1989. The Shiny Cowbird *Molothrus bonariensis* in the West Indian region - biogeographical and ecological implications. Pp. 519 - 540 *in* C.A. Woods (ed.), Biogeography of the West Indies - Past, Present, and Future. Sandhill Press. Gainesville, Fla.

Davies, N.B., and M. De L. Brooke. 1988. Cuckoos versus Reed Warblers: adaptations and counter-adaptations. Anim. Behav. 36: 262-284.

Davies, N.B., and M. De L. Brooke. 1989a. An experimental study of co-evolution between the cuckoo, *Cuculus canorus*, and its hosts. I. Host egg discrimination. J. Anim. Ecol. 58: 207-224.

Davies, N.B., and M. De L. Brooke. 1989b. An experimental study of co-evolution between the cuckoo, *Cuculus canorus*, and its hosts. II. Host egg markings, chick discrimination and general discussion. J. Anim. Ecol. 58: 225-236.

Dawkins, R., and J.R. Krebs. 1979. Arms races between and within species. Proc. R. Soc. Lond. Ser. B. 205: 489-511.

Eastzer, D., P.R. Chu, and A.P. King. 1980. The young cowbird: average or optimal nestling? Condor 82: 417-425.

Elliott, J.J., and R.S. Arbib, Jr. 1953. Origin and status of the House Finch in the eastern United States. Auk 70: 31-37.

Finch, D.M. 1983. Brood parasitism of the Abert's Towhee: timing, frequency, and effects. Condor 85: 355-359.

Friedmann, H. 1929. The Cowbirds, A Study in the Biology of Social Parasitism. C.C. Thomas, Springfield, Ill.

Friedmann, H. 1963. Host relations of the parasitic cowbirds. U.S. Natl. Mus. Bull. 233.

Friedmann, H., and L.F. Kiff. 1985. The parasitic cowbirds and their hosts. Proc. West. Found. Vert. Zool. 2: 226-304.

Friedmann, H., L.F. Kiff, and S.I. Rothstein. 1977. A further contribution to knowledge of the host relations of the parasitic cowbirds. Smithsonian Contr. Zool. 235: 1-75.

Hahn, D.C., and J.S. Hatfield. 1995. Parasitism at the landscape scale: cowbirds prefer forests. Conserv. Biol. 9: 1415-1424.

Hobson, K.A., and S.G. Sealy. 1989. Responses of Yellow Warblers to the threat of cowbird parasitism. Anim. Behav. 38: 510-519.

King, A.P. 1979. Variables affecting parasitism in the North American cowbird (*Molothrus ater*). Ph.D. diss. Cornell University, Ithaca.

Lowther, P.E. 1979. Nest selection by Brown-headed Cowbirds. Wilson Bull. 91: 118-122.

Lowther, P.E. 1993. Brown-headed Cowbird (*Molothrus ater*). *In* A. Poole and F. Gill (eds.), The Birds of North America, No. 47. Philadelphia: The Academy of Natural Sciences; Washington, D.C.: The America Ornithologists' Union.

Lowther, P.E., and R.F. Johnston. 1977. Influence of habitat on cowbird host selection. Kans. Ornithol. Soc. Bull. 28: 36-40.

Mark, D., and B.J. Stutchbury. 1994. Response of a forest-interior songbird to the threat of cowbird parasitism. Anim. Behav. 47: 275-280.

Martinez, J.G., M. Soler, and J.J. Soler. 1996. The effect of magpie breeding density and synchrony on brood parasitism by Great Spotted Cuckoos. Condor 98: 272-278.

Marvil, R.E., and A. Cruz. 1989. Impact of Brown-headed Cowbird parasitism on the reproductive success of the Solitary Vireo. Auk 106: 476-480.

Mason, P. 1986. Brood parasitism in a host generalist, the Shiny Cowbird: II. Host selection. Auk 103: 61-69.

Middleton, A.L.A. 1991. Failure of Brown-headed Cowbird parasitism in nests of the American Goldfinch. J. Field Ornithol. 62: 200-203.

Nakamura, H. 1990. Brood parasitism by the Cuckoo *Cuculus canorus* in Japan and the start of new parasitism on the Azure-winged Magpie *Cyanopica cyana*. Jap. J. Ornithol. 39: 1-18.

Neudorf, D.L., and S.G. Sealy. 1992. Reactions of four passerine species to threats of predation and cowbird parasitism: enemy recognition or generalized responses? Behaviour 123: 84-105.

Neudorf, D.L., and S.G. Sealy. 1994. Sunrise nest attentiveness in cowbird hosts. Condor 96: 162-169.

Ortega, C.P., and A. Cruz. 1992. Differential growth patterns of nestling Brown-headed Cowbirds and Yellow-headed Blackbirds. Auk 109: 368-376.

Payne, R.B. 1973. The breeding season of a parasitic bird, the Brown-headed Cowbird, in central California. Condor 75: 80-99.

Payne, R.B. 1977. The ecology of brood parasitism in birds. Ann. Rev. Ecol. Syst. 8: 1-28.

Post, W., T.K. Nakamura, and A. Cruz. 1990. Patterns of Shiny Cowbird parasitism in St. Lucia and southwestern Puerto Rico. Condor 92: 461-469.

Robertson, R.J., and R.F. Norman. 1977. The function and evolution of aggressive host behaviour towards the Brown-headed Cowbird (*Molothrus ater*). Can J. Zool. 55: 508-518.

Rothstein, S.I. 1975. An experimental and teleonomic investigation of avian brood parasitism. Condor 77: 250-271.

Rothstein, S.I. 1978. Mechanisms of avian egg-recognition: additional evidence for learned components. Anim. Behav. 26: 671-677.

Rothstein, S.I. 1982. Mechanisms of avian egg recognition: which egg parameters elicit responses by rejecter species? Behav. Ecol. Sociobiol. 11: 229-239.

Rothstein, S.I. 1990. A model system for coevolution: avian brood parasitism. Ann. Rev. Ecol. Syst. 21: 481-508.

Scott, D.M. 1963. Changes in the reproductive activity of the Brown-headed Cowbird within the breeding season. Wilson Bull. 75: 123-129.

Smith, J.N.M. 1981. Cowbird parasitism, host fitness, and age of the host female in an island Song Sparrow population. Condor 83: 152-161.

Smith, J.N.M. 1984. Age, experience, and enemy recognition by wild Song Sparrows. Behav. Ecol. Sociobiol. 14: 101-106.

Soler, M., and A.P. Møller. 1990. Duration of sympatry and coevolution between the Great Spotted Cuckoo and its magpie host. Nature 343:748-50.

Soler, M., and J.J. Soler. 1991. Growth and development of Great Spotted Cuckoos and their magpie host. Condor 93: 49-54.

Wiley, J.W. 1985. Shiny Cowbird parasitism in two avian communities in Puerto Rico. Condor 87: 167-176.

Wiley, J.W. 1988. Host selection by the Shiny Cowbird. Condor 90: 289-303.

Wiley, R.H., and M.S. Wiley. 1980. Spacing and timing in the nesting ecology of a tropical blackbird: comparison of populations in different environments. Ecol. Monogr. 50: 153-178.

2

Cowbird Parasitism and Productivity of House Finch Hosts

INTRODUCTION

Brood parasitism by the Brown-headed Cowbird often reduces host reproductive success. Generally hosts suffer reproductive cost because their eggs are removed or damaged by the parasite (Smith and Arcese 1994). The hatchability of remaining host eggs may be compromised (Payne 1977, Petit 1991). Furthermore, parasites frequently outcompete host nest mates for parental feedings (Clark and Robertson 1981). However, the degree to which cowbirds affect the productivity of their hosts is variable. Parasitism can cause a severe depressive effect on the reproductive output of some species (Grzybowski et al. 1986, Marvil and Cruz 1989) while other hosts are capable of rearing both the parasite and their own young (Røskaft et al. 1990).

Exploitation of new host populations by cowbirds has resulted largely from range expansions by these social parasites (Mayfield 1965, Post and Wiley 1977, Post et al. 1993, Rothstein 1994), but also may occur through changes in host distribution. The House Finch was introduced to eastern North America through the release of caged birds on Long Island, NY, in 1940 (Elliott and Arbib 1953). A founder population became established there, which increased in numbers and spread swiftly. Within 50 years the species had colonized much of the eastern United States and southeastern Canada (Hill 1993). In their native western range, House Finches are rarely parasitized by cowbirds (Friedmann 1966, Friedmann et al. 1977). As a result, little is known about the effects of parasitism on House Finch reproductive success. In contrast, eastern House Finches may be highly parasitized (Peck and James 1987). Because House Finches and cowbirds have only recently become associated in the east, the study of interactions between this host and parasite are of particular interest from a coevolutionary perspective.

I studied incidence of Brown-headed Cowbird parasitism and its effects on the productivity of recently established House Finches in southern Ontario. Occurrence of House Finches in Ontario was first documented in 1972 (Sprague and Weir 1984) and in 1978 the first nest was discovered, which also contained one cowbird egg (James 1978). Since that time numbers of House Finches have increased rapidly in the Province, most notably on the Niagara peninsula where the species established a foothold in the early 1980s (Kozlovic 1994). Currently, House Finches are common in many urban centres throughout southern Ontario. The purpose of the present study is to address two questions: (1) does cowbird activity have a significant impact on House Finch reproductive success, and (2) if so, do House Finches demonstrate anti-parasite behaviour that may mitigate the effects of parasitism?

MATERIALS AND METHODS

Study Site

The study was conducted during 1983 - 1985 at St. Catharines, Regional Municipality of Niagara, Ontario (43°10' N, 79°15' W). Observations were made in approximately 5 km^2 of the city bounded by Lake Ontario to the north and Martindale Pond to the west. The habitat was composed of suburban residential neighbourhoods interspersed with parks, sports fields and wooded ravines. Numerous ornamental trees including spruce (*Picea* spp.), juniper (*Juniperus* spp.), and white cedar (*Thuja occidentalis*) provided nesting sites for the House Finches.

Field Procedures

House Finch nests were found from late April to mid July. Observations of singing males or females carrying nest material were usually indicative of a nest site nearby. Nests were built 1.2 to 4.3 m above ground ($\bar{x} = 2.6$, SD = 0.71, $n = 74$) and contents easily observed with the aid of a six-foot (2m) stepladder and mirror attached to an extensible rod. Most nests were found during construction and following completion, were visited daily between 07:00 and 16:00 h to determine clutch initiation date, egg size, clutch size, fate of eggs during the laying period and incidence of cowbird parasitism.

The date of clutch initiation was determined explicitly by observation of the first egg laid or implicitly by backdating from the laying or hatching date of the last egg. House Finches usually lay 4 or 5 eggs (one egg per day). The modal incubation period from the laying of the last egg to its hatching was 13 days (Kozlovic 1987). Therefore, a total of 17 or 18 days, depending on the clutch size, was required from the laying of the first egg to the completion of incubation. Initiation date was not determined for clutches that were found after completion but failed before hatching. A clutch was deemed complete if it included at least three eggs and received no additional eggs for two successive days.

Eggs in each clutch were sequentially numbered at the larger end with an ink marker to indicate the order of laying. For each egg the maximum length and breadth were measured to the nearest 0.05 mm with dial calipers and egg mass (taken on day of laying) was determined with a 5-g Pesola® spring scale accurate to 0.05 g. In 1983 egg mass was not taken because measurements were done after clutches had been completed.

Frequency of cowbird parasitism was calculated as the proportion of active House Finch nests that contained at least one cowbird egg. Nests were considered active if parasitized or if a female House Finch was in attendance until at least three eggs were laid. Time of appearance of cowbird eggs in each clutch was measured in days from the date of the first finch egg laid. Finch eggs that disappeared from parasitized nests were assumed to have been removed by cowbirds (Rothstein 1975a).

Nests were visited every two or three days during incubation to determine nest survivorship and fate of individual eggs. Because the incubation period of cowbird eggs is shorter than that of the House Finch (Harrison 1978), daily nest visits were resumed several days before the expected hatch date of finch eggs so that the hatching date of cowbirds could be determined. Nests were monitored thereafter until nest failure or departure of all young from the nest to document number hatched, fate of young during the nestling period, number leaving nest, and nestling growth of House Finches.

In 1984 nestling growth of House Finches was determined from 7 parasitized (22 nestlings) and 11 unparasitized (33 nestlings) broods. For each nestling the following measurements were taken: bill length (from the anterior margin of the nostril to the tip of the bill), bill depth (from the ventral margin of the gnathotheca to the dorsal margin of the rhinotheca at the base of the bill), manus length (from the base of the alula to the fleshy distal tip of the manus), wing length (from the most anterior location of the wrist joint to the distal end of the longest primary, unflattened), tarsometatarsus length (from the notch at the tibiotarsal-tarsometatarsal joint to the most distal point of the bend at the tarsometatarsal-basal phalanx joint of digit III) and body mass. Linear measurements were made with dial calipers to the nearest 0.05

mm, except for wing length that was measured to the nearest 0.5 mm with a ruler. Body mass was taken using either 10- or 50-g Pesola® spring scales accurate to 0.1 and 0.25 g, respectively. Individual identification of young in a nest was through toenail-clipping (St. Louis et al. 1989). Nestlings were measured daily between 07:00 and 16:00 h from hatching (day 0) to day 14. Nests were visited at approximately the same time each day. Although nests were monitored for the entire nestling period, nestlings were not measured after day 14 to prevent young from leaving the nest prematurely.

Treatment of Data

Effects of cowbird parasitism, and year, on clutch initiation date, egg size, clutch size, number hatched and leaving the nest were examined with two-way analysis of variance (ANOVA; procedure GLM of SAS Institute, 1988) using ranked data. To prevent inflated degrees of freedom, analyses of egg size were performed using the mean size of eggs for each clutch before calculating means for effects of parasitism and year. Measures of House Finch hatching success (proportion of eggs from which young hatched), nesting success (proportion of hatchlings that departed the nest) and breeding success (proportion of eggs that became young, which departed the nest) were compared between parasitized and unparasitized nests after adjustment for the effects of number of eggs and number hatched using analysis of covariance (ANCOVA; procedure GLM of SAS Institute, 1988). My data include only eggs that were successfully incubated (i.e., at least one young hatched) and broods that were successfully reared (i.e., at least one finch departed the nest).

To increase the power of ANOVA and ANCOVA tests, degrees of freedom were preserved by removal of any nonsignificant interaction or year effects and rerunning the tests. In all tests, there was no significant interaction of parasitism with year (ANOVA or ANCOVA $F \leq 1.71$, $P \geq 0.1889$). Furthermore, there was no significant difference in egg size or reproductive parameters among years (ANOVA or ANCOVA $F \leq 3.07$, $P \geq 0.0555$).

To determine if cowbird parasitism influenced postnatal development of finches, nestling growth patterns were compared between samples of parasitized and unparasitized nests. A general linear model was employed to describe increase of bill size and wing length from hatching to 14 d and differences in growth rate were tested between samples using ANCOVA. Nonlinear growth of body mass and lengths of tarsometatarsus and manus was described using a logistic model (Ricklefs 1984):

$$[1] \qquad C_t = A\{1+\exp[-K(t-I)]\}^{-1}$$

where C_t is the magnitude of the character at age t, A is the asymptotic size of the character, K is the growth rate constant, and I is the inflection point of the growth curve. Growth curves were fitted to the data and growth parameters estimated using nonlinear least-squares regression (Gauss-Newton method, procedure NLIN of SAS

Institute, 1988). Differences in nestling growth between samples were tested using analysis of residual sum of squares (ARSS) (Chen et al. 1992). The coefficient of determination (r^2) was used as the measure of goodness-of-fit. Significance tests were carried out separately for each of the six nestling characters; however, this approach increased the likelihood of making a type-I error (Rice 1989). Therefore, probability values were adjusted for a group-wide significance level of 0.05 using the sequential Bonferonni technique outlined in Rice (1989). To avoid pseudoreplication, comparisons of growth were performed using the mean size of siblings at the same age.

RESULTS

Breeding Season of Host and Parasite

The breeding season of House Finches lasted about 3 months, with the first clutch found on 23 April and the last on 17 July (Fig. 2.1). Most breeding (72%) occurred from mid-May to late June. Timing of egg laying differed significantly among years ($F_{[2,75]} = 5.93$, $P = 0.0041$); breeding averaged about 18 days earlier in 1985 than in previous years (1983: $\bar{x}$ = 11 June, SD = 16 d, n = 30; 1984: $\bar{x}$ = 14 June, SD = 17 d, n = 24; 1985: $\bar{x}$ = 26 May, SD = 24 d, n = 24). Cowbird eggs were first observed in finch nests on 1 May and parasitism continued to 17 July (Fig. 2.1). Most parasitism (90%) occurred during May and June. The cowbird breeding season differed significantly among years ($F_{[2,26]} = 3.94$, $P = 0.0321$); the mean egg-laying date was 20 d earlier in 1985 than in either 1983 or 1984 (1983: $\bar{x}$ = 15 June, SD = 12 d, $n = 7$; 1984: $\bar{x}$ = 16 June, SD = 17 d, $n = 15$; 1985: $\bar{x}$ = 28 May, SD = 16 d, $n = 7$). Cowbird breeding coincided with the major portion of House Finch nesting; mean clutch initiation date did not differ significantly ($F_{[1,76]} = 1.90$, $P = 0.1721$) between parasitized and unparasitized clutches ($\bar{x}$ = 11 June, SD = 17 d, $n = 29$ and $\bar{x}$ = 5 June, SD = 22 d, $n = 49$, respectively).

Cowbird Parasitism

Thirty-three (40.2%) of a total of 82 House Finch nests observed contained at least 1 of the 43 cowbird eggs laid (Table 2.1). Frequency of parasitism varied significantly among years ($\chi^2 = 8.448$, df = 2, $P = 0.015$) and was highest in 1984. Cowbirds laid eggs at any time in the host egg-laying sequence (Table 2.2). Most cowbird eggs (76%) were laid within two days of the first House Finch egg laid and in one nest a single cowbird egg was laid 16 d after the House Finch clutch was begun, just as the finch eggs started to hatch. Mean appearance time of cowbird eggs during the House Finch laying period was 1.54 d (SD = 1.444, n = 24) after clutch initiation. Frequency distributions of cowbird eggs in finch nests are given in Table 2.3. A single cowbird egg was deposited in the majority (75.8%) of parasitized House Finch nests, and two eggs (18.2%) per nest was the next most frequent number. Two cowbird eggs were laid on the same day in each of three nests. Three cowbird eggs were found in only two (6.1%) nests one of which had no finch eggs. Mean number of cowbird eggs per parasitized nest, or intensity of parasitism, was 1.30 (SD = 0.59). Intensity of parasitism did not vary significantly among years (χ^2 = 1.524, df = 4, P = 0.822). To test if cowbirds parasitized nests randomly, data among years were combined. The number of cowbird eggs per nest was not significantly different (χ^2 = 4.043, df = 2, $P > 0.10$) from a truncated Poisson distribution (Orians et al. 1989). Seasonal variation in the number of cowbird eggs per parasitized nest is shown in Figure 2.2. House Finch nests with two or more cowbird eggs appeared from early May to mid-July. Based on differences of egg size and maculation (Dufty 1983), these nests appeared to contain eggs laid by more than one cowbird. Cowbird eggs hatched from 8 to 14 d after they appeared in finch nests ($\bar{x}$ = 11.5, SD = 1.366, n = 16). Of 30 cowbird eggs that were successfully incubated, 27 (90%) hatched. Cowbird eggs hatched 0 to 5 d in advance of finch eggs ($\bar{x}$ = 2.3, SD = 1.129, n = 20).

House Finch Reproduction

Egg Size

Egg sizes of House Finches in parasitized and unparasitized nests are given in Table 2.4. No significant differences between samples were found in egg length ($F_{[1,72]} = 0.00$, $P = 0.9513$), breadth ($F_{[1,72]} = 0.12$, $P = 0.7303$) or mass ($F_{[1,34]} = 0.90$, $P = 0.3488$).

Reproductive Success

Number of House Finch eggs in parasitized nests was significantly smaller (ANOVA $F_{[1,77]} = 6.54$, $P = 0.0125$) than in unparasitized nests (Table 2.5). Accordingly, parasitized nests experienced significantly fewer young hatched (ANOVA $F_{[1,52]} = 4.55$, $P = 0.0377$) than unparasitized nests. However, when samples were adjusted for variation in number of House Finch eggs in each nest, hatching success was not affected by parasitism (ANCOVA $F_{[1,51]} = 0.74$, $P = 0.3930$). Parasitized broods produced significantly fewer young that departed from the nest (ANOVA $F_{[1,19]} = 5.68$, $P = 0.0277$) than unparasitized broods. Parasitism did not have a significant effect (ANCOVA $F_{[1,18]} = 1.22$, $P = 0.2842$) on nesting success after variation in the number of young hatched in each nest was taken into account. Similarly, breeding success was not significantly different between samples when the number of House Finch eggs in each nest was the covariate (ANCOVA $F_{[1,18]} = 1.32$, $P = 0.2655$).

Nestling Growth

Growth of House Finch nestlings in parasitized and unparasitized nests is shown in Fig. 2.3. Comparison of nestling growth parameters between samples is given in Table 2.6. Both logistic and linear models provided reasonable descriptions of nestling growth (logistic model: r^2 approximation ≥ 0.97; linear model: r^2 approximation ≥ 0.90). There was no significant difference in overall growth of any nestling character between parasitized and unparasitized nests based on a sequential

Bonferonni adjustment of P-values (ARSS: body mass, $F_{[3,164]} = 1.986$, $P > 0.10$; tarsometatarsus length, $F_{[3,161]} = 1.039$, $P > 0.25$; manus length, $F_{[3,161]} = 3.366$, $0.01 < P < 0.025$; ANCOVA: wing length, $F_{[1,54]} = 1.64$, $P = 0.2054$; bill length, $F_{[1,163]} = 0.10$, $P = 0.7495$; bill depth, $F_{[1,163]} = 0.01$, $P = 0.9052$).

DISCUSSION

House Finches were commonly parasitized by Brown-headed Cowbirds at St. Catharines, Ontario; parasitism occurred in 40.2% of 82 nests observed in the three years of the study. Accordingly, the House Finch is regarded as a heavily parasitized host species in my study area (Mayfield 1965). Because House Finches in Ontario have a protracted egg-laying season, they are available as hosts for the entire cowbird breeding period. Cowbird egg-laying dates in the province range from 19 April to 5 August, with 50 percent of all nests parasitized during the period 28 May to 20 June (Peck and James 1987). At St. Catharines House Finches began to lay approximately one week in advance of cowbirds and have been observed breeding there as early as 19 March (Kozlovic 1988). Early breeding allows some House Finches to complete their first clutches before the onset of cowbird laying, and thus escape parasitism.

Cowbirds laid their eggs randomly in the nests of House Finches; previously parasitized nests were neither avoided nor favoured. Other studies have found both random and non-random distributions of parasitized nests (see Orians et al. 1989). Cowbirds may lay eggs in previously parasitized nests when few or no unparasitized host nests are available (Smith and Arcese 1994). This does not appear to be the reason for multiple parasitism at St. Catharines because unparasitized finch nests were available throughout the cowbird breeding season. Multiple parasitism tended to occur during the peak of the cowbird breeding season. In this respect, intensity of parasitism on House Finches is similar to that observed in other studies (Wolf 1987, Orians et al. 1989).

Despite frequent cowbird parasitism, House Finches sustained relatively little reproductive loss because of it. Parasitized finches had reduced clutches and hatched fewer young than unparasitized birds, but successfully reared most of their young. Cowbird parasitism often decreases host reproductive success (Rothstein 1990). This was observed at St. Catharines where cowbirds reduced the clutch size of parasitized House Finches by about one egg. Hatchability of the remaining eggs, however, was unaffected by parasitism, which suggests that the presence of cowbird eggs did not interfere with successful incubation of the smaller finch eggs (Payne 1977). Furthermore, finch nestlings were equally likely to depart from parasitized and unparasitized nests. Percent of eggs hatched and young that left the nest were not significantly reduced in parasitized nests of the Dark-eyed Junco (*Junco hyemalis*, Wolf 1987). Similarly, the proportion of Song Sparrow (*Melospiza melodia*) young that survived to six days and four weeks was not influenced by parasitism (Smith 1981). Interestingly, Middleton (1977) found that hatching and fledging success of parasitized Amercian Goldfinches (*Carduelis tristis*) was higher than in unparasitized nests. In contrast, Black-capped (*Vireo atricapillus*) and Solitary vireos (*Vireo solitarius*) experienced very low fledging success when parasitized (Grzybowski et al. 1986, Marvil and Cruz 1989). Although House Finches experienced a reduction of reproductive output through the removal of eggs by cowbirds, this initial cost of parasitism appears to have had no effect on the subsequent success of remaining House Finch eggs.

Overall growth of House Finch nestlings was not influenced by the presence of cowbirds. Other studies have also found that having cowbird young as nest mates had little or no effect on the development of host young (Hofslund 1957, Murphy 1986, Wolf 1987, Petit 1991, Smith and Arcese 1994). In these cases foster parents successfully reared both their own and parasite young. This was not true of House Finches because cowbird young did not survive in the nests of this host. No cowbirds were reared apparently because they were fed a granivorous diet by their foster parents unsuitable for cowbird growth and maturation; in another study malnourished cowbirds survived on average only 3 d after hatching (Kozlovic et al. 1996). As a result, cowbird young were effectively not detrimental to host nestlings for most of the nestling period.

Frequency of parasitism on House Finches shows considerable geographical variation both in its native western and introduced eastern ranges. Ehrlich et al. (1988) considered the House Finch to be a common host in the east and incidence of parasitism there can be very high; at Guelph, Ontario 88% of House Finch nests contained cowbird eggs (Graham 1987). But reports of parasitism are few in other parts of the eastern range. Bull (1974) noted only three instances of parasitism in New York; two of which occurred on Long Island (Friedmann et al. 1977). Parasitism was also found at Salem, North Carolina, in a small colony of House Finches, which included at least four breeding pairs (Potter 1978, Potter and Whitehurst 1981). Only 2 cowbird eggs were detected in 350 nests in southeastern Michigan (Hill 1993). Based on data from nest records, incidence of parasitism is 11% throughout the northeastern United States (Wootton 1986). Compared to their eastern counterparts, western House Finches are rarely parasitized. Only 20 cases of parasitism have been reported in the literature for House Finches in their native range (Friedmann 1929, 1963, 1966; Friedmann et al. 1977; Friedmann and Kiff 1985) and data from nest records indicate that only 1% of nests there contain cowbird eggs (Wootton 1986).

Greater frequency of parasitism on House Finches in eastern North America may be attributed to a higher density of cowbirds there or to a difference in the availability of host species (Wootton 1986). Breeding Bird Survey (BBS) data (1966-1994, Sauer et al. 1996) indicate that relative abundance of cowbirds is not significantly greater in the east ($t = 0.847$, df = 39, $P = 0.4022$) than in the west. Average number of birds observed per BBS route in each state or province ranged from 2.15 to 18.87 ($\bar{x} = 8.05$, SD = 3.74, $n = 28$) and 1.72 to 13.63 ($\bar{x} = 6.99$, SD = 3.69, $n = 13$) for eastern and western regions, respectively (see Robbins et al. 1986, for descriptions of BBS regions). Frequency of cowbird parasitism on House Finches may be related to the abundance of hosts. Recent population declines of Neotropical migrants in North America (Robbins et al. 1989, Askins et al. 1990) may reduce cowbird opportunities for parasitism among native nesting species. Concomitant exponential growth of the House Finch population in the east (Robbins et al. 1986), however, has increasingly provided cowbirds there access to this additional host species.

Higher frequency of parasitism also may be the result of a recent association between a host and parasite. New hosts may experience greater frequency of parasitism than traditional hosts (Nakamura 1990). Hosts of the Brown-headed Cowbird can be classified as either accepters or rejecters of cowbird eggs and rejection behaviour, which most typically involves ejection of the cowbird egg from the nest, is convincingly explained as an evolved response by hosts in response to parasitism (Rothstein 1975a, 1975b). Because parasitism of rejecter species almost always fails, selection should favour parasitism of only accepter hosts. Species encountered for the first time by cowbirds may be "perceived" by these social parasites as accepters because, in the absence of parasitism, the hosts have had no opportunity to evolve rejection behaviour. As a result, novel hosts, which would constitute suitable species in this case, may be favoured by cowbirds and thus sustain a high incidence of parasitism.

Cowbirds of eastern North America appear to have had no previous contact with House Finches. Colonization of the East by cowbirds during the last century likely occurred through an eastward expansion from their native range, which originally occupied much of the mid-west (Mayfield 1965). Before their introduction, House Finches occurred mainly west of the Great Plains and were not in contact with the eastern cowbird population. Frequent parasitism found in this study suggests that cowbirds may parasitize House Finches, at least initially. However, failure of parasitism in House Finch nests suggests that cowbirds may be under selection pressure to avoid this host.

At St. Catharines, House Finches accepted all cowbird eggs save in a nest containing only three cowbird eggs, which was abandoned. House Finches will accept cowbird eggs if there are no finch eggs present (Kozlovic, unpubl. data), and nests experimentally parasitized with artificial cowbird eggs (Rothstein 1975a). Desertion of parasitized nests by House Finches has been noted only twice (Hanna 1933, Hensley 1959). Because cowbirds are often reared at the expense of host young, selection should favour rejection of cowbird eggs by hosts, as an anti-parasite defence (Rothstein 1975b). The failure of some hosts to evolve rejection behaviour remains perplexing. Rohwer and Spaw (1988) suggested that hosts may accept cowbird eggs because rejection is not feasible; in some cases the cost of rejecting may exceed that of accepting the parasite (Rohwer et al. 1989, Røskaft et al. 1990, 1993, Sealy 1995). Alternatively, rejection behaviour may not yet have evolved as an anti-parasite defence in accepter species (Rothstein 1975b, 1990; Ward et al. 1996). Parasitized finches did not experience a significant decrease in nesting or breeding success compared to unparasitized individuals. Furthermore, finches were reared even in situations involving multiple parasitism. Consequently, rejection of cowbird eggs does not appear to be selectively advantageous for House Finches.

Acceptance of cowbird eggs does not imply that hosts show no anti-parasite behaviour. The cost of parasitism to House Finches occurs through the removal of their eggs by cowbirds. Therefore, finches would be expected to demonstrate adaptations that would reduce the likelihood of being parasitized. Indeed, House Finches do respond aggressively to cowbirds and breeding pairs can successfully drive off the parasite from their nest (Kozlovic, pers. obs.). Many accepter species recognize cowbirds as threats (Robertson and Norman 1977, Briskie and Sealy 1989, Neudorf and Sealy 1992) and their aggressive behaviour may serve either to distract or supplant the parasite from the nest. However, host aggression, particularly among small species, is often not sufficient defence against parasitism and its conspicuousness may even assist cowbirds in locating the nests of potential hosts (Robertson and Norman 1976, Uyehara and Narins 1995). Given the high frequency of parasitism found in the present study, host aggression is probably not regularly effective in preventing parasitism of House Finch nests.

Aggressive behaviour of House Finches towards cowbirds is probably not a phenomenon that has emerged since contact of these two species in eastern North America. Both species are co-distributed in their western ranges and studies indicate that hosts showing a history of sympatry with cowbirds are more likely to behave aggressively towards the parasite than those experiencing cowbird parasitism for the first time (Robertson and Norman 1976, Briskie et al. 1992). Conceivably, individuals that founded the eastern finch population could recognize cowbirds as threats. Since that time selection for host aggression in the east probably persists through continued association of House Finches and cowbirds (see Cruz and Wiley 1989).

Table 2.1. Frequency of Brown-headed Cowbird parasitism of House Finch nests at St. Catharines, Ontario.

Year	Nests observed	Nests parasitized	Cowbird eggs
1983	33	10 (30.3)[a]	14
1984	25	16 (64.0)	20
1985	24	7 (29.2)	9

[a] (percent)

Table 2.2. Number of cowbird eggs laid during the House Finch laying and incubation period at St. Catharines, Ontario.

	Days after clutch initiation						
	0	1	2	3	4	5	16
1983	1						1
1984	5	4	5		1	1	
1985	1	2	1	2	1		

Table 2.3. Frequency distributions of cowbird eggs laid in House Finch nests at St. Catharines, Ontario.

	Cowbird eggs per nest		
Year	1	2	3
1983	7(70.0)[a]	2(20.0)	1(10.0)
1984	13(81.3)	2(12.5)	1(6.3)
1985	5(71.4)	2(28.6)	

[a] Number of nests containing a particular number of cowbird eggs (percent).

Table 2.4. Measurements of House Finch eggs in relation to cowbird parasitism at St. Catharines, Ontario.

Egg	Parasitized nests	Unparasitized nests
Length (mm)	19.68±0.98(27)[a]	19.56±0.86(47)
Breadth (mm)	14.41±0.61(27)	14.40±0.50(47)
Mass (mm)	2.24±0.23(19)	2.16±0.22(17)

[a] mean ± SD (number of nests).

Table 2.5. Reproductive success of House Finches in relation to cowbird parasitism at St. Catharines, Ontario.

	Parasitized nests	Unparasitized nests
Number of eggs	3.50±1.20(30)[a]	4.22±0.74(49)
Number hatched[b]	2.87±1.49(23)	3.74±1.00(31)
Hatching success (%)[b]	80.5	87.2
Number leaving nest[c]	2.64±1.21(11)	3.80±0.79(10)
Nesting success (%)[c]	82.9	92.7
Breeding success (%)[c]	74.4	84.4

[a] Mean ± SD (number of nests).
[b] Successfully incubated clutches (see text).
[c] Successfully reared broods (see text).

Table 2.6. Growth parameters of House Finch nestlings in relation to cowbird parasitism at St. Catharines, Ontario. In logistic equations of body mass, tarsometatarsus and manus length, A is the asymptotic size of the character, I is the inflection point of the growth curve, and K is the growth rate constant. In linear equations of increase in wing and bill size, b is the slope.

Character	Parasitized nests (n=7)	Unparasitized nests (n=11)
Body mass (g)		
A (g)	20.66±0.388[a]	19.32±0.361
I (days)	5.41±0.148	4.90±0.137
K (day^{-1})	0.396±0.017	0.434±0.020
Tarsometatarsus length (mm)		
A (mm)	18.55±0.237	18.30±0.288
I (days)	3.08±0.111	2.85±0.131
K (day^{-1})	0.335±0.013	0.352±0.017
Manus length (mm)		
A (mm)	16.79±0.240	17.07±0.226
I (days)	2.78±0.125	2.69±0.112
K (day^{-1})	0.32±0.014	0.33±0.013
Wing length (mm)		
b (mm day^{-1})	3.540±0.204	3.992±0.258
Bill length (mm)		
b (mm day^{-1})	0.285±0.006	0.282±0.007
Bill depth (mm)		
b (mm day^{-1})	0.238±0.005	0.237±0.007

[a] mean ± SE.

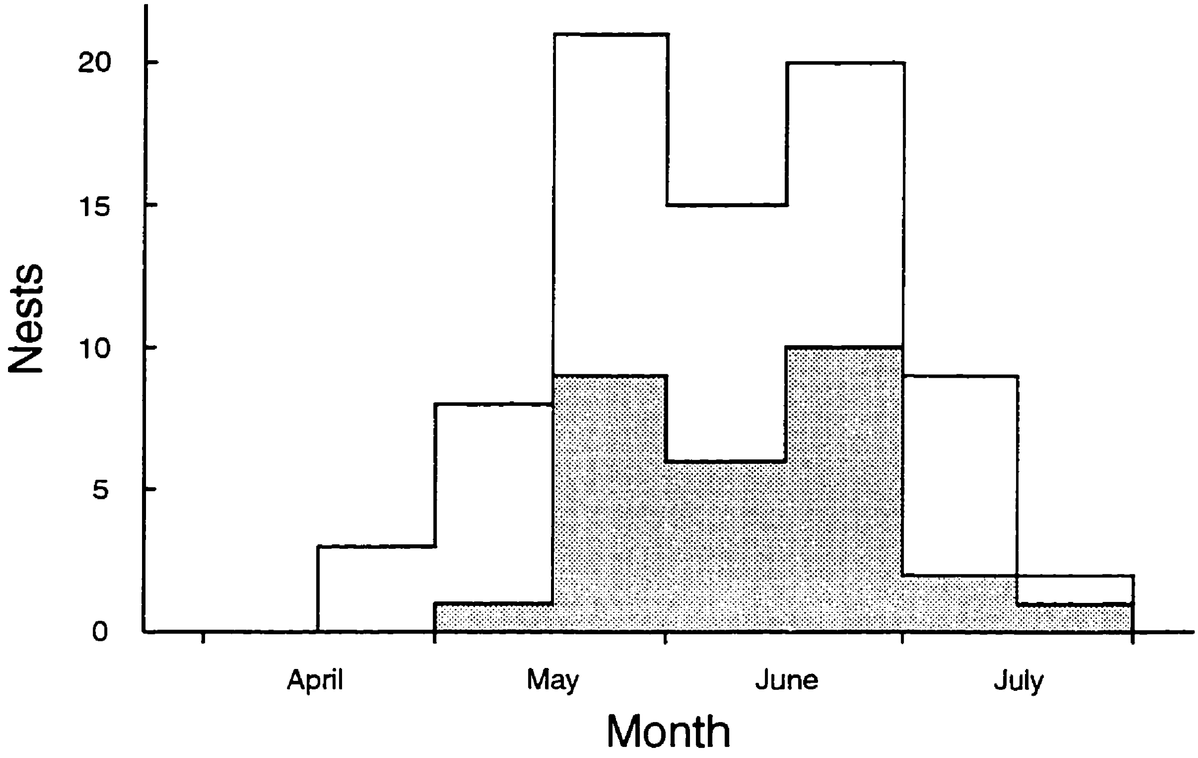

Fig. 2.1. Frequency distributions of House Finch clutch initiation date at St. Catharines, Ontario (1983-1985) for all nests (open histogram) and nests parasitized by the Brown-headed Cowbird (shaded histogram). Histogram class is 0.5 month.

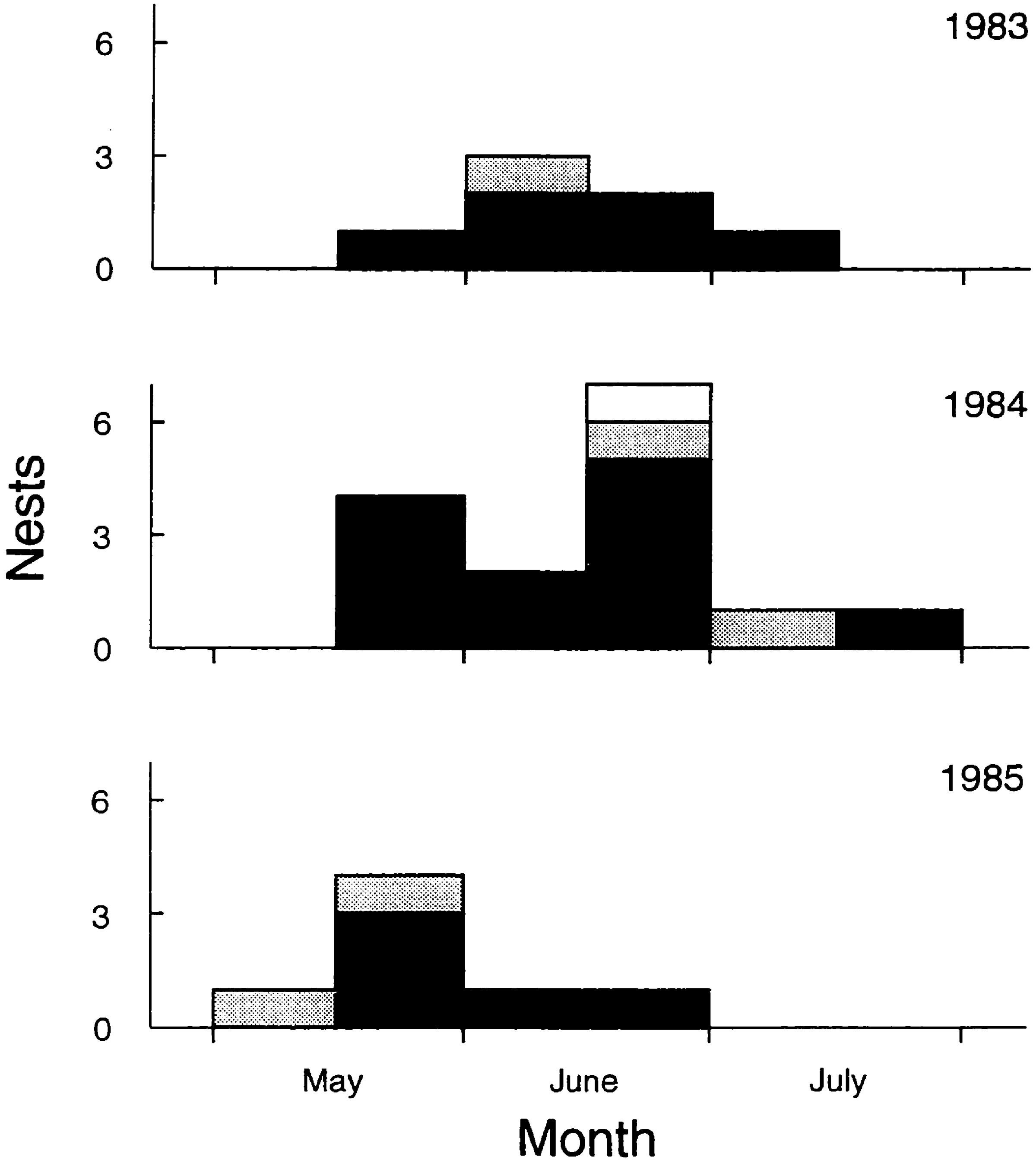

Fig. 2.2. Seasonal variation in the number of House Finch nests containing one (solid histogram), two (shaded histogram) and three (open histogram) cowbird eggs per nest in 1983, 1984 and 1985 at St. Catharines, Ontario. Histogram class is 0.5 month.

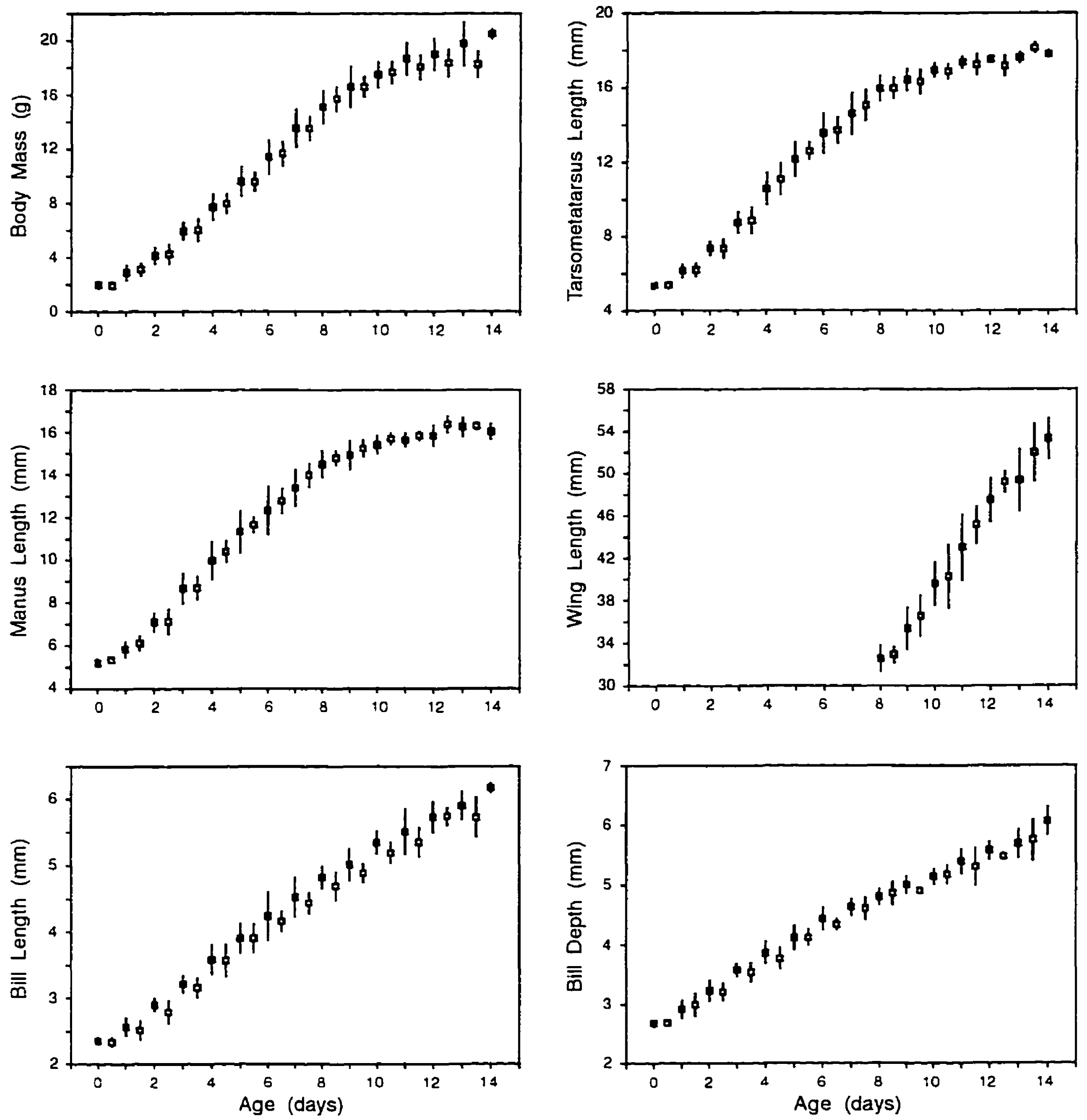

Fig. 2.3. Growth of House Finches in nests parasitized (solid squares, *n* = 7 broods) and unparasitized (open squares, *n* = 11 broods) by the Brown-headed Cowbird at St. Catharines, Ontario. Day 0 is day of hatch. Plotted values are the mean ± 1 SD. Nestling growth curves for unparasitized nests are offset by 0.5 d.

LITERATURE CITED

Askins, R.A., J.F. Lynch, and R. Greenberg. 1990. Population declines in migratory birds in eastern North America. Pp. 1-57 *in* D.M. Power (ed.), Current Ornithology. Volume 7. Plenum Press, New York, New York.

Briskie, J.V., and S.G. Sealy. 1989. Changes in nest defence against a brood parasite over the breeding cycle. Ethology 82: 61-67.

Briskie, J.V., S.G. Sealy, and K.A. Hobson. 1992. Behavioral defenses against avian brood parasitism in sympatric and allopatric host populations. Evolution 46: 334-340.

Bull, J. 1974. The Birds of New York State. Doubleday, Natural History Press, New York.

Chen, Y., D.A. Jackson, and H.H. Harvey. 1992. A comparison for von Bertalanffy and polynomial functions in modelling fish growth data. Can. J. Fish. Aquat. Sci. 49: 1228-1235.

Clark, K.L., and R.J. Robertson. 1981. Cowbird parasitism and evolution of anti-parasite strategies in the Yellow Warbler. Wilson Bull. 93: 249-258.

Cruz, A., and J.W. Wiley. 1989. The decline of an adaptation in the absence of a presumed selection pressure. Evolution 43: 55-62.

Dufty, A.M., Jr. 1983. Variation in the egg markings of the Brown-headed Cowbird. Condor 85: 109-111.

Ehrlich, P.R. D.S. Dobkin, and D. Wheye. 1988. The Birder's Handbook, A Field Guide to the Natural History of North American Birds. Simon and Schuster Inc., New York.

Elliott, J.J., and R.S. Arbib, Jr. 1953. Origin and status of the House Finch in the eastern United States. Auk 70: 31-37

Friedmann, H. 1929. The Cowbirds, A Study in the Biology of Social Parasitism. C.C. Thomas, Springfield, Ill.

Friedmann, H. 1963. Host relations of the parasitic cowbirds. U.S. Natl. Mus. Bull. 233.

Friedmann, H. 1966. Additional data on the host relations of the parasitic cowbirds. Smithsonian Misc. Coll. 149: 1-12.

Friedmann, H., and L.F. Kiff. 1985. The parasitic cowbirds and their hosts. Proc. West. Found. Vert. Zool. 2: 226-304.

Friedmann, H., L.F. Kiff, and S.I. Rothstein. 1977. A further contribution to knowledge of the host relations of the parasitic cowbirds. Smithsonian Contr. Zool. 235: 1-75.

Graham, D.S. 1987. Frequent cowbird parasitism of House Finches (*Carpodacus mexicanus*) at Guelph, Ontario. Ont. Birds 5: 116-117.

Grzybowski, J.A., J.T. Marshall, and R.B. Clapp. 1986. History and current population status of the Black-capped Vireo in Oklahoma. Am. Birds 40: 1151-1161.

Hanna, W.C. 1933. House Finch parasitized by Dwarf Cowbird and Black Phoebe nests occupied by House Finch. Condor 35: 205.

Harrison, C. 1978. A Field Guide to the Nests, Eggs and Nestlings of North American Birds. William Collins Sons and Co. Ltd., Glasgow.

Hensley, M.M. 1959. Notes on the nesting of selected species of birds of the Sonoran Desert. Wilson Bull. 71: 86-92.

Hill, G.E. 1993. House Finch (*Carpodacus mexicanus*). *In* A. Poole and F. Gill (eds.), The Birds of North America, No. 46. Philadelphia: The Academy of Natural Sciences; Washington, D.C.: The American Ornithologists' Union.

Hofslund, P.B. 1957. Cowbird parasitism of the Northern Yellow-throat. Auk 74: 42-48.

James, R.D. 1978. Nesting of the House Finch (*Carpodacus mexicanus*) in Ontario. Ont. Field Biol. 32 :30-32.

Kozlovic, D.R. 1987. Differentiation of morphology and reproductive traits in the House Finch (*Carpodacus mexicanus*): a comparison between native and introduced populations. M.Sc. thesis, Brock University, St. Catharines, Ontario.

Kozlovic, D.R. 1988. Early nesting by House Finches in Ontario. Ont. Birds 6: 18-22.

Kozlovic, D.R. 1994. The House Finch in Ontario. Pp. 298-306 *in* M.K. McNicholl and J.L. Cranmer-Byng (eds.), Ornithology in Ontario. Spec. Publ. No. 1, Ontario Field Ornithologists. Hawk Owl Publ., Whitby.

Kozlovic, D.R., R.W. Knapton, and J.C. Barlow. 1996. Unsuitability of the House Finch as a host of the Brown-headed Cowbird. Condor 98: 253-258.

Marvil, R.E., and A. Cruz. 1989. Impact of Brown-headed Cowbird parasitism on the reproductive success of the Solitary Vireo. Auk 106: 476-480.

Mayfield, H. 1965. The Brown-headed Cowbird, with old and new hosts. Living Bird 4: 13-28.

Middleton, A.L.A. 1977. Effect of cowbird parasitism on American Goldfinch nesting. Auk 94: 304-307.

Murphy, M.T. 1986. Brood parasitism of Eastern Kingbirds by Brown-headed Cowbirds. Auk 103: 626-628.

Nakamura, H. 1990. Brood parasitism by the Cuckoo *Cuculus canorus* in Japan and the start of new parasitism on the Azure-winged Magpie *Cyanopica cyana*. Jap. J. Ornithol. 39: 1-18.

Neudorf, D.L., and S.G. Sealy. 1992. Reactions of four passerine species to threats of predation and cowbird parasitism: enemy recognition or generalized responses? Behaviour 123: 84-105.

Orians, G.H., E. Røskaft, and L.D. Beletsky. 1989. Do Brown-headed Cowbirds lay their eggs at random in the nests of Red-winged Blackbirds? Wilson Bull. 101: 599-605.

Payne, R.B. 1977. The ecology of brood parasitism in birds. Ann. Rev. Ecol. Syst. 8: 1-28.

Peck, G.K., and R.D. James. 1987. Breeding birds of Ontario: nidiology and distribution. Volume 2: Passerines. Life Sci. Misc. Publ. Royal Ontario Museum, Toronto.

Petit, L.J. 1991. Adaptive tolerance of cowbird parasitism by Prothonotary Warblers: a consequence of nest-site limitation. Anim. Behav. 41: 425-432.

Post, W., A. Cruz, and D.B. McNair. 1993. The North American invasion pattern of the Shiny Cowbird. J. Field Ornithol. 64: 32-41.

Post, W., and J.W. Wiley. 1977. The Shiny Cowbird in the West Indies. Condor 79: 119-121.

Potter, E.F. 1978. Notes on the breeding birds of the Carolinas. Chat 42: 71-76.

Potter, E.F., and G.T. Whitehurst. 1981. Cowbirds in the Carolinas. Chat 45: 57-68.

Rice, W.R. 1989. Analyzing tables of statistical tests. Evolution 43: 223-225.

Ricklefs, R.E. 1984. Components of variance in measurements of nestling European Starlings (*Sturnus vulgaris*) in southeastern Pennsylvania. Auk 101: 319-333.

Robbins, C.S., D. Bystrak, and P.H. Geissler. 1986. The breeding bird survey: its first fifteen years, 1965-1979. U.S. Fish and Wildl. Serv. Resour. Publ. 157.

Robbins, C.S., J.R. Sauer, R.S. Greenberg, and S. Droege. 1989. Population declines in North American birds that migrate to the Neotropics. Proc. Natl. Acad. Sci. 86: 7658-7662.

Robertson, R.J., and R.F. Norman. 1976. Behavioral defenses to brood parasitism by potential hosts of the Brown-headed Cowbird. Condor 78: 166-173.

Robertson, R.J., and R.F. Norman. 1977. The function and evolution of aggressive host behaviour towards the Brown-headed Cowbird (*Molothrus ater*). Can. J. Zool. 55: 508-518.

Rohwer, S., and C.D. Spaw. 1988. Evolutionary lag versus bill-size constraints: a comparative study of the acceptance of cowbird eggs by old hosts. Evol. Ecol. 2: 27-36.

Rohwer, S., C.D. Spaw, and E. Røskaft. 1989. Costs to Northern Orioles of puncture-ejecting parasitic cowbird eggs from their nests. Auk 106: 734-738.

Røskaft, E., G.H. Orians, and L.D. Beletsky. 1990. Why do Red-winged Blackbirds accept eggs of Brown-headed Cowbirds? Evol. Ecol. 4: 35-42.

Røskaft, E., S. Rohwer, and C.D. Spaw. 1993. Cost of puncture ejection compared with costs of rearing cowbird chicks for Northern Orioles. Ornis. Scand. 24: 28-32.

Rothstein, S.I. 1975a. An experimental and teleonomic investigation of avian brood parasitism. Condor 77: 250-271.

Rothstein, S.I. 1975b. Evolutionary rates and host defences against avian brood parasitism. Am. Nat. 109: 161-176.

Rothstein, S.I. 1990. A model system for coevolution: avian brood parasitism. Ann. Rev. Ecol. Syst. 21: 481-508.

Rothstein, S.I. 1994. The cowbird's invasion of the far west: history, causes and consequences experienced by host species. Pp. 301-315 *in* J.R. Jehl, Jr. and N.K. Johnson (eds.), A Century of Avifaunal Change in Western North America. Stud. Avian Biol. No. 15. Cooper Ornithological Society, Sacramento.

SAS Institute. 1988. SAS/STAT User's Guide, Release 6.03 Edition. SAS Institute Inc., Cary, NC.

St. Louis, V.L., J.C. Barlow, and J.-P.R.A. Sweerts. 1989. Toenail-clipping: a simple technique for marking individual nidicolous chicks. J. Field Ornithol. 60: 211-215.

Sauer, J.R., S. Schwartz, B.G. Peterjohn, and J.E. Hines. 1996. The North American Breeding Bird Survey Home Page. Version 95.1. Patuxent Wildlife Research Center, Laurel, MD.

Sealy, S.G. 1995. Burial of cowbird eggs by parasitized Yellow Warblers: an empirical and experimental study. Anim. Behav. 49: 877-889.

Smith, J.N.M. 1981. Cowbird parasitism, host fitness, and age of the host female in an island Song Sparrow population. Condor 83: 152-161.

Smith, J.N.M., and P. Arcese. 1994. Brown-headed Cowbirds and an island population of Song Sparrows: a 16-year study. Condor 96: 916-934.

Sprague, R.T., and R.D. Weir. 1984. The Birds of Prince Edward County, 2nd edition. Kingston Field Naturalists. Kingston, Ontario.

Uyehara, J.C., and P.M. Narins. 1995. Nest defense by Willow Flycatchers to brood-parasitic intruders. Condor 97: 361-368.

Ward, D., A.K. Lindholm, and J.N.M. Smith. 1996. Multiple parasitism of the Red-winged Blackbird: further experimental evidence of evolutionary lag in a common host of the Brown-headed Cowbird. Auk 113: 408-413.

Wolf, L. 1987. Host-parasite interactions of Brown-headed Cowbirds and Dark-eyed Juncos in Virginia. Wilson Bull. 99: 338-350.

Wootton, J.T. 1986. Clutch-size differences in western and introduced eastern populations of House Finches: patterns and hypotheses. Wilson Bull. 98: 459-462.

3

Availability of the House Finch as a Host of the Brown-headed Cowbird

INTRODUCTION

Brown-headed Cowbirds are generalist brood parasites that choose their hosts, in part, on the basis of habitat. Cowbirds prefer to lay in nests that are located in shrub habitat rather than in open grasslands or forest interiors (Mayfield 1965, Lowther and Johnston 1977, Brittingham and Temple 1983). In this respect, the cowbird is very much a parasite of "edge" species that inhabit the transition zone between forest and grasslands. Cowbirds may prefer this successional habitat over other habitats because 1) it is adjacent to open grassy areas where they feed and can have easy access to host rich areas (Weins 1963, Rich 1978, Rothstein et al. 1984), 2) hosts may be more willing to accept cowbird eggs because they are more recently associated with cowbirds and have not yet evolved anti-parasite defences (Mayfield

1965), 3) edge habitat is more varied in structure and therefore can support a greater density of hosts species (Lowther and Johnston 1977), which may provide greater opportunities for parasitism.

Urban habitats are similar to natural forest-grassland ecotones in several respects and thus may be suitable breeding areas for cowbirds. Urban areas are often products of former agricultural communities and are usually near cultivated land where cowbirds may gather in large numbers to forage (Rothstein et al. 1986). Urban environments are distinguished by a variety of vegetational elements and land uses that have resulted in a complex mosaic-like landscape (Oelke 1981). In this way human settlement has provided new opportunities for species to breed and forage, and thus contributed importantly to the diversity of urban habitat (Emlen 1974). Furthermore. some cowbird host species may occur in greater density in urban than non urban areas (Emlen 1974, Tweit and Tweit 1986, Mills et al. 1989). However, the importance of urban habitat as an area of cowbird breeding is poorly understood (Middleton 1988).

The House Finch, a host of the Brown-headed Cowbird, is a relatively new species to eastern North America (Elliott and Arbib 1953). Since their introduction to Long Island, NY, in 1940, House Finches have quickly increased in numbers and spread throughout the eastern United States and southeastern Canada (Hill 1993). Colonization of House Finches has been largely facilitated by human activity and the species remains most abundant in highly developed areas. Presence of House Finches in the east has effectively altered the structure of the existing cowbird host community there. But what proportion of the host community do House Finches represent? House Finch numbers have increased exponentially in the east (Robbins et al. 1986); however, estimates of finch abundance to date have been based on data collected either from wintering populations or breeding birds in primarily non urban habitat (Robbins et al. 1986, Root 1988, Price et al. 1995) and not from urban habitat where House Finches are most prevalent. The purpose of the present study was to determine the availability of House Finches as hosts of cowbirds. Frequencies of breeding House Finches and other species were assessed in urban and non urban habitat and rate of cowbird parasitism was related to host abundance.

MATERIALS AND METHODS

Field Sites

Field work for this study was conducted at four sites in Ontario, Canada: Orillia (44° 36' N, 79° 26' W), Simcoe County; Barrie (44° 22' N, 79° 42' W), Simcoe County; Guelph (43° 34' N, 80° 16' W), Wellington County; St. Catharines (43° 10' N, 79° 15' W), Regional Municipality of Niagara (see Fig. 5.1). Study sites were in areas of suburban development (hereafter referred to as urban habitat) at each location: Orillia, a 4.7 km^2 area located between mixed forest, agricultural land, and Lake Couchiching; Barrie, a 3.8 km^2 area on the southwest shore of Kempenfelt Bay, Lake Simcoe contiguous with an industrial area and mixed forest; Guelph, a 4.3 km^2 area approximately 2 km east of the Speed River in a region of extensive agriculture; St.

Catharines, a 5 km^2 area bounded by Martindale Pond to the west and Lake Ontario to the north in a region of fruit growing. Habitat at each study site included residential neighbourhoods interspersed with wooded ravines, sports fields and public parks landscaped with deciduous and coniferous shrubs and trees.

Cowbird and Host Abundance

To determine the relative abundance (number of individuals) of cowbirds and their hosts at each study site, counts of adult birds were made during the months of May, June and July. Surveys were conducted at St. Catharines in 1990 - 1992, at Orillia and Barrie in 1992 - 1993, and at Guelph in 1993. Counts were done within 2 h after sunrise along strip-transects (number of transects: Orillia, N = 29; Barrie, N = 31; Guelph, N = 15; St. Catharines, N = 105) throughout each of the study sites. Each transect was approximately 500 m long, 50 m wide and required 20-25 min. to complete. All transects were along streets. The starting point and direction of each transect was determined randomly. Birds were not counted during rain or very windy conditions. Flying birds were not recorded unless they perched within the count corridor; however, all cowbirds observed were noted. Cowbirds noted included birds observed both during transect counts and during other fieldwork (see Chapters 4 and 5, Appendix 1). The relative abundance of each cowbird host at each study site was determined using only passerines known to breed there (Cadman et al. 1987, Peck and James 1987, Appendix 2). Species parasitized but not known to have reared the parasite, and cavity nesting species (Friedmann 1963, Friedmann and Kiff 1985, Peck and James 1987) were not considered in analyses. The former group included the Blue Jay (*Cyanocitta cristata*) and American Crow (*Corvus brachyrhynchos*). Cavity nesting species are seldom used as hosts because cowbirds are often unable to parasitize them. This group included Great Crested Flycatcher (*Myiarchus crinitus*), Purple Martin (*Progne subis*), Tree Swallow (*Tachycineta bicolor*), Black-capped Chickadee (*Parus atricapillus*), Red-breasted Nuthatch (*Sitta canadensis*), White-breasted Nuthatch (*S. carolinensis*), House Wren (*Troglodytes aedon*), European Starling (*Sturnus vulgaris*) and House Sparrow (*Passer domesticus*). Cowbird and House Finch abundance was compared among the study sites with analysis of variance. The data were square root transformed (Sokal and Rohlf 1981) and significance was tested at the alpha 0.05 level using randomization tests based on 5000 iterations (Manly 1991a). Randomization testing is particularly well suited for these data because of the large occurrence of tied values among the samples (Manly 1991b).

I compared host abundance at each study site with data collected in 1994 from four Breeding Bird Survey (BBS) routes nearby: Orillia (44°43' N, 79°38' W), Simcoe County; Sunnydale Corners (44°25' N, 80°00' W), Simcoe County; Arkell (43°23' N, 80°19' W), Wellington County; Welland (43°01' N, 79°17' W), Regional Municipality of Niagara. These routes followed roads through largely non urban areas of the Great Lakes and St. Lawrence River plains (Robbins et al. 1986). Data from these areas (hereafter referred to as non urban habitat) were used to estimate host abundance beyond locations of urban development that I sampled. BBS data were collected at 50, 3-min. stops that are 0.8 km apart (Robbins et al. 1986), whereas I counted all birds along the entire length of each transect. The detectability of species may be influenced by the counting method used as well as differences in vegetation structure and composition and behaviour of the birds themselves between habitats (Edwards et al. 1981, Oelke 1981, Verner 1985). These sources of bias precluded statistical comparison between urban and non urban samples. Therefore, host abundance is presented simply as the frequency of each species at each site. Names of field sites were used to identify locations of both urban and non urban habitat.

RESULTS

Number of hosts in areas of urban habitat was smaller compared to non urban habitat (Table 3.1). Urban habitat contained about half the number of species that were recorded in non urban situations in each area. Guelph showed the greatest paucity of cowbird hosts among urban sites. Most hosts observed in urban habitat were also common to non urban habitat; however, hosts observed at urban sites made up a considerably smaller proportion of the host community in the non urban habitats both in terms of number of species and individuals observed there (Table 3.2).

Frequency of the 15 most abundant hosts in urban habitat together with frequencies of these hosts in non urban habitat is shown in Fig. 3.1. These species represented the bulk of hosts ($\geq$0.71) observed in urban habitat and included virtually all ($\geq$0.99) of the individuals recorded there. The most common species in urban habitats at Orillia, Barrie and Guelph were House Finch, American Robin (*Turdus migratorius*), Common Grackle (*Quiscalus quiscula*), Song Sparrow (*Melospiza melodia*), American Goldfinch (*Carduelis tristis*) and Chipping Sparrow (*Spizella passerina*), which represented more than 87% of the host commumity at each site. These species together with Northern Cardinal (*Cardinalis cardinalis*) and Cedar Waxwing (*Bombycilla cedrorum*) accounted for 98% of individuals observed in the urban habitat at St. Catharines. Of these species, the most frequently observed was the House Finch. It comprised about 25% of the host community at Orillia and Barrie, 28% at Guelph and was most abundant at St. Catharines where 53% of all individuals observed were House Finches.

In contrast, the House Finch was relatively rare in non urban habitat. It represented less than 2% of individuals at Orillia, Barrie and Guelph, but the species remained the most abundant host in non urban habitat at St. Catharines where it accounted for 15% of hosts. Common hosts in non urban habitat included Red-winged Blackbird (*Agelaius phoenicius*), American Robin, Song Sparrow, Common Grackle, Chipping Sparrow and American Goldfinch. Red-winged Blackbirds were the most common non urban host species (19%) at Barrie, but were not observed in the urban habitat there. Frequencies of other cowbird hosts are given in Table 3.3.

Species that eject cowbird eggs from their nest, or rejecter species (Rothstein 1975), comprised a large proportion of the host community, particularly in the urban habitats. The most common rejecter species here was the American Robin, which represented about 20% of individuals. Other rejecter species observed were Eastern Kingbird (*Tyrannus tyrannus*), Gray Catbird (*Dumetella carolinensis*), Brown Thrasher (*Toxostoma rufum*), Cedar Waxwing, Warbling Vireo (*Vireo gilvus*, Sealy 1996), and Baltimore Oriole (*Icterus galbula*). Cowbirds may frequently lay eggs in the nests of rejector species (Scott 1977), but because rejection almost always occurs (Rothstein 1975) parasitism of these hosts is rarely successful. The number of species that accept cowbird eggs, or accepter species (Rothstein 1975), may be a more appropriate measure of the host community. Among these species, House Finches represented about 35% of individuals in urban habitat at Orillia, Barrie, and Guelph and 65% of hosts at St. Catharines. In non urban habitat, the species comprised less than 3% of hosts except at St. Catharines where House Finch abundance increased to 19%.

Cowbird frequency was similar in both urban and non urban habitat among sites. Cowbirds represented 2.4 - 4.1% of the urban avian community, which included both accepter and rejecter species, and comprised 1.3 - 2.7% of individuals in non urban habitat. House Finch and cowbird abundance in urban habitat is shown in Fig. 3.2. In urban habitat finches showed highly significant ($P = 0.001$) variation in numbers; birds were twice as abundant at St. Catharines compared to the other sites. A randomized multiple comparisons test revealed no significant ($P > 0.05$) differences among years at St. Catharines or among the remaining samples. In contrast, there was no significant difference ($P = 0.61$) in the number of cowbirds observed among the urban study sites. This was also true when comparisons were made using male (P = 0.61) and female (P = 0.13) counts separately.

DISCUSSION

House Finches were the most frequent cowbird host of urban habitats. They comprised only a small proportion of the host community in non urban habitat except at St. Catharines where they were the most abundant species. House Finch abundance among the study sites and between habitats reflects the history of colonization of this species in Ontario. House Finches were first reported in the Province in 1972 and occurred only sporadically in southern Ontario until the late 1970s (Kozlovic 1994). The species became established on the Niagara peninsula in the early 1980s and subsequently spread along the shores of Lakes Erie and Ontario and then to the north. Among the study sites, House Finches were first reported breeding at St. Catharines in 1980 (Foley 1983) and at Guelph in 1985 (Weir 1985). The species most recently colonized Orillia and Barrie, the two northern sites, and birds have occurred regularly there only since the late 1980s (Kozlovic 1994).

Other studies have found that urbanization has had a positive influence on House Finch breeding. House Finches were among the most abundant species in urban habitat but occurred sparsely in non urban situations (Emlen 1974, Tweit and Tweit 1986, Mills et al. 1989). In the present study, House Finches were more abundant in urban than non urban habitat, but increase of the population at many urban centres has resulted in birds spreading into surrounding non urban areas of Ontario. Recent, large invasions of finches were reported into rural areas of Bruce, Frontenac, Leeds and Grenville, Peterborough, Prince Edward (Weir 1988a, 1988b) and Durham (Bain and Henshaw 1990, 1992) counties. First time breeding records were noted in Bruce County in 1988 and in Dufferin and Muskoka counties in 1995 (Peck 1996). These regions lie just south of the Canadian Shield, which marks the northern boundary of the range of the species in southern Ontario (Kozlovic 1994). On the Shield there are extensive areas of mixed forest and limited human settlement that provide few opportunities for House Finches to breed and disperse. Accordingly, they have been observed only in small numbers there. Intensive development and agriculture in the extreme southern portion of the Province has created an ideal environment for House Finches, particularly at St. Catharines, and continuing growth of the population there has likely fueled the spread of birds northwards. Although St. Catharines has experienced recent declines in the numbers of House Finches, their numbers continue to increase at other urban sites (Kozlovic 1994).

Cowbirds occurred at about the same frequency between urban and non urban habitats. Rothstein et al. (1984) observed large groups of cowbirds in areas close to human activity. Airola (1986) found that frequency of cowbird parasitism was strongly and positively associated with the degree of habitat disturbance. Marvil and Cruz (1989) noted most parasitized Solitary Vireo (*Vireo solitarius*) nests near settled areas. Similarly, Chipping Sparrows experienced higher levels of parasitism in urban than non urban areas (Middleton 1988). In contrast, several studies have reported cowbirds to be less abundant in urban than non urban settings (Emlen 1974, Campbell and Dagg 1976, Mills et al. 1989). Middleton (1988) found that American Goldfinch nests were not parasitized in urban habitat and concluded that the urban environment may provide a refuge from brood parasites for this species. This does not appear to be true for House Finches, which may experience a high frequency of parasitism in urban settings. At St. Catharines the average frequency of parasitism was 40.2% during the period 1983 - 85 (Chapter 2). Although incidence of parasitism was not assessed in non urban habitat, the high frequencies of parasitism at St. Catharines indicate that the urban habitat there is frequented by cowbirds.

Cowbirds demonstrate diurnal movements from breeding to distinct and often separate feeding areas (Rothstein et al. 1980, 1984, Thompson 1994). Birds depart from breeding sites by midday to congregate at feeding and roosting areas up to 7 km away. Although I did not follow the movements of individuals, cowbirds were present in urban habitat primarily in the morning and rarely in the afternoon (Appendix 1), which suggests that they foraged elsewhere. The urban habitats that I surveyed may have been attractive to cowbirds because they contained high host densities (Verner and Ritter 1983, Airola 1986, Rothstein et al. 1986). The large numbers of breeding House Finches there would provide cowbirds with numerous opportunities for parasitism. The development of southern Ontario would indicate that cowbirds there are rarely distant from areas of human activity including urban habitat. Urban habitats may therefore be important for breeding cowbirds.

Although individual cowbirds do not appear to be host specific (Fleischer 1985), they may form search images for common host species (Friedmann et al. 1977). If hosts available to cowbirds are equally likely to be parasitized then the frequency of parasitism should be proportional to the abundance of nesting species. In urban habitats, therefore, House Finches should be the most highly parasitized species. Nest records show that House Finches are among the most highly parasitized hosts species observed in urban habitats (Peck and James 1987). Other accepter species that were frequently found in urban habitat also sustained relatively high parasitism. These species were Northern Cardinal, Chipping and Song sparrows, which showed levels of parasitism of 21.1%, 32% and 23.2%, respectively (Peck and James 1987). However, some common hosts in urban habitat may be infrequently parasitized. For example, American Goldfinches begin to breed near the end of the cowbird breeding season and therefore only a small number of nests are parasitized (Middleton 1977, Peck and James 1987). Common Grackles are among the most abundant species of urban habitats yet only 0.2% of their nests contain cowbird eggs (Peck and James 1987). This may be because grackles roost in their nests and are less easily displaced by cowbirds than smaller hosts (Neudorf and Sealy 1994).

Frequencies of parasitism for common rejecter species such as American Robin, Gray Catbird, Cedar Waxwing and Baltimore Oriole were 0.3%, 1.5%, 7.5%

and 6%, respectively (Peck and James 1987), but do not represent actual frequencies of parasitism because these species commonly eject cowbird eggs from their nest (Rothstein 1975). For example, Scott (1977) determined that the actual frequency of parasitism for the Gray Catbird may be a high as 44%; however, frequency of parasitism of catbirds did not reflect host availability because other less common hosts were more heavily parasitized. Scott (1977) attributed the lower parasitism of catbirds to their attentiveness at the nest, which may have reduced or prevented parasitism. Other studies, too, have found that cowbirds do not necessarily parasitize their hosts according to host abundance (Friedmann 1963, Rothstein 1976). A cowbird search image for common hosts may apply only to accepter species because the behaviour of rejecters towards parasites may influence their availability as hosts. Furthermore, frequency of parasitism may be affected by the structure of the host community (Mason 1986). Cowbirds may have experienced opportunities for parasitism unique to urban habitats. This may be a result of the very high densities of House Finches in my study areas. I do not know if House Finches experience similarly high frequencies of parasitism in non urban as in urban habitat. However, the aformentioned growing presence of House Finches in non urban environments in Ontario suggests that the structure of host communities of these areas are also undergoing change.

The ease with which cowbirds locate nests may be related to host behaviour. Cowbirds appear to find nests of potential hosts by observing their nest building activities (Friedmann 1929, Payne 1973, 1977), and although host activity is not essential for nest discovery (Norman and Robertson 1975) it seems to be an important factor (Hoy and Ottow 1964, Thompson and Gottfried 1976, 1981). High frequency of parasitism of House Finch nests suggests that cowbirds have little difficulty in locating their nests. This may be due to the conspicuous nature of House Finch breeding activities (Kozlovic pers. obs.). Female finches seem to make little effort to conceal their nest building. They gather nest material often in the immediate vicinity of the nest site and carry it directly to the site of construction. In addition to natural supports, nests are often placed in human-made structures such a awnings, light fixtures and hanging potted plants. These nests may be more noticeable to Brown-headed Cowbirds than those in natural sites and may, as a result, sustain higher levels of parasitism (Mason 1986). During nest construction and egg laying, male finches sing vigorously at great length from prominent perches near the nest site. This may draw the attention of cowbirds and aid them in locating nests (Gochfeld 1979). House Finches are semicolonial and nest in loose aggregations where there is suitable habitat (Thompson 1960a, 1960b). These concentrations of finches may allow cowbirds to monitor the activity of several finch pairs simultaneously and may also reduce the time required for nest searching.

Habitat composition may also influence the detectability of nests by social parasites. The absence of suitable vantage points from which cowbirds may observe host activity can limit their ability to find nests (Payne 1973, Gochfeld 1979, Freeman et al. 1990). Urban settings offer numerous opportunities for cowbirds to observe the activities of their hosts. Cowbirds can perch high above ground on a variety of objects such as light standards, utility wires and buildings to survey the surrounding habitat (Kozlovic pers. obs.). Furthermore, urban habitat contains relatively less vegetation than non urban habitat (Mills et al. 1989). As a result, cowbirds may be better able to find nests in urban habitat because there is less vegetation to obscure host activities than in non urban areas.

The presence of House Finches in eastern North America has greatly altered the cowbird host community particularly in urban areas where finches are most abundant. High parasitism of House Finch nests demonstrates that urban habitat is an important breeding area for cowbirds. Large concentrations of House Finches may attract cowbirds to urban areas. Here cowbirds may be as abundant as in non urban situations. Continued growth of the House Finch population suggests that the species is becoming increasingly common even in non urban areas as was observed at St. Catharines. Widespread availability of House Finches to cowbirds suggests that this host may play an important role in influencing cowbird reproductive success.

Table 3.1. Number of host species of the Brown-headed Cowbird in urban and non urban habitats.

	Number of host species	
Site	Urban	Non urban
Orillia	20	40
Barrie	21	43
Guelph	11	40
St. Catharines	18	32

Table 3.2. Proportion of cowbird hosts common to both urban and non urban habitats.

	Urban hosts found in non urban habitat		Non urban hosts found in urban habitat	
Site	Species	Individuals	Species	Individuals
Orillia	0.85	0.99	0.42	0.63
Barrie	0.86	0.99	0.42	0.48
Guelph	1.00	1.00	0.28	0.62
St. Catharines	0.83	0.99	0.41	0.72

Table 3.3. Frequency of occurrence (%) in all birds counted of uncommon hosts of the Brown-headed Cowbird found in non urban and urban habitat. Values for urban habitat appear in bold type.

	Location			
Species	Orillia	Barrie	Guelph	St.Cath.
Eastern Kingbird *Tyrannus tyrannus*			1.61	1.60
Eastern Wood-Pewee *Contopus virens*		1.38	1.75	0.58 **0.04**
Eastern Phoebe *Sayornis phoebe*	3.77	0.79	0.29	0.29
Least Flycatcher *Empidonax minimus*	0.40	0.59	1.02	
Horned lark *Eremophila alpestris*		2.76	0.29	0.87
Barn Swallow *Hirundo rustica*	4.76		2.05	3.92
Ruby-crowned Kinglet *Regulus calendula*	**0.28**	**0.13**		
Wood Thrush *Hylocichla mustelina*		1.38	0.44	
Veery *Catharus fuscescens*				
Gray Catbird *Dumetella carolinensis*	0.60 **0.28**	0.59		1.74
Brown Thrasher *Toxostoma rufum*	1.39		0.29	
Warbling Vireo *Vireo gilvus*			2.92	0.29
Blue-winged Warbler *Vermivora pinus*				0.15
Golden-winged Warbler *Vermivora chrysoptera*	0.40			
Tennessee Warbler *Vermivora peregrina*		0.13		
Nashville Warbler *Vermivora ruficapilla*	1.79	0.39	0.15	
Northern Parula *Parula americana*	**0.14**			
Black-and-white Warbler *Mniotilta varia*	0.60 **0.14**	0.39 **0.13**		
Chestnut-sided Warbler *Dendroica pensylvanica*	0.40	0.39	0.44	**0.08**
Black-throated Green Warbler *Dendroica virens*		0.59		
Pine Warbler *Dendroica pinus*		0.20	0.29	
Yellow Warbler *Dendroica petechia*		2.17 **0.13**	4.39	1.60

	Location			
Species	Orillia	Barrie	Guelph	St.Cath.
Mourning Warbler *Oporornis philadelphia*	1.98	0.39	0.29	
Ovenbird *Seiurus aurocapillus*	1.79	2.56	0.29	
Northern Waterthrush *Seiurus noveboracensis*			0.15	
Common Yellowthroat *Geothlypis trichas*	1.98	0.59	3.36	0.29
American Redstart *Setophaga ruticilla*	0.20	0.20	0.15	
Rose-breasted Grosbeak *Pheucticus ludovicianus*	0.99	1.78 **0.13**	1.61	0.15 **0.08**
Indigo Bunting *Passerina cyanea*	0.40	0.99	0.58	0.73
Eastern Towhee *Pipilo erythrophthalmus*		0.20		0.15
Grasshopper Sparrow *Ammodramus savannarum*	0.79	0.39	0.29	
Vesper Sparrow *Pooecetes gramineus*	0.20	0.99	0.15	0.87
Savannah Sparrow *Passerculus sandwichensis*	5.36	10.26	3.22	3.63
Field Sparrow *Spizella pusilla*	0.40	0.39	0.73	0.58
White-throated Sparrow *Zonotrichia albicollis*	0.60	0.20		
Swamp Sparrow *Melospiza georgiana*	1.19		1.17	**0.04**
Bobolink *Dolichonyx oryzivorus*	8.33	4.73	5.99	1.31
Eastern Meadowlark *Sturnella magna*	3.17	1.58	2.34	1.89
Orchard Oriole *Icterus spurius*				0.15
Baltimore Oriole *Icterus galbula*			1.32	
Scarlet Tanager *Piranga olivacea*	0.20	0.39 **0.13**		0.15
Pine Siskin *Carduelis pinus*	**0.28**			

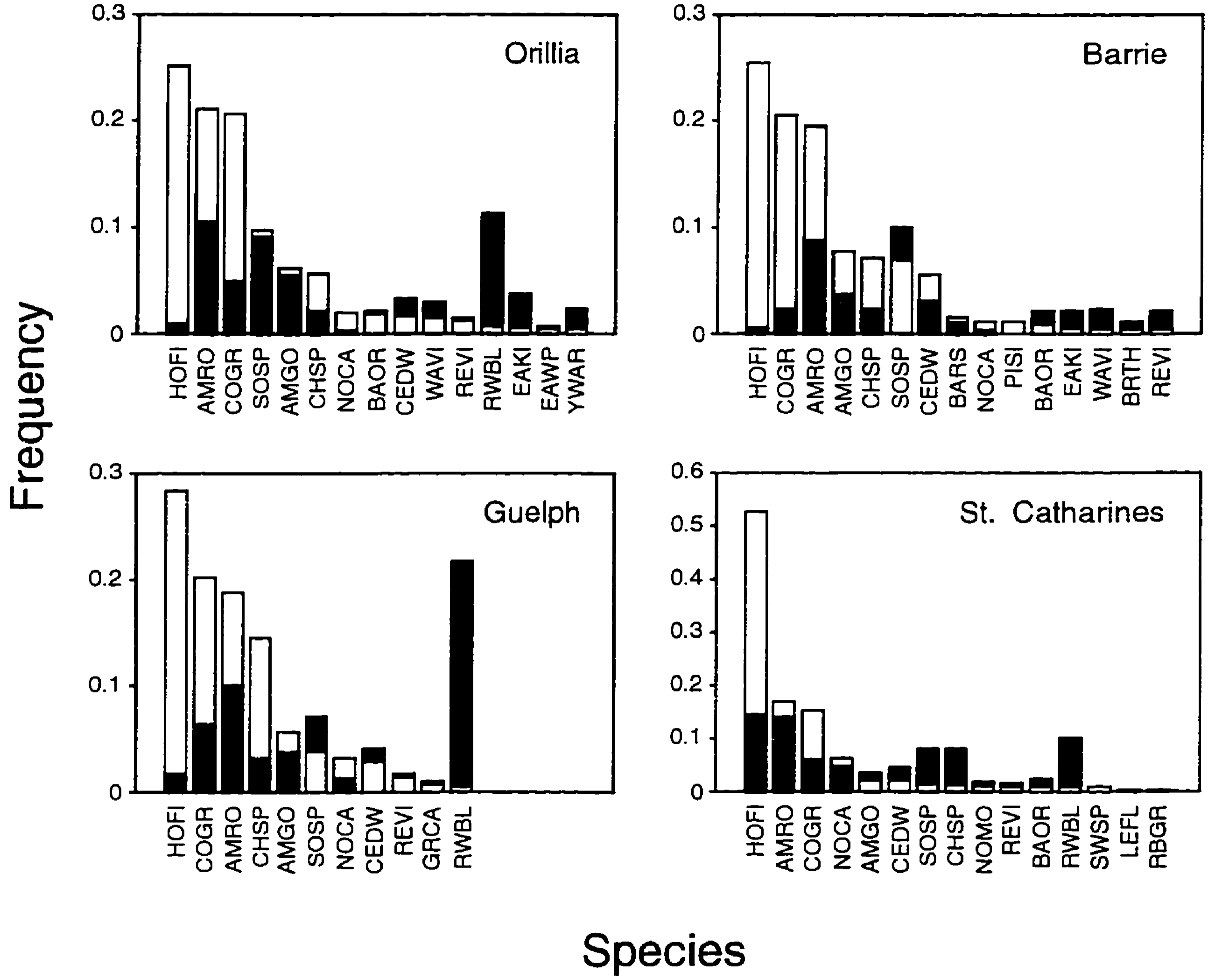

Fig. 3.1. Frequency of occurrence (%) of common hosts of the Brown-headed Cowbird (*Molothrus ater*) at four sites in Ontario in urban (open bars) and non urban (solid bars) habitat. Bars for species found in both habitats are superimposed. Data for non urban habitat are from the Breeding Bird Survey recorded in 1994. Years of

study and total number of transects conducted in urban habitat at each site are as follows: Orillia: 1992 - 1993, $n = 29$; Barrie: 1992 - 1993, $n = 31$; Guelph: 1993, $n = 15$; St. Catharines: 1990 - 1992, $n = 105$. Data for urban habitat were pooled between or among years. Species acronyms are as follows: AMGO, American Goldfinch (*Carduelis tristis*); AMRO, American Robin (*Turdus migratorius*); BAOR, Baltimore Oriole (*Icterus galbula*); BARS, Barn Swallow (*Hirundo rustica*); BRTH, Brown Thrasher (*Toxostoma rufum*); CEDW, Cedar Waxwing (*Bombycilla cedrorum*); CHSP, Chipping Sparrow (*Spizella passerina*); COGR, Common Grackle (*Quiscalus quiscula*); EAKI, Eastern Kingbird (*Tyrannus tyrannus*); EAWP, Eastern Wood-Pewee (*Contopus virens*); GRCA, Gray Catbird (*Dumetella carolinensis*); HOFI, House Finch; LEFL, Least Flycatcher (*Empidonax minimus*); NOCA, Northern Cardinal (*Cardinalis cardinalis*); NOMO, Northern Mockingbird (*Mimus polyglottos*); PISI, Pine Siskin (*Carduelis pinus*); RBGR, Rose-breasted Grosbeak (*Pheucticus ludovicianus*); REVI, Red-eyed Vireo (*Vireo olivaceus*); RWBL, Red-winged Blackbird (*Agelaius phoeniceus*); SOSP, Song Sparrow (*Melospiza melodia*); SWSP, Swamp Sparrow (*M. georgiana*); WAVI, Warbling Vireo (*V. gilvus*); YWAR, Yellow Warbler (*Dendroica petechia*).

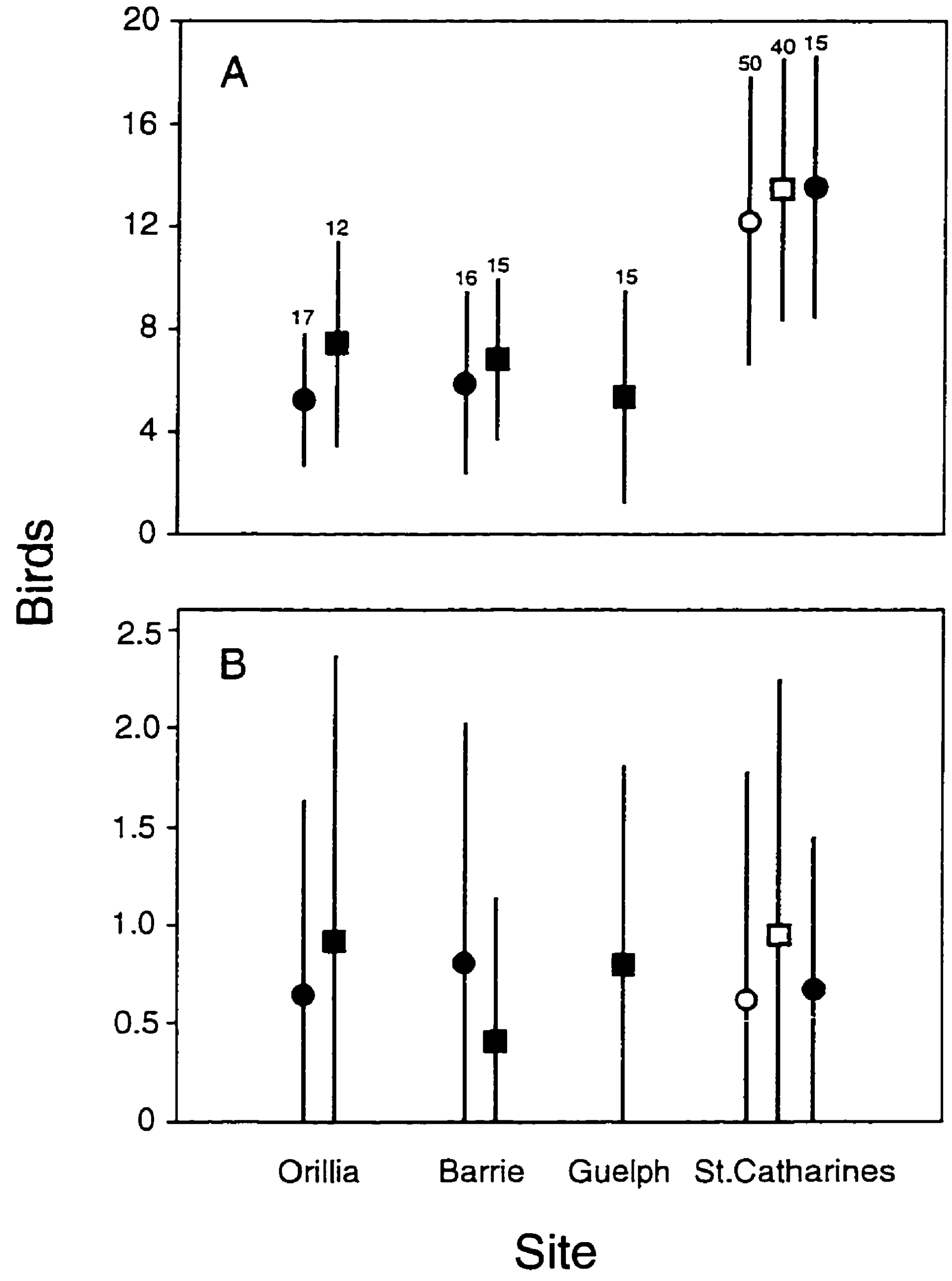

Fig. 3.2. Number of House Finches (A) and Brown-headed Cowbirds (B) at four urban sites in southern Ontario in 1990 (○), 1991 (□), 1992 (●) and 1993 (■). Symbols represent the mean ± 1 SD number of birds observed per transect. Number of transects that were conducted appears above plotted values.

LITERATURE CITED

Airola, D.A. 1986. Brown-headed Cowbird parasitism and habitat disturbance in the Sierra Nevada. J. Wildl. Manage. 50: 571-575.

Bain, M., and B. Henshaw (eds.). 1990. Annual bird report, Durham region, Ontario, 1990. M. Bain and B. Henshaw Publ.

Bain, M., and B. Henshaw (eds.). 1992. Annual bird report, Durham region, Ontario, 1991. M. Bain and B. Henshaw Publ.

Brittingham, M.C., and S.A. Temple. 1983. Have cowbirds caused forest songbirds to decline? Bioscience 33: 31-35.

Cadman, M.D., P.F.J. Eagles, and F.M. Helleiner (compilers). 1987. Atlas of the Breeding Birds of Ontario. University of Waterloo Press, Waterloo.

Campbell, C.A., and A.I. Dagg. 1976. Bird populations in downtown and suburban Kitchener-Waterloo, Ontario. Ont. Field Biol. 30: 1-22.

Edwards, D.K., G.L. Dorsey, and J.A. Crawford. 1981. A comparison of three avian census methods. Pp. 170 - 176 *in* C.J. Ralph and J. M. Scott (eds.), Estimating Numbers of Terrestrial Birds. Stud. Avian Biol. No. 6. Cooper Ornithological Society.

Elliott, J.J., and R.S. Arbib, Jr. 1953. Origin and status of the House Finch in the eastern United States. Auk 70: 31-37.

Emlen, J.T. 1974. An urban bird community in Tucson, Arizona: derivation, structure, regulation. Condor 76: 184-197.

Fleischer, R.C. 1985. A new technique to identify and assess the dispersion of eggs of individual brood parasites. Behav. Ecol. Sociobiol. 17: 91-99.

Foley, M.E. 1983. Large numbers of House Finches in St. Catharines, Ontario. Ontario Birds 2: 56-60.

Freeman, S., D.F. Gori, and S. Rohwer. 1990. Red-winged Blackbirds and Brown-headed Cowbirds: some aspects of a host-parasite relationship. Condor 92: 336-340.

Friedmann, H. 1929. The Cowbirds, A Study in the Biology of Social Parasitism. C.C. Thomas, Springfield, Ill.

Friedmann, H. 1963. Host relations of the parasitic cowbirds. U.S. Natl. Mus. Bull. 233.

Friedmann, H., and L.F. Kiff. 1985. The parasitic cowbirds and their hosts. Proc. West. Found. Vert. Zool. 2: 225-304.

Friedmann, H., L.F. Kiff, and S.I. Rothstein. 1977. A further contribution to knowledge of the host relations of the parasitic cowbirds. Smithsonian Contrib. Zool. 235: 1-75.

Gochfeld, M. 1979. Brood parasite and host coevolution: interactions between Shiny Cowbirds and two species of meadowlarks. Am. Nat. 113: 855-870.

Hill, G.E. 1993. House Finch (*Carpodacus mexicanus*). *In* A. Poole and F. Gill (eds.), The Birds of North America, No. 46. Philadelphia: The Academy of Natural Sciences; Washington, D.C.: The American Ornithologists' Union.

Hoy, G., and J. Ottow. 1964. Biological and oological studies of the molothrine cowbirds (Icteridae) of Argentina. Auk 81: 186-203.

Kozlovic, D.R. 1994. The House Finch in Ontario. Pp. 298-306 *in* M.K. McNicholl and J.L. Cranmer-Byng (eds.), Ornithology in Ontario. Spec. Publ. No. 1, Ontario Field Ornithologists. Hawk Owl Publ., Whitby.

Lowther, P.E., and R.F. Johnston. 1977. Influences of habitat on cowbird host selection. Kans. Ornithol. Soc. Bull. 28: 36-40.

Manly, B.F.J. 1991a. RT, a program for randomization testing. Version 1.01. Centre for Applications of Statistics and Mathematics, University of Otago, Dunedin.

Manly, B.F.J. 1991b. Randomization and Monte Carlo Methods in Biology. Chapman and Hall, London.

Marvil, R.E., and A. Cruz. 1989. Impact of Brown-headed Cowbird parasitism on the reproductive success of the Solitary Vireo. Auk 106: 476-480.

Mason, P. 1986. Brood parasitism in a host generalist, the Shiny Cowbird: II. Host selection. Auk 103: 61-69.

Mayfield, H. 1965. The Brown-headed Cowbird, with old and new hosts. Living Bird 4: 13-28.

Middleton, A.L.A. 1977. Effect of cowbird parasitism on American Goldfinch nesting. Auk 94: 304-307.

Middleton, A.L.A. 1988. The urban environment and it potential as a refuge from brood parasitism by the Brown-headed Cowbird. Pp. 1802-1808 *in* H. Ouellet (ed.), Acta XIX Congressus Internationalis Ornithologici. Volume II. National Museum of Natural Sciences, Ottawa.

Mills, G.S., J.B. Dunning, Jr., and J.M. Bates. 1989. Effects of urbanization on breeding bird community structure in southwestern desert habitats. Condor 91: 416-428.

Neudorf, D.L., and S.G. Sealy. 1994. Sunrise nest attentiveness in cowbird hosts. Condor 96: 162-169.

Norman, R.F., and R.J. Robertson. 1975. Nest-searching behavior in the Brown-headed Cowbird. Auk 92: 610-611.

Oelke, H. 1981. Limitations of estimating bird populations because of vegetation structure and composition. Pp. 316 - 321 *in* C.J. Ralph and J.M. Scott (eds.), Estimating Numbers of Terrestrial Birds. Stud. Avian Biol. No. 6. Cooper Ornithological Society.

Payne, R.B. 1973. The breeding season of a parasitic bird, the Brown-headed Cowbird, in central California. Condor 75: 80-99.

Payne, R.B. 1977. The ecology of brood parasitism in birds. Ann. Rev. Ecol. Syst. 8: 1-28.

Peck, G.K. 1996. Ontario nest records scheme, twenty-seventh report (1956 - 1995). Royal Ontario Museum.

Peck, G.K., and R.D. James. 1987. Breeding birds of Ontario: nidiology and distribution. Volume 2: passerines. Life Sci. Misc. Publ. Royal Ontario Museum, Toronto.

Price, J., S. Droege, and A. Price. 1995. The Summer Atlas of North American Birds. Academic Press, San Diego.

Rich, T.D.G. 1978. Cowbird parasitism of Sage and Brewer's sparrows. Condor 80: 348.

Robbins, C.S., D. Bystrak, and P.H. Geissler. 1986. The breeding bird survey: its first fifteen years, 1965-1979. U.S. Fish Wildl. Serv., Resour. Publ. 157.

Root, T. 1988. Atlas of Wintering North American Birds. University of Chicago Press, Chicago.

Rothstein, S.I. 1975. An experimental and teleonomic investigation of avian brood parasitism. Condor 77: 250-271.

Rothstein, S.I. 1976. Experiments on defenses Cedar Waxwings use against cowbird parasites. Auk 93: 675-691.

Rothstein, S.I., J. Verner, and E. Stevens. 1980. Range expansion and diurnal changes in dispersion of the Brown-headed Cowbird in the Sierra Nevada. Auk 97: 253-267.

Rothstein, S.I., J. Verner, and E. Stevens. 1984. Radio-tracking confirms a unique diurnal pattern of spatial occurrence in the parasitic Brown-headed Cowbird. Ecology 65: 77-88.

Rothstein, S.I., D.A. Yokel, and R.C. Fleischer. 1986. Social dominance, mating and spacing systems, female fecundity, and vocal dialects in captive and free-ranging Brown-headed Cowbirds. Pp. 127-185 *in* R.F. Johnston (ed.), Current Ornithology. Volume 3. Plenum Press, New York.

Scott, D.M. 1977. Cowbird parasitism on the Gray Catbird at London, Ontario. Auk 94: 18-27.

Sealy, S.G. 1996. Evolution of host defenses against brood parasitism: implications of puncture-ejection by a small passerine. Auk 113: 346-355.

Sedgwick, J.A., and F.L. Knopf. 1988. A high incidence of Brown-headed Cowbird parasitism of Willow Flycatchers. Condor 90: 253-256.

Sokal, R.R., and F.J. Rohlf. 1981. Biometry. 2nd edition. W.H. Freeman and Co., San Francisco.

Thompson, C.F., and B.M. Gottfried. 1976. How do cowbirds find and select nests to parasitize? Wilson Bull. 88: 673-675.

Thompson, C.F., and B.M. Gottfried. 1981. Nest discovery and selection by Brown-headed Cowbirds. Condor 83: 268-269.

Thompson, F.R., III. 1994. Temporal and spatial patterns of breeding Brown-headed Cowbirds in the midwestern United States. Auk 111: 979-990.

Thompson, W.L. 1960a. Agonistic behavior in the House Finch part I: annual cycle and display patterns. Condor 62: 245-271.

Thompson, W.L. 1960b. Agonistic behavior in the House Finch part II: factors in aggressiveness and sociality. Condor 62: 378-402.

Tweit, R.C., and J.C. Tweit. 1986. Urban development effects on the abundance of some common resident birds of the Tucson area of Arizona. Amer. Birds 40: 431-436.

Verner, J. 1985. Assessment of counting techniques. Pp. 247 - 302 *in* R.F. Johnston (ed.), Current Ornithology. Volume 2. Plenum Press, Chicago.

Verner, J., and L.V. Ritter. 1983. Current status of the Brown-headed Cowbird in the Sierra National Forest. Auk 100: 355-368.

Weir, R.D. 1985. The spring migration. Ontario region. Am. Birds 39: 291-296.

Weir, R.D. 1988a. The winter season. Ontario region. Am. Birds 42: 256-261.

Weir, R.D. 1988b. The nesting season. Ontario region. Am. Birds 42: 1281-1286.

Wiens, J.A. 1963. Aspects of cowbird parasitism in southern Oklahoma. Wilson Bull. 75: 130-139.

4

Unsuitability of the House Finch as a Host of the Brown-headed Cowbird

INTRODUCTION

The Brown-headed Cowbird is an obligate brood parasite that lays its eggs in the nests of many host species, which provide parental care (Friedmann and Kiff 1985). For parasitism to be successful, hosts must not only accept and incubate cowbird eggs (some species routinely reject these eggs; Rothstein 1975) but they also must provide the nestling parasite with adequate nourishment for proper development. The food of cowbird hosts varies widely from animal to plant material (Martin et al. 1951), but almost all feed their young primarily animals. Some taxa, however, feed their young plant material and failure of cowbird parasitism in the nests of these species is believed to be the result of inadequate diet (Eastzer et al. 1980, Middleton 1991).

The House Finch is an occasional host of the Brown-headed Cowbird (Friedmann 1966, Friedmann et al. 1977). This finch feeds on a variety of plant materials, but most of the diet consists of weed seeds. The few animals taken are mainly aphids and caterpillars (Woods 1968). Like other members of the Carduelinae, House Finches are unusual among cowbird hosts in that they feed their young primarily plant material. The food is given to nestlings by regurgitation; it is neither partially digested nor does it contain nutritive secretions from the adult (Newton 1972). Similar diets fed to cowbirds by other species are insufficient, which implies that the House Finch, too, would be unable to rear the parasite. The purpose of the present study was to determine the frequency of successful parasitism on House Finch nestling, and hence the suitability of this species as a host of the Brown-headed Cowbird.

MATERIALS AND METHODS

Data were collected at sites in southern Ontario in the towns of Barrie, Guelph, Orillia, and St. Catharines, from May to August 1983-1985 and 1990-1993. House Finch nests were found by systematically searching through residential neighbourhoods for singing territorial males or evidence of nest construction. Nests were commonly placed in ornamental conifers near dwellings and were positioned 0.9 to 6.0 m ($\bar{x}$=2.44, SD=0.729, n=373) above ground. Most nests were easily reached using a six-foot (2 m) stepladder. The contents of higher nests were observed with the aid of a small mirror positioned on the end of a telescopic pole. Parasitized nests contained cowbird eggs, cowbird nestlings or both. These nests were monitored daily at approximately the same time except in 1992 and 1993 when nests were visited twice per week. The fate of most cowbird nestlings was determined but data on their growth and survivorship were taken only from individuals that were observed daily from hatching (day 0). Cowbird nestlings in a nest were marked uniquely by toenail-clipping (St. Louis et al. 1989). Nestling body mass was measured using 10- and 50-g Pesola® spring scales accurate to 0.1 and 0.25 g, respectively. Wing chord and length of ninth primary (tip of feather to the point of emergence from the skin) were taken to the nearest 0.05 mm using dial calipers. Nestlings that disappeared were assumed to have died in the nest, the corpse having been removed by the foster parents (Welty and Baptista 1988). Predation of cowbirds was ruled out if the nest continued to hold House Finch eggs and/or young.

A nestling cardueline stores food temporarily in its distensible gullet before digestion (Newton 1972). In House Finch nestlings the full gullet appears as a large bulge on the right side of the neck, the contents of which can be easily observed through the thin, translucent skin. Initial observations of House Finch diet were made by external examination of the gullet. All young appeared to be receiving plant material mostly in the form of seeds. Finch and cowbird diets were studied more thoroughly by examination of nestling feces. At St. Catharines fresh feces were collected from young during nest visits throughout the 1991 breeding season. Each sample was sealed in a separate vial and later stored at -20° C. Samples were taken when House Finches and cowbirds were 0-8 and 2-5 days old, respectively. One-hundred and thirteen fecal samples were collected from 67 House Finches at 23 nests and four samples were taken from two cowbirds at two nests. Upon examination, the samples were moistened with 70% ethanol, teased apart with dissecting needles, and the constituents identified under a binocular dissecting microscope. A drawback of using fecal samples for the analysis of diet is the fragmented nature of the food (Rosenberg and Cooper 1990). This is less of a concern with nestlings as their feces retain an undigested residue. Nonetheless, food became increasingly difficult to identify with age of nestlings because samples from older young contained relatively more digested food.

Growth coefficients were calculated for increase in body mass based on a logistic model of growth (Ricklefs 1984). The relative growth rate, K, asymptotic body mass, and time required to complete 10 to 90% of the asymptote, $t_{10\text{-}90}$, were determined using nonlinear least-squares regression (Gauss-Newton method, NLIN of SAS Institute 1988). Because sample sizes varied greatly among age groups of cowbirds, the data were weighted according to sample size. Thus, body mass values for each age group were accurately represented in the calculation of growth parameters. Cowbird growth data from Scott (1979) were similarly analyzed. The logistic model provided a suitable description of growth (r^2 approximation ≥ 0.8433).

RESULTS

The Brown-headed Cowbird parasitized 99 (24.4%) of 406 House Finch nests observed. Parasitized nests contained a total of 127 cowbird eggs. Of these, 79 survived through the incubation period and produced 67 (84.8%) nestlings. In addition, 11 cowbirds of varying age were discovered after they had hatched. No cowbird was successfully reared in a House Finch nest. Nestlings that perished in the nest were either found dead there (35.6%), or removed (64.4%) by the foster parents. Two discarded corpses were found on the ground near their respective nests. Only one cowbird fledged. It left the nest at age 14 d but was found dead the following day. Proportional survivorship of cowbird nestlings is shown in Fig. 4.1. The average survival time was only 3.2 d (SD=2.87, *n*=25). Two birds did not survive beyond their day of hatching, whereas only one individual survived to 14 d.

Cowbird hatchlings had a mean body mass of 2.79 g (SD=0.273, *n*=23) and body mass increased in a largely linear fashion over the entire growth period (Fig. 4.2). Two nestlings failed to gain mass beyond two and five days of age and one individual lost mass after two days of age. The maximum nestling mass recorded was 22 g. Specific growth parameters for cowbirds reared by House Finches and other species are given in Table 4.1. Cowbird growth was severely retarded in House Finch nests. Cowbirds achieved an estimated asymptotic body mass that was 22.4% smaller than in nests of other hosts. The relatively smaller growth rate, *K*, approximately doubled the time required for growth.

Nestling cowbirds developed teleoptiles, but barbs did not emerge from the sheaths of most individuals. The single cowbird that fledged had well developed plumage when it left the nest. It showed substantial growth of barbs of all feather tracts and attained wing chord and ninth primary lengths of 63.00 mm and 33.15 mm, respectively.

House Finch diet consisted almost entirely of plant material including whole seeds, cotyledons (primary embryonic leaves) and the seed coats that cover them, plant fragments and pulp. Most seeds were small and ranged in length from 1 to 4 mm. Animals were identified in only eight (7.1%) samples and included eight mites (Acari), three springtails (Collembola) and three aphids (Aphididae). Grit first appeared in the meals of one-day-old House Finches. Samples of cowbird diet contained only plant material consisting mostly of whole seeds and seed parts and appeared to be largely undigested with very little indistinguishable plant material present.

DISCUSSION

Results indicate that the House Finch is an unsuitable host of the Brown-headed Cowbird. All attempts at parasitism failed with most cowbird nestlings perishing in the nest. There are no reports in the literature of cowbird nestlings in House Finch nests. Most of the existing records of parasitism mention the presence of cowbird eggs in House Finch nests (Friedmann 1963, Friedmann et al. 1977, Friedmann and Kiff 1985 and references therein), but provide no account of cowbird hatching success or nestling survivorship. Some data on cowbird nestling life in eastern North America are provided by the American Nest Records Card Program and in at least two cases corroborate the results of this study. Three records indicate cowbirds surviving from at least 2 to 10 d before predation of nest contents, or observations ended. Another nest contained one dead cowbird nestling of unknown age with two unhatched finch eggs. One observer reported the disappearance of a two-to-six d old cowbird from a nest that also held two finch nestlings that later fledged successfully. The disappearance of cowbird nestlings is implied in four other instances, including one record from Oregon. Presumably, cowbird nestlings that disappeared from these nests had perished there and their bodies were removed by the foster parents. Given these findings, the probability of survival of cowbirds in House Finch nests appears to be exceedingly small.

Despite this high level of mortality, cowbird nestlings occasionally fledge from House Finch nests. In the present study, only one cowbird survived to leave its nest but either died of malnutrition (see below) or received no foster-parental care thereafter. Wauer (1964:299) reported an exception observed in California in which a fledgling cowbird (*M. a. obscurus*) was seen being fed by a House Finch. The rearing of cowbirds by this host appears to be very rare.

The type of diet that parents feed to their offspring is important in determining host suitability. Most passerines feed their young with arthropods and nestling diets show considerable overlap among sympatric species (Orians and Horn 1969, Maher

1979). Thus, there appears to be little restriction among hosts concerning the food of nestlings; a variety of species appear to provide equally adequate diets to cowbird young (see Norris 1947, Scott 1979). However, cowbirds fail to survive in nests of hosts that feed their nestlings regurgitated seeds, fruit or other plant material. Hatchling Brown-headed Cowbirds died, most within six days, after being placed in nests of the House Sparrow (*Passer domesticus*, Eastzer et al. 1980), which may feed their young large quantities of plant material (Bent 1958). Cowbirds survived an average of only 2 days in American Goldfinch (*Carduelis tristis*) nests. Most cowbirds died by the fourth day and only one survived 12 days (Middleton 1991). Cowbirds may fledge from Cedar Waxwing (*Bombycilla cedrorum*) nests but occasionally die after three days when parents start to feed their young fruit rather than insects (Rothstein 1976). House Finches gave cowbird nestlings a specific diet consisting mainly of seeds. The failure of cowbirds to thrive on this food is additional evidence that this species is unlikely to survive on the special nestling diets of some granivorous or frugivorous species.

Most altricial young grow rapidly (Ricklefs 1968), which requires a protein rich diet (O'Connor 1984). Food low in protein content may arrest growth severely (Johnson 1971, Roudybush and Grau 1986, Boag 1987). The poor development of cowbirds witnessed in House Finch nests appears to be the result of protein deficiency. Nestling body mass did not follow a sigmoidal pattern typical of normal growth (Ricklefs 1968) and never attained the asymptotic level or fledging mass of cowbirds reared by suitable hosts. The body mass of two cowbirds did not increase, whereas another individual experienced weight recession. Feather growth was delayed and required additional time (about 4 days for the only individual that fledged) to achieve sizes observed for cowbirds 10 days old (Scott 1979). Unlike suitable hosts, House Finches feed their young a diet that is limited in protein. Seeds and particularly fruits are generally low in protein (Newton 1972:179, Morton 1973, O'Connor 1984, Johnson et al. 1985). Furthermore, plant proteins often lack one or several of the "essential" amino acids that cannot be synthesized by the animal itself (Needham 1964, Parrish and Martin 1977, Sedinger 1990). Cowbirds in finch nests received a minuscule quantity of animal food, probably inadvertently consumed by foraging parents, that was grossly insufficient to meet their protein requirements.

The failure of cowbird parasitism on House Finch nesting may lend insight in the evaluation of host suitability by cowbirds. Because there is no reproductive success in parasitism of House Finches, they should be avoided by cowbirds. The frequency of parasitism observed in this study was relatively high; however, this may be a result of the recent association of this host and parasite in Ontario (Kozlovic 1994). Therefore, cowbirds may be under strong selection against choosing House Finches as hosts after the two species come into contact. Indeed, parasitism rate has decreased markedly with time of association between this host and parasite in eastern North America (see Chapter 5).

Table 4.1. Specific growth parameters of nestling Brown-headed Cowbirds.

Host	n	Asymptote[a] (g)	Adult Body Mass[b] (g)	Ratio (R)	Growth Rate[c] (K)	($t_{10\text{-}90}$)	Source
Ovenbird, Wood Thrush	2	30.0	43.5	0.69	0.576	7.6	Ricklefs 1968[d]
Red-winged Blackbird, Song Sparrow, Yellow Warbler	8	28.8	43.5	0.66	0.597	7.4	Scott 1979
House Finch	23	22.8	43.5	0.52	0.318	13.8	present study

[a] Estimated final body mass of nestling growth.

[b] From Ricklefs (1968).

[c] Logistic growth rate constant, K, and time required to complete 10 to 90 percent of the asymptote, $t_{10\text{-}90}$.

[d] Data from Norris (1947).

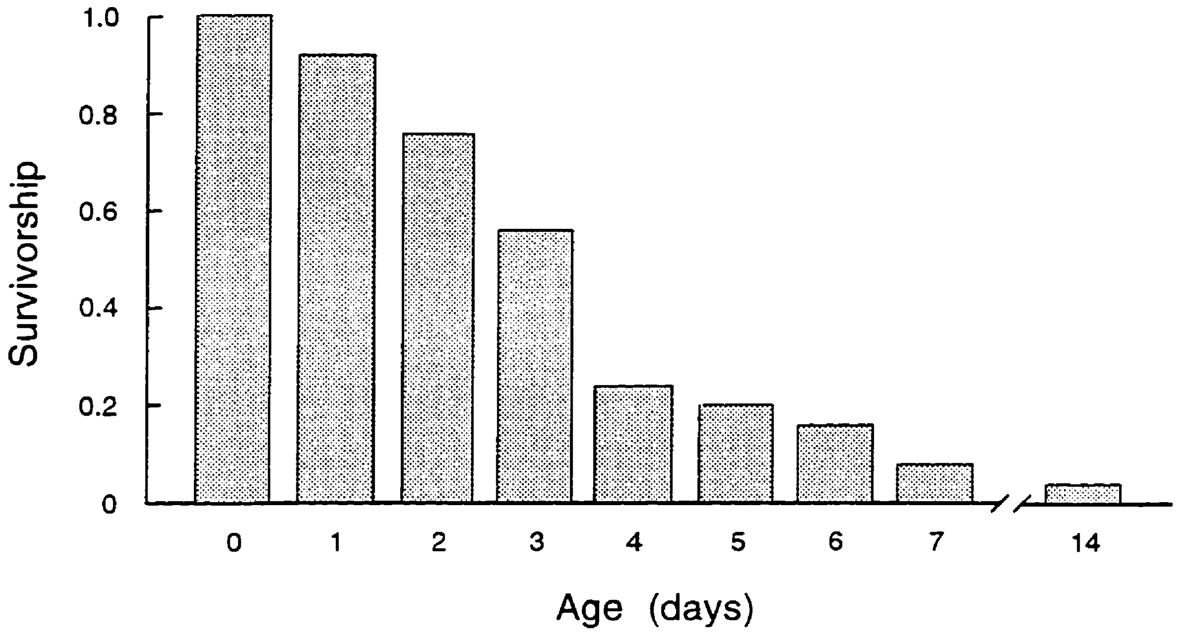

Fig. 4.1. Proportional survivorship of Brown-headed Cowbirds (original n=25) from hatching (0) to 14 d in nests of the House Finch.

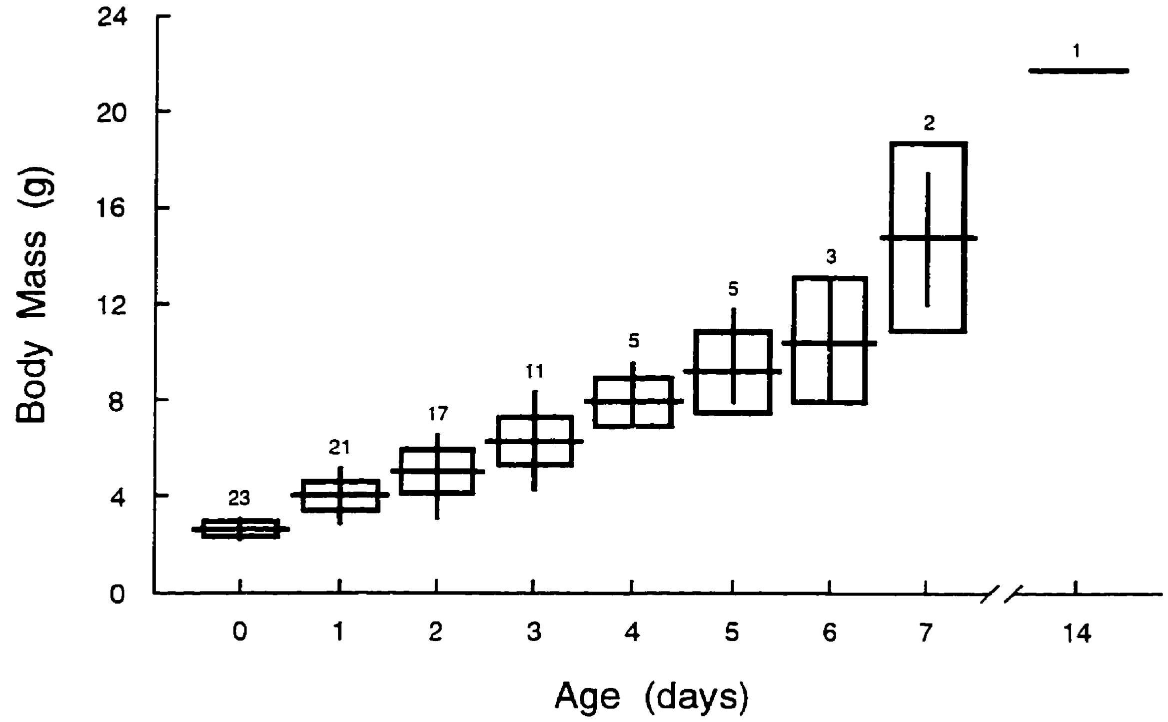

Fig. 4.2. Increase of body mass of Brown-headed Cowbirds from hatching (0) to 14 d in nests of the House Finch. Horizontal bars indicate sample means, vertical bars the range, and the rectangles enclose ± 1 standard deviation. Sample size is shown above plotted values.

LITERATURE CITED

Bent, A.C. 1958. Life histories of North American blackbirds, orioles, tanagers, and allies. U.S. Natl. Mus. Bull. 211.

Boag, P.T. 1987. Effects of nestling diet on growth and adult size of Zebra Finches (*Poephila guttata*). Auk 104: 155-166.

Eastzer, D., P.R. Chu, and A.P. King. 1980. The young cowbird: average or optimal nestling? Condor 82: 417-425.

Friedmann, H. 1963. Host relations of the parasitic cowbirds. U.S. Natl. Mus. Bull. 233.

Friedmann, H. 1966. Additional data on the host relations of the parasitic cowbirds. Smithsonian Misc. Coll. 149: 1-12.

Friedmann, H., and L.F. Kiff. 1985. The parasitic cowbirds and their hosts. Proc. West. Found. Vert. Zool. 2: 225-304.

Friedmann, H., L.F. Kiff, and S.I. Rothstein. 1977. A further contribution to knowledge of the host relations of the parasitic cowbirds. Smithsonian Contr. Zool. 235: 1-75.

Johnson, N.F. 1971. Effects of levels of dietary protein on Wood Duck growth. J. Wildl. Mangmt. 35: 798-802.

Johnson, R.A., M.F. Willson, J.N. Thompson, and R.I. Bertin. 1985. Nutritional values of wild fruits and consumption by migrant frugivorous birds. Ecology 66: 819-827.

Kozlovic, D.R. 1994. The House Finch in Ontario. Pp. 298-306 *in* M.K. McNicholl and J.L. Cranmer-Byng (eds.). Ornithology in Ontario. Spec. Publ. No. 1, Ontario Field Ornithologists. Hawk Owl Publ., Whitby.

Maher, W.J. 1979. Nestling diets of prairie passerine birds at Matador, Saskatchewan, Canada. Ibis 121: 437-452.

Martin, A.C., H.S. Zim, and A.L. Nelson. 1951. American Wildlife and Plants, A Guide to Wildlife Food Habits. McGraw-Hill, New York.

Middleton, A.L.A. 1991. Failure of Brown-headed Cowbird parasitism in nests of the American Goldfinch. J. Field Ornithol. 62: 200-203.

Morton, E.S. 1973. On the evolutionary advantages and disadvantages of fruit eating in tropical birds. Am. Nat. 107: 8-22.

Needham, A.E. 1964. The Growth Process in Animals. Pitman and Sons Ltd., London.

Newton, I. 1972. Finches. William Collins Sons and Co. Ltd., Glasgow.

Norris, R.T. 1947. The cowbirds of Preston Frith. Wilson Bull. 59: 83-103.

O'Connor, R.J. 1984. The Growth and Development of Birds. John Wiley and Sons Ltd., Chichester.

Orians, G.H., and H.S. Horn. 1969. Overlap in foods and foraging of four species of blackbirds in the potholes of central Washington. Ecology 50: 930-938.

Parrish, J.W., Jr., and E.W. Martin. 1977. The effect of dietary lysine level on the energy and nitrogen balance of the Dark-eyed Junco. Condor 79: 24-30.

Ricklefs, R.E. 1968. Patterns of growth in birds. Ibis 110: 419-451.

Ricklefs, R.E. 1984. Components of variance in measurements of nestling European Starlings (*Sturnus vulgaris*) in southeastern Pennsylvania. Auk 101: 319-333.

Rosenberg, K.V., and R.J. Cooper. 1990. Approaches to avian diet analysis. Pp. 80-90 *in* M.L. Morrison, C.J. Ralph, J. Verner, and J.R. Jehl, Jr. (eds.), Avian Foraging: Theory, Methodology, and Applications. Stud. Avian Biol. No. 13. Cooper Ornithological Society.

Rothstein, S.I. 1975. An experimental and teleonomic investigation of avian brood parasitism. Condor 77: 250-271.

Rothstein, S.I. 1976. Cowbird parasitism of the Cedar Waxwing and its evolutionary implications. Auk 93: 498-509.

Roudybush, T.E., and C.R. Grau. 1986. Food and water interrelations and the protein requirement for growth of an altricial bird, the Cockatiel (*Nymphicus hollandicus*). J. Nutr. 116: 552-559.

SAS Institute. 1988. SAS/STAT User's Guide, Release 6.03 Edition. SAS Institute Inc., Cary, NC.

St. Louis, V.L., J.C. Barlow, and J.-P.R.A. Sweerts. 1989. Toenail-clipping: a simple technique for marking individual nidicolous chicks. J. Field Ornithol. 60: 211-215.

Scott, T.W. 1979. Growth and age determination of nestling Brown-headed Cowbirds. Wilson Bull. 91: 464-466.

Sedinger, J.S. 1990. Are plant secondary compounds responsible for negative apparent metabolizability of fruits by passerine birds? A comment on Izhaki and Safriel. Oikos 57: 138-140.

Wauer, R.H. 1964. Ecological distribution of the birds of the Panamint Mountains, California. Condor 66: 287-301.

Welty, J.C., and L.F. Baptista. 1988. The Life of Birds. Saunders, New York.

Woods, R.S. 1968. *Carpodacus mexicanus frontalis* (Say), House Finch. Pp. 290-314 *in* A.C. Bent (O.L. Austin, Jr. [ed.]), Life histories of North American cardinals, grosbeaks, buntings, towhees, finches, sparrows, and allies. U.S. Natl. Mus. Bull. 237.

5

Cowbird Parasitism of House Finches is Related to Their Time in Sympatry

INTRODUCTION

The fitness of an avian brood parasite depends on its choice of host. Because hosts available to parasites may comprise a diverse group of species that can vary greatly in their ability to rear parasites, not all hosts may be suitable for parasitism. For instance, female parasites may realize no reproductive success from the nests of hosts that provide inappropriate foster parental care (Mason 1986a, Davies and Brooke 1989, Middleton 1991). On the other hand, some hosts may reject parasite eggs (Rothstein 1975). The quality of a host, therefore, is likely an important factor in determining the nature of host-parasite interactions. A parasite may become more effective in its parasitism by evolving specificity on a single host species or related groups of species (Friedmann 1929). Alternatively, a generalist approach also may be an effective strategy because it distributes the parasitic burden among many hosts, thus reducing the likelihood that any one host will evolve anti-parasite behaviour (Payne 1977, Davies and Brooke 1989).

The Brown-headed Cowbird is an extreme host generalist that routinely parasitizes many North America species (Friedmann 1963, Friedmann et al. 1977, Friedmann and Kiff 1985). Mayfield (1965a) considered cowbirds to be truly opportunistic in host selection, depositing their eggs randomly among hosts (see also Buech 1982, Fleischer 1985, Orians et al. 1989). Others have reported non-random distributions of cowbird eggs among nests (Preston 1948, Elliott 1977, Lowther 1984), which suggests that cowbirds practice some host selection. The notion that some level of host discrimination may occur is supported by additional studies reporting different frequencies of parasitism among species. Some species may be used almost exclusively as hosts (Hatch 1983) while others experience virtually no cowbird parasitism even though they are available as hosts and accept cowbird eggs (Friedmann 1963, Rothstein 1976).

The origin or evolutionary path leading to observed patterns of host exploitation are often difficult to elucidate because most studies of social parasitism involve host and parasite populations that have had long histories of sympatry. One way to obviate the lack of firm data on how such patterns are established involves monitoring the frequency of parasitism in actively colonizing populations of either parasites or hosts. The recent establishment of the House Finch in eastern North

America provides such an opportunity. House Finches experience considerable geographical variation in frequency of parasitism. They are rarely parasitized in their native western range (Friedmann et al. 1977, Wootton 1986, Brown 1994) yet may be frequently parasitized by cowbirds in the east (Graham 1987a, Peck and James 1987, this study). These findings are of particular note as the House Finch is an unsuitable cowbird host (Kozlovic et al. 1996). There now exists a unique opportunity to investigate the dynamics of brood parasitism early in the history of interaction between the cowbird and an actively colonizing host (Kozlovic et al. op. cit.).

Natural History of the Brown-headed Cowbird and House Finch in North America

Brown-headed Cowbirds are native to the grasslands of the Great Plains. The species appears to have been largely confined to this region until the eighteenth century when European settlement provided additional habitat in the east. Extensive clearing of forests for agriculture and livestock created an environment favourable to cowbirds and promoted their spread (Friedmann 1929, Mayfield 1965b). By 1790 the species was common in Pennsylvania and New York (Friedmann 1929) and apparently widespread in the northeast by the late 1800s. More recently, cowbirds have invaded the far west (Rothstein 1994). Cowbirds of the Southwest that occurred along the Colorado River and farther east began to colonize southern California around 1900. The population spread quickly through the state reaching the north coastal region by 1941. Cowbirds continued to claim new territory west of the Cascades and reached southern British Columbia, the current extent of the range, by 1955. Presently, cowbirds occur in southern Canada, throughout the conterminous United States south to southern Mexico (Lowther 1993).

The House Finch occurs naturally in western North America, west of the Great Plains, from southern British Columbia to southern Mexico (Hill 1993). It occupies a variety of habitats from deserts to open coniferous forests and prefers edge habitat near water. House Finches are frequently associated with humans and are common in many urban situations where they nest about dwellings. In 1940 the species became established in the east through the release of caged birds on Long Island, NY (Elliott and Arbib 1953). This finch has since dispersed throughout the eastern United States and southeastern Canada. In addition, incursion of the western population has occurred into the midwest (Seltman 1989) where parent and naturalized populations have recently merged and continue to increase in number (Podrebarac and Finck 1991).

Colonization by House Finches has resulted in contact with new cowbird populations, thus host and parasite have been associated for varying periods of time in the east. House Finches near the release site have been sympatric with cowbirds for over half a century whereas those near the periphery of their distribution have only just encountered the parasite. This situation is particularly well suited for the study of host-parasite interactions for several reasons. First, frequency of parasitism can be studied in a known time frame. Colonization of House Finches has been well documented (Mundinger and Hope 1982, Sauer et al. 1996), thus duration of sympatry between host and parasite may be determined precisely among locations. Both species interact mainly in disturbed areas. Human settlements have provided both a vehicle for spread and abundant habitat for both species. Finally, both species are common and widely distributed, which allows incidence of parasitism to be examined locally and throughout the colonized distribution.

Predictions

Because host species vary in quality, individual female cowbirds experience differential reproductive success based, in part, on the hosts that they use (Scott and Lemon 1996). Natural selection favours individuals that maximize their fitness. One approach that cowbirds may employ in maximizing their fitness is to avoid parasitizing unsuitable hosts. House Finches are unsuitable hosts (Kozlovic et al. 1996), which may explain why the species is rarely parasitized in its native western range. If this represents host avoidance by cowbirds, then low parasitism should also be the rule in the colonized eastern range, given time. Because House Finches represent a new host species in the east and because cowbirds are opportunistic parasites, cowbird parasitism may be high in areas of new sympatry. However, continued association of host and parasite should result in a decrease of parasitism over time. Consequently, in areas of long-standing sympatry in the East little parasitism should be observed. By examining frequency of parasitism among populations where House Finches and cowbirds have been sympatric for different periods of time, I show that frequency of parasitism is related to duration of sympatry and appears to represent a change in host preference by cowbirds.

MATERIALS AND METHODS

Study Sites

Field work for this study was conducted at Goleta, Santa Barbara County, California and four localities in Ontario, Canada: Orillia, Simcoe County; Barrie, Simcoe County; Guelph, Wellington County; St. Catharines, Regional Municipality of Niagara (Fig. 5.1). Study sites included suburban residential neighbourhoods with wooded ravines, public parks and sports fields (see Chapter 3).

The Goleta study site lies on the Pacific slope of southern California where both House Finches and cowbirds are common (Garret and Dunn 1981). House Finches have probably occurred in southern coastal California long before humans settled the area. Brown-headed cowbirds began to colonize Santa Barbara County in 1915 and were well established there by 1933 (Rothstein 1994). Study sites in Ontario were located in the southern portion of the Province south and northeast of Lake Ontario. Cowbirds were observed here in the 1880s (McIlwraith 1886) and have become a common breeding species throughout southern Ontario (Graham 1987b). House Finches were first reported in Ontario in 1972 and colonized the province with considerable speed thereafter (Dunn 1987; Kozlovic 1987, 1994). The species became established first on the Niagara peninsula, between Lakes Ontario and Erie, and breeding was noted at St. Catharines in 1980 (Foley 1983). The population expanded quickly along the northern shores of Lakes Erie and Ontario during the early 1980s. Birds started to appear in Guelph in 1984 (Kozlovic 1994) and two nests were found there in 1985 (Weir 1985). Subsequent spread occurred into rural regions and northwards. Birds began to appear regularly at Barrie and Orillia by 1987 (Kozlovic 1994). Currently, House Finches are common in southern Ontario, south of the Canadian Shield, and continue to claim new territory; however, the species remains most abundant in urban centres.

Goleta is a site of long-standing contact between cowbirds and House Finches. Therefore, frequency of parasitism here is probably reflective of relatively longer history of interaction between the two species. In contrast, duration of sympatry between the populations in Ontario has been rather short. Barrie and Orillia represented areas where House Finches and cowbirds became associated in the last 9 years. At Guelph and St. Catharines contact between the species has been for 12 and 16 years, respectively.

Nest Examination

During the period 1983 - 1993 I monitored a total of 476 House Finch nests among the five study sites. Sampling localities together with years, dates of observation and number of nests found are given in Table 5.1. Most nests were discovered during construction or egg laying. Nests were checked every day during 1983 - 1991, and twice per week in other years. All nest visits were made between 07:00 - 16:00 hrs. I was able to observe nests up to 5 m with the aid of a 2-m stepladder and a mirror attached to the end of an extensible pole. Frequency of parasitism was determined for all active House Finch nests. Nests were considered to be active if they held at least three House Finch eggs or were parasitized (see King 1979). To permit individual identification, House Finch and cowbird eggs were numbered inconspicuously at the broad end using an indelible ink marker. Because cowbird nestlings did not survive in House Finch nests, foster parents frequently removed their corpses (Kozlovic et al. 1996). Consequently, status of parasitism could not be determined for nests that contained only House Finch young when found.

Breeding Records

Incidence of cowbird parasitism on House Finches was examined throughout eastern North America using nest records. Data were obtained from the North American Nest Record Card Program, Ontario Nest Record Scheme, Quebec Nest Record Card Program and the Maritime Nest Record Program. These nest record programs provide contributors with record cards to document nesting species, nest location, habitat type, number of eggs, nestlings and cowbird parasitism for each nest found. The accuracy of each nest record depends on the observer's ability to distinguish cowbird eggs from host eggs. Parasitism of House Finch nests is easily recognized because cowbird eggs are larger and heavily maculated compared to those of the host. Therefore, I believe that nest records provided reliable documentation of parasitism of House Finches.

Colonization times for House Finches were determined using Breeding Bird Survey (BBS) data from 1966 - 1994 maintained by the U.S. National Biologcial Survey. The main purpose of the BBS is to monitor population trends of North American birds, but survey data also can be used to detect changes in their breeding distributions. Surveys are conducted annually, on a single day at the peak of the nesting season, throughout the United States and Canada. Each BBS participant records the number of birds observed along a predetermined route at fifty 3-min. stops 0.8 km apart (Robbins et al. 1986). Because data are collected by experienced observers who often cover the same route each year, expansion of the House Finch range has been accurately documented. The eastern House Finch population spread both by diffusion and "jump" dispersal (Mundinger and Hope 1982), the latter method resulting in dissemination of individuals in advance of the main population. Consequently, birds were observed on some BBS routes several years before records began to show annual occurrence of House Finches. Records of jump dispersal, to some extent, reflect subsequent spread of the species but are a premature measure of colonization time of the population as a whole. Therefore, I considered House Finches to have colonized an area after they began to appear annually on a BBS route.

Great Circle (nautical) distances were calculated from the point of introduction to the location of 906 House Finch nests (Fig. 5.2) based on latitude and longitude coordinates. In order to minimize the likelihood of incorporating records of birds from the western population, only nests within a 1000 km radius of the point of introduction were used. This sample included 883 (97.5%) of all (906) eastern records for which the status of parasitism could be determined. House Finches were released at three closely grouped sites on Long Island (Kozlovic 1994) and one, Hicksville (40° 47' N, 73° 32' W), was chosen to represent the origin of the eastern population in the present study. Frequency of cowbird parasitism on House Finches was determined for three time (1965 - 1974, 1975 - 1984, 1985 - 1994) and five distance (km) categories (0 - 200, >200 - 400, >400 - 600, >600 - 800, >800 -1000), and variation of frequency of parasitism among samples was tested using multidimensional contingency analysis (Everitt 1977). The assumption of random sampling of year and distance variates cannot be strictly satisfied in this case because time of parasitism is, in part, dependent on the colonization process. In other words, House Finches must occupy new territory before parasitism of their nests can occur there. A test of mutual independence of the variables proved highly significant ($\chi^2 = 329.72$, df = 13, $P < 0.001$), but associations among all variables cannot be assumed. Several hypotheses of partial independence may be formulated to investigate relationships between variables; however, the null model of interest here is that parasitism is independent of time and distance from the point of origin of the eastern population. Hence, independence between year and distance is inconsequential and was not considered. Frequency of parasitism also was examined in relation to length of time that House Finches and cowbirds have been associated in the east. BBS data were used to determine the time of colonization of finches in 50 km intervals from the release point of the population. Frequency of parasitism was then compared with time in sympatry of host and parasite.

RESULTS

Frequency of Parasitism Among Study Sites

Cowbird parasitism on House Finches was not recorded at Goleta, California, but was common in Ontario and varied considerably among sites and years (Fig. 5.3). Average frequency of parasitism at Orillia and Barrie was 53.1 and 45.5%, respectively. Frequency of parasitism did not differ significantly ($\chi^2 < 0.39$, df = 1, $P > 0.25$) between years at each location. Finches at Guelph experienced the highest frequency of parasitism, of 87.5% in 1986; however, in 1993 frequency of parasitism decreased significantly ($\chi^2 = 7.73$, df = 1, $P < 0.01$) to 22.7%. At St. Catharines average frequency of parasitism was 40.2% during 1983 - 1985 and decreased significantly ($\chi^2 = 71.08$, df = 5, $P < 0.001$) during the six years that the population there was studied. During 1990 - 1992 the average frequency of parasitism at St. Catharines was 5.3% and did not differ significantly ($\chi^2 = 0.55$, df = 2, $P > 0.25$) among years.

Number of cowbird eggs per parasitized nest varied from 1.00 to 1.44 among the study sites (Table 5.2). Multiple parasitism (>1 cowbird egg per nest) was common (22.2%) and differences in size and maculation of cowbird eggs suggests that laying by more than one female in the same nest was likely (Dufty 1983). Two cowbird eggs per nest was the most common form of multiple parasitism. Two nests at Orillia and Barrie contained four cowbird eggs and no finch eggs. Similarly, one nest at St. Catharines in 1983 contained only three cowbird eggs. Presumably, all finch eggs in these nests had been removed by successive female cowbirds (Rothstein 1975). During 1990 -1992 multiple parasitism was not observed at St. Catharines where House Finches and cowbirds have been associated the longest among the study sites.

Frequency of Parasitism in Eastern North America

Overall fequency of parasitism for eastern North America, including data from field sites and nest records, was 18.4% (165 of 883 nests). Fig. 5.4 illustrates frequency of parasitism in relation to time and distance from the origin of the colonizing House Finch population. There are no data for the period 1965 - 1974 beyond 400 km from the release site because this distance marked the extent of the finch distribution at that time (Bystrak 1981). To eliminate empty cells, data from the earlier two decades were combined within their respective distance classes before statistical analysis. Among remaining samples, there was a highly significant (χ^2 =

108.31, df = 9, $P < 0.001$) relationship between frequency of parasitism and time and distance. Frequency of parasitism both decreases with time within each distance class and increases with distance in each decade to a maximum of 800 km (Fig. 5.4). During 1985 - 1994, parasitism was not detected at the centre of the colony and was greatest nearer the periphery of the distribution. Small samples for distance categories of >800 - 1000 in 1985 - 1994 and >600 - 800 and >800 - 1000 in 1975 - 1984 indicate that House Finches have just colonized these regions and, as a result, frequency of parasitism here is likely underestimated. Because these low levels of parasitism may have influenced results, data beyond 600 km were removed and the statistic recalculated. Despite truncation of the data set, a strong relationship between frequency of parasitism and time and distance was still evident ($\chi^2 = 22.61$, df = 5, $P < 0.001$).

Change in frequency of parasitism in relation to time in sympatry of host and parasite is shown in Fig. 5.5. There is a highly significant ($\chi^2 = 22.07$, df = 4, $P < 0.0001$) association between frequency of parasitism and time that House Finches and cowbirds have co-occurred. Frequency of parasitism was greatest (27.9%) soon after the two species came into contact but consistently decreased by approximately 7% during each subsequent time period. Parasitism was not detected after 20 years, which included records of sympatry to 35 years.

DISCUSSION

Frequency of Parasitism Over Time

Change in frequency of cowbird parasitism on House Finches over time may provide insight into how host-parasite interactions influence host choice by cowbirds. Parasitism was highest in areas of new sympatry between House Finches and cowbirds but very low or nonexistent in regions of relatively long-standing sympatry both in the native and colonized range. Several studies have shown that hosts experience high parasitism soon after first contact with social parasites (Friedmann 1963, Wiley 1985, Cruz et al. 1989, Nakamura 1990, Post et al. 1990). In areas of recent sympatry, hosts may lack effective anti-brood parasite defences (Robertson and Norman 1977, Briskie et al. 1992, Rothstein 1975, 1990) and thus are vulnerable to parasitism. Before introduction to eastern North America, House Finches were co-distributed with cowbirds in their native, western range where they had been exposed to the parasite for a considerable period of time. House Finches respond aggressively towards cowbirds (see Chapter 2), but this behaviour does not appear to be sufficient defence against parasitism.

On the other hand, eastern populations of cowbirds have had little or no experience with House Finches. Eastern House Finches represent a new host for the cowbird and because such hosts are unlikely to have evolved anti-brood parasite defences, cowbirds may "perceive" them as suitable hosts. Indeed, the high frequency of parasitism recorded in some locations during the present study suggest that House

Finches are parasitized opportunistically when first encountered by cowbirds. If parasitism is sustained at a high level, host populations may experience local decrease in numbers (Mayfield 1983, Wiley 1985), but this is not the case for finch populations in the east because frequency of parasitism decreased steadily to zero. In Ontario parasitism decreased eight fold at St. Catharines and four fold at Guelph within six years. This trend also was evident throughout the eastern colonized range, with no parasitism detected where there has been contact for more than 20 years. Hahn and Hatfield (1995) studied frequency of cowbird parasitism on field, edge and forest-nesting species in southeastern New York state. House Finches, which have been sympatric with cowbirds there for at least 25 years, were not parasitized, although other hosts of field and edge habitat experienced frequencies of parasitism in excess of 20%, while those of forest habitat were parasitized by as much as 65%.

Reductions of parasitism in the east are not due to the evolution of effective host defences by House Finches, which accept all cowbird eggs in their nests. House Finches neither desert their nests nor do they eject cowbird eggs from their nests when parasitized (Rothstein 1975, pers. obs.). I suggested (Chapter 2) that House Finches have not evolved rejection behaviour because it is not selectively advantageous to the finches. Proportions of finches that hatched and left the nest are not significantly different in parasitized compared to unparasitized nests, thus House Finch reproductive success appears to be little affected by cowbird parasitism. If observed decrease of frequency of parasitism in the east is not a result of host response to parasitism, it may represent changes in host and parasite numbers or changes in host preference.

Population Trends

Decrease in parasitism over time may reflect changes in relative abundance of cowbirds and House Finches. Campaigns to control cowbird numbers have proven effective in reducing parasitism on threatened species at the local level (e.g., Mayfield 1983); broad scale reductions of cowbird numbers may have a similar effect on common host species. According to BBS results cowbirds are declining significantly in more regions than they are increasing (Sauer et al. 1996). For example, the cowbird population in Ontario has shown a significant decrease of 5.5% per year since 1980. In contrast, House Finch numbers there have increased by 58% per year over the same period. If frequency of cowbird parasitism is simply related to host abundance, frequency of parasitism may be expected to decrease as cowbirds become fewer while House Finch numbers increase.

Population size does not appear to be the only factor determining frequency of parasitism in the east. First, although cowbirds have shown an overall decline, their numbers are increasing or have remained unchanged in many areas particularly in the coastal regions from New England to Florida (Sauer et al. 1996). Second, House Finch numbers appear to have stabilized in some parts of the eastern range. Numbers have not shown increases in the New York City area since the mid 1970s (Bosakowski

1986). Finally, frequency of parasitism in Ontario does not appear to be governed solely by parasite and host numbers. Despite reported reductions of cowbirds in Ontario (Sauer et al. 1996), frequencies of parasitism were relatively high among the study sites and did not reflect relative proportions of cowbirds and House Finches. Cowbird abundance was not significantly different among the study sites in Ontario while House Finches were twice as abundant at St. Catharines compared to the other study sites in the Province (see Fig. 3.2). Frequency of parasitism at St. Catharines during 1990 - 1992 was only 10% that observed at Orillia and Barrie and not 50% as might be expected if parasitism were based on host abundance alone. By the same token, magnitude of parasitism at Orillia, Barrie and Guelph ought to have been similar because both cowbird and House Finch numbers were not significantly different among these localities. However, parasitism at Guelph was about half that observed at the two more northern sites and about four times greater than at St. Catharines.

One approach to investigating the effect of species availability on incidence of parasitism involves determining level of parasitism after populations stabilize. In stable populations of cowbirds and House Finches frequency of parasitism also may be expected to arrive at some constant level. Compared to eastern North America, western populations of House Finches and cowbirds have been relatively stable since 1966 (Sauer et al. 1996). Parasitism on House Finches in the west is very low and was zero at Goleta, where cowbirds were present. Similarly, the low frequency of parasitism at St. Catharines during 1990 - 1992. as well as lack of parasitism observed in those parts of the east where the species have been sympatric for more than 20 years suggests that other factors are involved in the parasitism of House Finches by cowbirds.

Selection on Cowbirds

Because cowbird parasitism is unsuccessful in House Finch nests, individual female cowbirds that do not parasitize House Finches would be expected to experience greater reproductive success than those that include House Finches among their hosts. Some host species have evolved anti-brood parasite defences in order to mitigate the negative effects of parasitism on their reproductive success (Rothstein 1990). If parasites do not respond with more effective counter adaptations, parasitism fails and parasites must switch to alternative hosts.

Kozlovic et al. (1996) determined that failure of parasitism in House Finch nests is due to an inadequate, granivorous diet provided to cowbird young by their foster parents. Although the diet of adult cowbirds may include plant material (Bent 1958), cowbird nestlings are unable to survive on a purely granivorous diet. This limitation appears to be the result of an opportunistic parasitic habit that is adapted to the average or common nestling food among hosts, which includes a high-protein diet of invertebrates (Martin et al. 1951). The House Finch is atypical among cowbird hosts in that its nestlings receive a granivorous rather than insect diet.

The House Finch is not the only host that is unsuitable to Brown-headed Cowbirds for dietary reasons. Cowbirds are not able to survive in the nests of other hosts that provide their young large quantities of either fruit or seeds (Table 5.3). Dietary barriers to parasitism also are characteristic of other generalist brood parasites. Granivorous hosts of the Shiny Cowbird (*Molothrus bonariensis*), Screaming Cowbird (*M. rufoaxillaris*) and Common Cuckoo (*Cuculus canorus*) are unsuitable (Table 5.3). Furthermore, hosts that have unsuitable diets for parasite young also are rarely parasitized and some potential hosts of the Shiny Cowbird that have diets of plant material are not known to have been parasitized (references in Table 5.3). Host diet, therefore, appears to be an important factor in host choice among generalist brood parasites. The fact that hosts with inappropriate diets for parasite young are infrequently parasitized suggests that reproductive loss suffered by parasites in the nests of these species is sufficient to be acted upon by natural selection, which would favour exclusion of unsuitable species from the suite of hosts used. Because Brown-headed Cowbirds cannot survive in House Finch nests, decrease of parasitism may reflect selection pressure on cowbirds to avoid this host species.

The rate at which parasitism on House Finches may be expected to decrease over time will depend on the intensity of selection on cowbird reproductive success; strong selection pressure can induce evolution over comparatively short periods of time (e.g., Boag and Grant 1981, Schluter and McPhail 1992). Although the Brown-headed Cowbird is known to parasitize over 200 species throughout North America

(Friedmann and Kiff 1985), individual cowbirds do not have access to this number of hosts. Female cowbirds maintain home ranges or territories (Dufty 1982, Darley 1983) and, therefore, may be exposed to a relatively small number of host species in a given breeding season. For example, avian communities in Ontario may include as few as 11 cowbird hosts. Furthermore, the probability of cowbird young surviving to breeding age is very low (Scott and Ankney 1980). Because cowbirds have a given number of eggs to distribute among hosts, the type and number of hosts species chosen will have a bearing on cowbird reproductive success.

House Finches are the most abundant host species available to cowbirds in some avian communities in Ontario (see Fig. 3.1). In addition, House Finches are heavily parasitized when first encountered by the parasite. Consequently, cowbirds may experience considerable reproductive loss in the nests of House Finches. Therefore, selection on cowbirds to avoid parasitizing House Finches may be strong. Changes in host preference have been noted in other species of generalist brood parasites. For example, the Siberian Meadow Bunting (*Emberiza cioides*), once a main host of the cuckoo (*Cuculus canorus*), is now rarely parasitized presumably due to the evolution of effective egg discrimination ability by the host within 60 years (Nakamura 1990). Shiny Cowbird parasitism on Rufous-collared Sparrows (*Zonotrichia capensis*) dropped significantly soon after colonization of a more effective host, the White-browed Blackbird (*Sturnella superciliaris*, Fraga 1978, 1983). Shiny Cowbirds also have recently colonized islands of the Caribbean, yet potentially unsuitable hosts there are not parasitized (Table 5.3). Apparently, Shiny Cowbirds have developed aversions to these newly encountered species within 50 years of colonizing the area. House Finches have been in contact with cowbirds in eastern North America for about 50 years. Observations of frequency of parasitism over time in Ontario indicate that changes in host preference may occur rapidly.

Briskie et al. (1992) found that some cowbird hosts possessed cowbird egg rejection behaviour even in the absence of parasitism. They suggested rejection behaviour may be genetically controlled and maintained in allopatric populations through introgression of rejecter alleles from host populations sympatric with cowbirds. Gene flow of House Finch avoidance alleles could hasten the rate at which cowbird parasitism decreases over time. Introgression of cowbirds could occur from areas where they are sympatric with House Finches into surrounding allopatric cowbird populations. Thus, colonizing House Finches may encounter cowbird populations which already have avoidance alleles for this host.

However, gene flow for this trait may be largely restricted to the east. The fact that House Finches are heavily parasitized soon after cowbirds encountered them suggests that cowbird alleles for avoiding House Finches were not established in eastern North America. This is consistent with the notion that colonizing cowbird populations originated in the midwest, an area largely devoid of House Finches, where there would be no opportunity for cowbirds to evolve avoidance alleles for this host or that the persistence of such alleles in the absence of House Finches is associated with a cost to cowbirds (e.g., avoidance of suitable host species). Selection for such alleles would likely occur in the presence of House Finches because this host is common and unsuitable for parasitism.

Learning by Cowbirds

Brood parasites may ascertain the suitability of hosts by monitoring the development of their young in nests they have parasitized. Cowbirds repeatedly visit parasitized nests (Mayfield 1961 and references therein) at which time they may remove eggs of the host or other cowbirds (Rothstein 1990). Rothstein (1976) suggested that during these visits cowbirds could gain information concerning host suitability and develop host preferences through learning. He argued that returning to parasitized nests is of adaptive value to cowbirds because unsuitable hosts, those that reject parasitic eggs by ejecting them from the nest, would be recognized and, presumably, could be avoided by brood parasites at future encounters. Although House Finches do not reject cowbird eggs, failure of parasitism does occur after parasitic young hatch. Cowbird nestlings survive on average only 3 days in House Finch nests (Kozlovic et al. 1996), and thus nests of this host are free of cowbird young for most of the nestling period.

Cowbirds have been observed visiting nests containing host young (Dubois 1956, Post and Wiley 1977, Carter 1986). Furthermore, Hahn and Fleischer (1995) found that adult female cowbirds associate with their recently fledged offspring during the breeding season and suggested that these associations could have been fostered through nest visits by females to monitor their young. Cowbirds monitoring the nests of House Finches may observe failure of parasitism during the nestling period as do other species of cowbirds (Post and Wiley 1977, Carter 1986) and some species of cuckoos (Soler at al. 1995). Nest visits during the nestling period would be of highly adaptive value because they would provide cowbirds with information not only on species that accept cowbird eggs but also those that can successfully rear the parasite. Cowbird response to unsuitable hosts through learning could result in rapid changes in host preference. Negative feedback may enhance selection on cowbirds to avoid House Finches, particularly when parasitism, as in the case of this host, may result in considerable reproductive loss.

Another mechanism by which brood parasites could develop host preference is through imprinting (Payne 1977). Nestling Cuckoos (*C. canorus*) are believed to imprint on their host species and later, as adults, parasitize only that species (Glue and Morgan 1972). Rothstein (1976) thought imprinting an unlikely model of host choice in cowbirds because cowbirds do not appear to exhibit host specificity. Brown-headed Cowbirds (Fleischer 1985) as well as Bronzed (*Molothrus aeneus*, Carter 1986) and Shiny Cowbirds (Mason 1986b) distribute their eggs among a variety of hosts and show no tendency to parasitize foster species. Furthermore, feeding of the same cowbird nestling by more than one hosts species may be common (Klein and Rosenberg 1986) suggesting that nestling cowbirds do not discriminate among species with respect to foster parental feedings. Nonetheless, Woodward (1983) observed fledgling cowbirds soliciting feedings from their host species while usually ignoring other species. He also reported three instances of cowbird fledglings being "adopted" by a pair of host-conspecific birds and suggested that fledgling cowbirds recognize host species but not necessarily individuals of that species. Rothstein (1976) also pointed out that if cowbirds imprint on hosts that reared them, one is left to explain the continued parasitism of unsuitable host species. Hosts that are considered to be unsuitable for cowbirds, for instance those that eject cowbird eggs from their nests, occasionally rear the parasite (Friedmann and Kiff 1985). Even small recruitment of cowbirds from the nests of rejecter species may be sufficient to maintain parasitism of these hosts. Kozlovic et al. (1996) observed no rearing to independence of cowbirds by House Finches. Furthermore, departure of cowbirds from the nests of this host appears to be extremely rare (Wauer 1964, Kozlovic et al. 1996, Van Twest pers. comm.). Dwindling numbers of cowbirds that recognize the House Finch as a potential host species could depress incidence of parasitism over time. Lack of cowbird parasitism on House Finch populations after 20 years of sympatry at least does not refute imprinting as a possible model of cowbird host choice.

Thus, decrease in brood parasitism by Brown-headed Cowbirds on House Finches appears to represent a response to an unsuitable host species. Failure of parasitism in House Finch nests may select for cowbirds that avoid of this host. Discrimination among hosts by cowbirds may evolve either through their differential reproductive success with various hosts or parasite response to failure of parasitism. On the other hand, imprinting may effectively serve to narrow the range of host species available to cowbirds by removing from the population, through unsuccessful parasitism, those individuals with the proclivity to parasitize House Finches. The above-mentioned responses may be considered adaptive because they function to maximize cowbird fitness. Accordingly, frequency of parasitism on House Finches was seen to decrease with time. The fact that changes in host preference occurred relatively rapidly is testimony to a parasitic habit that can be both opportunistic and yet responsive to host selective pressures.

Table 5.1. Numbers of House Finch nests examined directly.

Locality	Year	Dates of Observation	Number of Nests
Goleta	1984	2 March - 20 May	70
Orillia	1992	5 May - 30 July	31
	1993	14 June - 5 August	18
Barrie	1992	6 May - 30 July	36
	1993	11 June - 3 August	19
Guelph	1993	10 June - 29 July	22
St. Catharines	1983	20 May - 3 August	33
	1984	25 May - 5 August	25
	1985	26 April - 3 August	24
	1990	1 May - 13 August	68
	1991	3 May - 2 July	57
	1992	11 May - 5 August	73

Table 5.2. Frequency distributions of House Finch nests in Ontario containing one or more cowbird eggs.

			Number of cowbird eggs				
Location	Year	N[a]	1	2	3	4	$\bar{x} \pm$ SD
Orillia	1992	18	12	5		1	1.44 ± 0.784
	1993	8	7	1			1.13 ± 0.350
Barrie	1992	16	11	4		1	1.44 ± 0.814
	1993	9	8	1			1.11 ± 0.333
Guelph	1993	5	4	1			1.20 ± 0.447
St. Catharines	1983	10	7	2	1		1.40 ± 0.699
	1984	16	13	2	1		1.25 ± 0.577
	1985	7	5	2			1.29 ± 0.488
	1990	3	3				1.00 ± 0.000
	1991	4	4				1.00 ± 0.000
	1992	3	3				1.00 ± 0.000

[a] Number of nests.

Table 5.3. Species either unsuitable as hosts or not known as hosts of some common brood parasites.

Parasite	Unsuitable hosts[a]	Not known as host[b]
Brown-headed Cowbird (*Molothrus ater*)	Cedar Waxwing[c] (*Bombycilla cedrorum*) House Sparrow[d] (*Passer domesticus*) American Goldfinch[d] (*Carduelis tristis*)	
Shiny Cowbird (*M. bonariensis*)	Bronze Manakin[d] (?)[e] (*Lonchura cucullata*) House Sparrow[d] Hooded Siskin[d] (*Carduelis magellanica*) Saffron Finch[d] (?) (*Sicalis flaveola*) Grassland Yellow-Finch[d] (*Sicalis luteola*)	Nutmeg Manakin[d] (*Lonchura punctulata*) Bananaquit[f] (*Coereba flaveola*) Stripe-headed Tanager[c] (*Spindalis zena*) Yellow-faced Grassquit[d] (*Tiaris olivacea*) Black-faced Grassquit[d] (*T. bicolor*) Puerto Rican Bullfinch[d] (*Loxigilla portoricensis*) Lesser Antillean Bullfinch[d] (*Loxigilla noctis*) Streaked Saltator[d] (*Saltator albicollis*)
Screaming Cowbird (*M. rufoaxillaris*)	Saffron Finch[d]	
Common Cuckoo (*Cuculus canorus*)	Greenfinch[d] (*Carduelis chloris*) Oriental Greenfinch (?) (*Carduelis sinica*) Linnet[d] (*Carduelis cannabina*) Bullfinch[d] (*Pyrrhula pyrrhula*)	

(Table 5.3 continued)

[a] Glue and Morgan (1972), Rothstein (1976), Friedmann et al. (1977), Eastzer et al. (1980), Wiley (1988), Davies and Brooke (1989), Nakamura (1990), Middleton (1991), Alvarez (1994).
[b] Wiley (1985, 1988), Mason (1986a), Post et al. (1990).
[c] Frugivorous.
[d] Granivorous.
[e] Probably unsuitable but not confirmed.
[f] Nectarivorous.

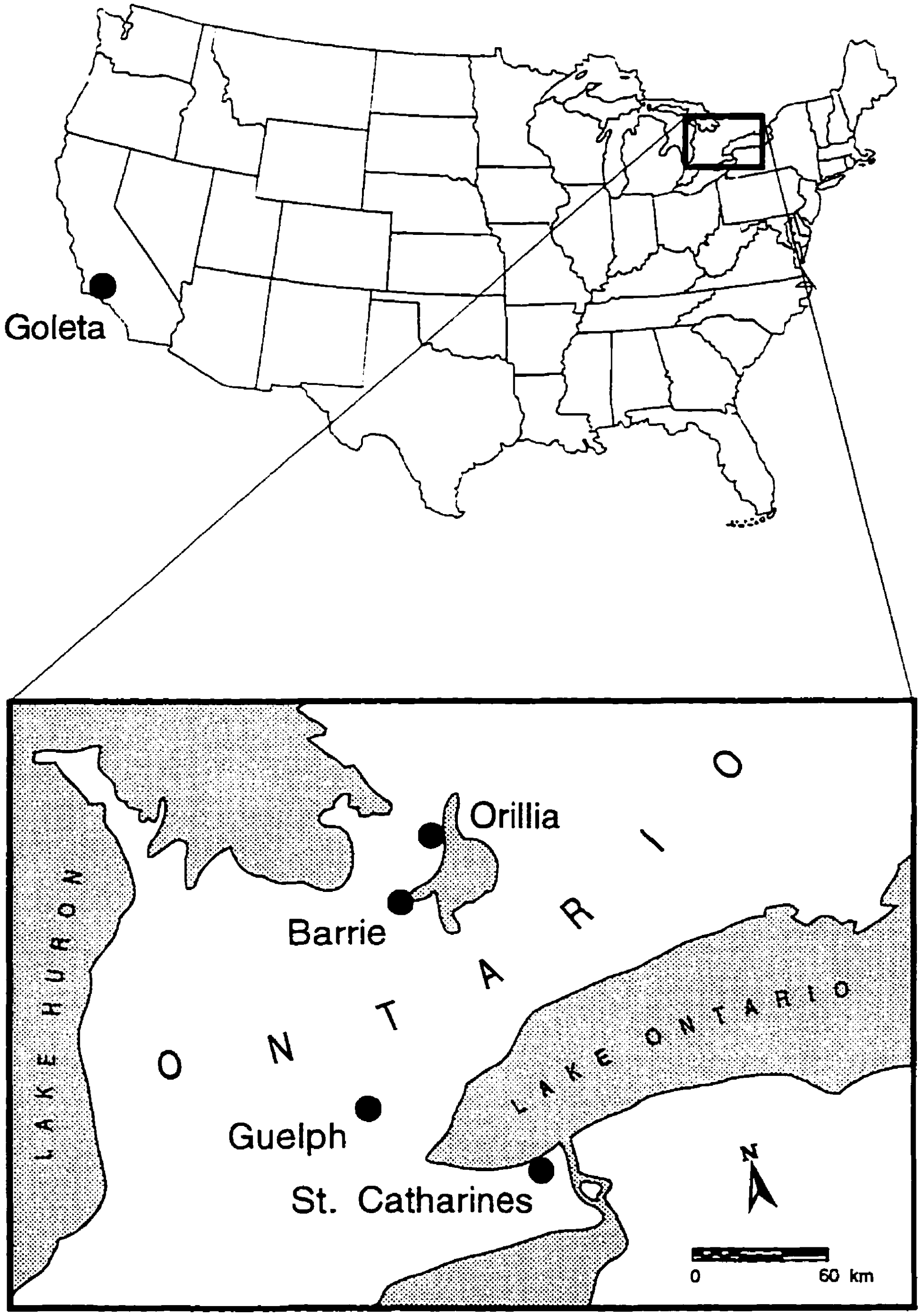

Fig. 5.1. Locations of sites used to determine frequency of Brown-headed Cowbird parasitism on House Finch nests in southern Ontario and California.

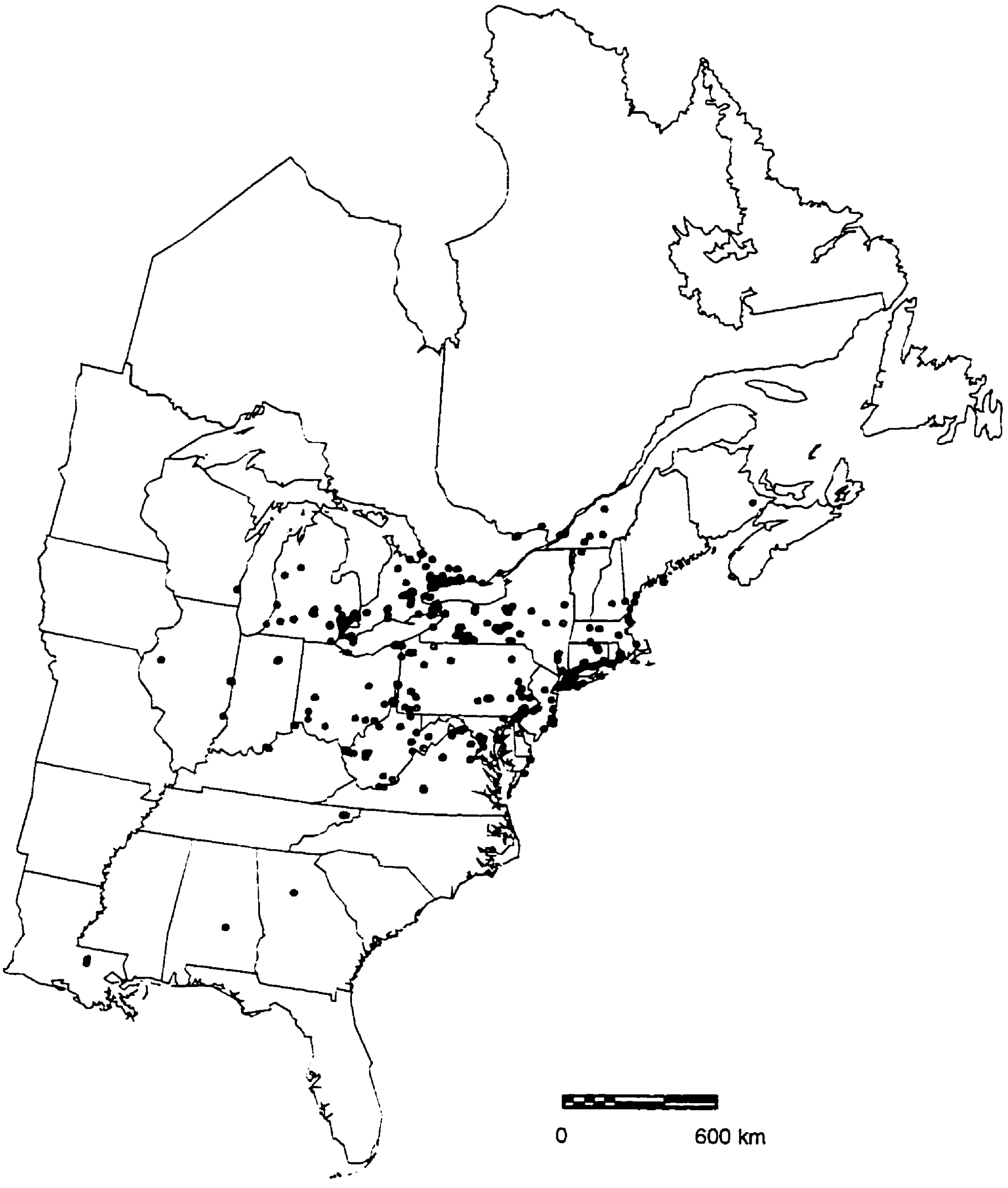

Fig. 5.2. Locations of House Finch nests (N = 906) recorded in eastern North America.

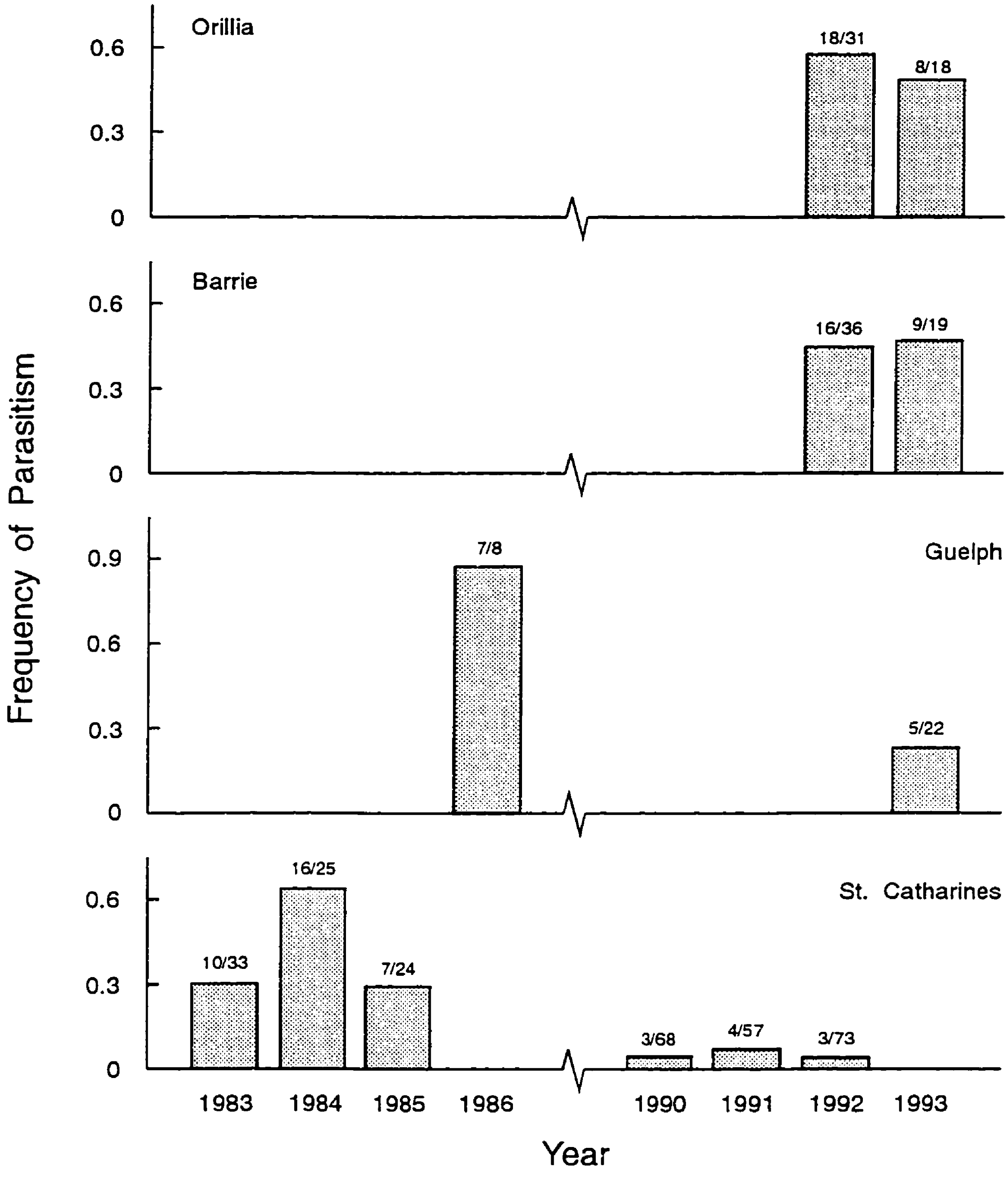

Fig. 5.3. Frequency of Brown-headed Cowbird parasitism on House Finch nests at four sites in Ontario. Fractions above bars indicate the number of nests parasitized out of the number of nests observed. Data for Guelph in 1986 are from Graham (1987a).

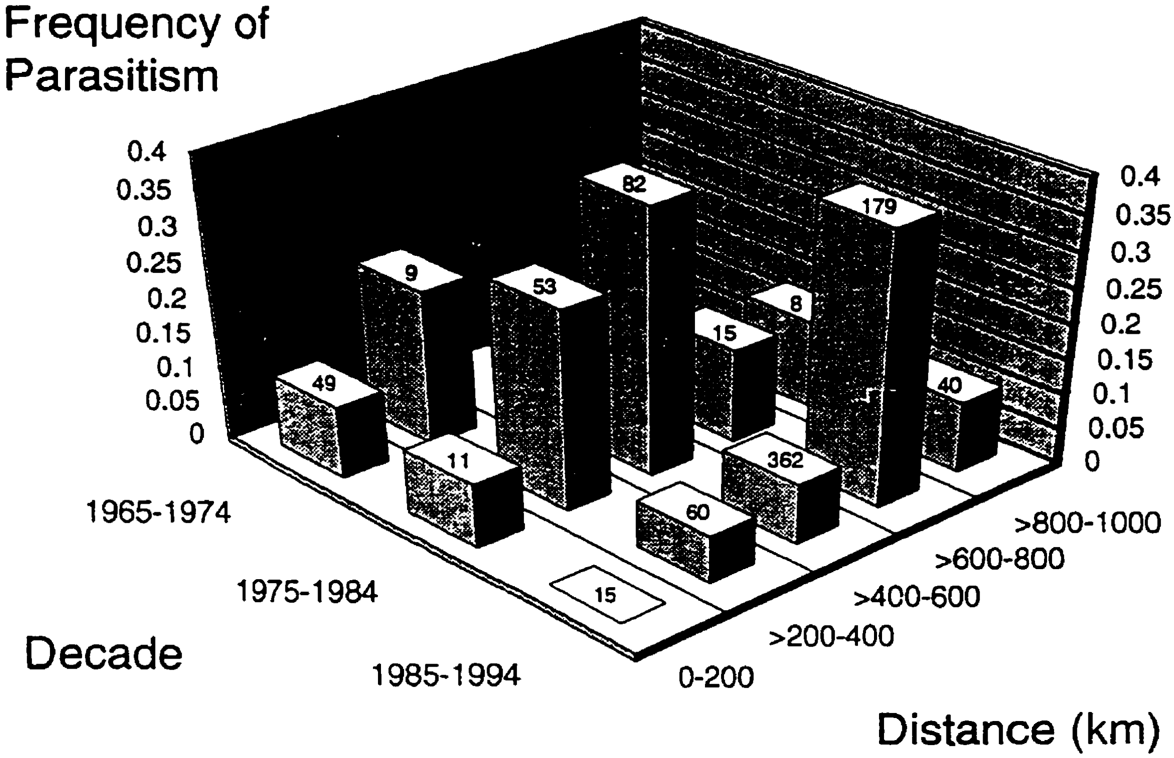

Fig. 5.4. Frequency of Brown-headed Cowbird parasitism on House Finches in relation to year and distance from the point of origin of the host population in eastern North America. Sample sizes appear above bars.

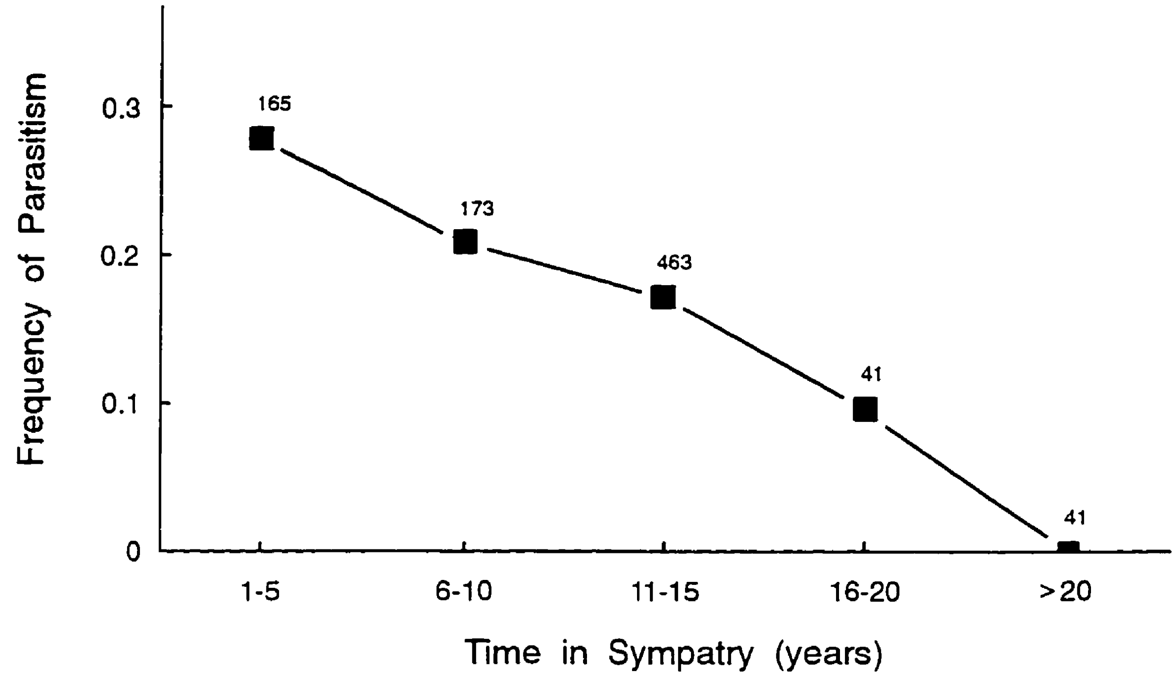

Fig. 5.5. Relationship between frequency of parasitism and time that Brown-headed Cowbirds and House Finches have coexisted in eastern North America. Sample sizes appear above plotted values.

LITERATURE CITED

Alvarez, F. 1994. A gens of Cuckoo *Cuculus canorus* parasitizing Rufous Bush Chat *Cercotrichas galactotes.* J. Avian Biol. 25: 239-243.

Bent, A.C. 1958. Life histories of North American blackbirds, orioles, tanagers, and allies. U.S. Natl. Mus. Bull. 211.

Boag, P.T., and P.R. Grant. 1981. Intense natural selection in a population of Darwin's finches (Geospizinae) in the Galápagos. Science 214: 82-85.

Bosakowski, T. 1986. Winter population trends of the House Finch and ecologically similar species in northeastern New Jersey. Am. Birds 40: 1105-1110.

Briskie, J.V., S.G. Sealy, and K.A. Hobson. 1992. Behavioral defenses against avian brood parasitism in sympatric and allopatric host populations. Evolution 46: 334-340.

Brown, B.T. 1994. Rates of brood parasitism by Brown-headed Cowbirds on riparian passerines in Arizona. J. Field Ornithol. 65: 160-168.

Buech, R.R. 1982. Nestling ecology and cowbird parasitism of Clay-colored, Chipping and Field sparrows in a Christmas tree plantation. J. Field Ornithol. 53: 363-369.

Bystrak, D. 1981. The North American breeding bird survey. Pp. 34-41 *in* C.J. Ralph and J.M. Scott (eds.), Estimating Numbers of Terrestrial Birds. Stud. Avian Biol. No. 6. Cooper Ornithological Society.

Carter, M.D. 1986. The parasitic behavior of the Bronzed Cowbird in south Texas. Condor 88: 11-25.

Cruz, A., J.W. Wiley, T.K. Nakamura, and W. Post. 1989. The Shiny Cowbird *Molothrus bonariensis* in the West Indian region - biogeographical and ecological implications. Pp. 519 - 540 *in* C.A. Woods (ed.), Biogeography of the West Indies - Past, Present and Future. Sandhill Press. Gainesville, Fla.

Darley, J.A. 1983. Territorial behaviour of the female Brown-headed Cowbird (*Molothrus ater*). Can. J. Zool. 61: 65-69.

Davies, N.B., and M. De L. Brooke. 1989. An experimental study of co-evolution between the cuckoo, *Cuculus canorus*, and its hosts. I. Host egg discrimination. J. Anim. Ecol. 58: 207-224.

Dubois, A.D. 1956. A cowbird incident. Auk 73: 286.

Dufty, A.M., Jr. 1982. Movements and activities of radio-tracked Brown-headed Cowbirds. Auk 99: 326-327.

Dufty, A.M., Jr. 1983. Variation in the egg markings of the Brown-headed Cowbird. Condor 85: 109-111.

Dunn, E.H. 1987. Using atlas data to monitor changes in House Finch distribution. Pp. 574-575 *in* M.D. Cadman, P.F.J. Eagles, and F.M. Helleiner (compilers), Atlas of the Breeding Birds of Ontario. University of Waterloo Press, Waterloo.

Eastzer, D., P.R. Chu, and A.P. King. 1980. The young cowbird: average or optimal nestling? Condor 82: 417-425.

Elliott, J.J., and R.S. Arbib, Jr. 1953. Origin and status of the House Finch in the eastern United States. Auk 70: 31-37.

Elliott, P.F. 1977. Adaptive significance of cowbird egg distribution. Auk 94: 590-593.

Everitt, B.S. 1977. The Analysis of Contingency Tables. Chapman and Hall Ltd., London.

Fleischer, R.C. 1985. A new technique to identify and assess the dispersion of eggs of individual brood parasites. Behav. Ecol. Sociobiol. 17: 91-99.

Foley, M.E. 1983. Large numbers of House Finches in St. Catharines, Ontario. Ontario Birds 2:56-60.

Fraga, R.M. 1978. The Rufous-collared Sparrow as a host of the Shiny Cowbird. Wilson Bull. 90: 271-284.

Fraga, R.M. 1983. Parasitismo de cría del renegrido (*Molothrus bonariensis*) sobre el chingolo (*Zonotrichia capensis*): nuevas observaciones y conclusiones. Hornero 12, No. Extraord.: 245-255.

Friedmann, H. 1929. The Cowbirds, A Study in the Biology of Social Parasitism. C.C. Thomas, Springfield, Ill.

Friedmann, H. 1963. Host relations of the parasitic cowbirds. U.S. Natl. Mus. Bull. 233.

Friedmann, H., and L.F. Kiff. 1985. The parasitic cowbirds and their hosts. Proc. West. Found. Vert. Zool. 2: 225-304.

Friedmann, H., L.F. Kiff, and S.I. Rothstein. 1977. A further contribution to knowledge of the host relations of the parasitic cowbirds. Smithsonian Contrib. Zool. 235: 1-75.

Garrett, K., and J. Dunn. 1981. Birds of Southern California: Status and Distribution. Los Angeles Audubon Society, Los Angeles.

Glue, D., and R. Morgan. 1972. Cuckoo hosts in British habitats. Bird Study 19: 187-192.

Graham, D.S. 1987a. Frequent cowbird parasitism of House Finches (*Carpodacus mexicanus*) at Guelph, Ontario. Ont. Birds 5: 116-117.

Graham, D. 1987b. Brown-headed Cowbird, Vacher à tête brune, *Molothrus ater*. Pp. 482-483 *in* M.D. Cadman, P.F.J. Eagles, and F.M. Helleiner (compilers), Atlas of the Breeding Birds of Ontario. University of Waterloo press, Waterloo.

Hahn, D.C., and R.C. Fleischer. 1995. DNA fingerprint similarity between female and juvenile Brown-headed Cowbirds trapped together. Anim. Behav. 49: 1577-1580.

Hahn, D.C., and J.S. Hatfield. 1995. Parasitism at the landscape scale: cowbirds prefer forests. Conserv. Biol. 9: 1415-1424.

Hatch, S.A. 1983. Nestling growth relationships of Brown-headed Cowbirds and Dickcissels. Wilson Bull. 95: 669-671.

Hill, G.E. 1993. House Finch (*Carpodacus mexicanus*). *In* A. Poole and F. Gill (eds.), The Birds of North America, No. 46. Philadelphia: The Academy of Natural Sciences; Washington, D.C.: The American Ornithologists' Union.

Klein, N.K., and K.V. Rosenberg. 1986. Feeding of Brown-headed Cowbird (*Molothrus ater*) fledglings by more than one "host" species. Auk 103: 213-214.

Kozlovic, D.R. 1987. House Finch, Roselin familier, *Carpodacus mexicanus*. Pp. 492-493 *in* M.D. Cadman, P.F.J. Eagles and F.M. Helleiner (compilers), Atlas of the Breeding Birds of Ontario. University of Waterloo Press, Waterloo.

Kozlovic, D.R. 1994. The House Finch in Ontario. Pp. 298-306 *in* M.K. McNicholl and J.L. Cranmer-Byng (eds.), Ornithology in Ontario. Spec. Publ. No. 1, Ontario Field Ornithologists. Hawk Owl Publ., Whitby.

Kozlovic, D.R., R.W., Knapton, and J.C. Barlow. 1996. Unsuitability of the House Finch as a host of the Brown-headed Cowbird. Condor 98: 253-258.

Lowther, P.E. 1984. Cowbird nest selection. Wilson Bull 96: 103-107.

Lowther, P.E. 1993. Brown-headed Cowbird (*Molothrus ater*). *In* A. Poole and F. Gill (eds.), The Birds of North America, No. 47. Philadelphia: The Academy of Natural Sciences; Washington, D.C.: The American Ornithologists' Union.

Martin, A.C., H.S. Zim, and A.L. Nelson. 1951. American Wildlife and Plants, A Guide to Wildlife Food Habits. McGraw-Hill, New York.

Mason, P. 1986a. Brood parasitism in a host generalist, the Shiny Cowbird: I. The quality of different species as hosts. Auk 103: 52-60.

Mason, P. 1986b. Brood parasitism in a host generalist, the Shiny Cowbird: II. Host selection. Auk 103: 61-69.

Mayfield, H.F. 1961. Vestiges of a proprietary interest in nests by the Brown-headed Cowbird parasitizing the Kirtland's Warbler. Auk 78: 162-166.

Mayfield, H.F. 1965a. Chance distribution of cowbird eggs. Condor 67: 257-263.

Mayfield, H. 1965b. The Brown-headed Cowbird, with old and new hosts. Living Bird 4: 13-28.

Mayfield, H.F. 1983. Kirtland's Warbler, victim of its own rarity? Auk 100: 974-976.

McIlwraith, T. 1886. The Birds of Ontario. A. Lawson and Co., Hamilton.

Middleton, A.L.A. 1991. Failure of Brown-headed Cowbird parasitism in nests of the American Goldfinch. J. Field Ornithol. 62: 200-203.

Mundinger, P.C., and S. Hope. 1982. Expansion of the winter range of the House Finch: 1947-79. Am. Birds 36:347-353.

Nakamura, H. 1990. Brood parasitism by the Cuckoo *Cuculus canorus* in Japan and the start of new parasitism on the Azure-winged Magpie *Cyanopica cyana*. Jap. J. Ornithol. 39: 1-18.

Orians, G.H., E. Røskaft, and L.D. Beletsky. 1989. Do Brown-headed Cowbirds lay their eggs at random in the nests of Red-winged Blackbirds? Wilson Bull. 101: 599-605.

Payne, R.B. 1977. The ecology of brood parasitism in birds. Ann. Rev. Ecol. Syst. 8: 1-28.

Peck, G.K., and R.D. James. 1987. Breeding birds of Ontario: nidiology and distribution. Volume 2: passerines. Life Sci. Misc. Publ. Royal Ontario Museum, Toronto.

Podrebarac, D.K., and E.J. Finck. 1991. The winter distribution of the House Finch in Kansas. Kansas Ornith. Soc. Bull. 42: 33-36

Post, W., T.K. Nakamura, and A. Cruz. 1990. Patterns of Shiny Cowbird parasitism in St. Lucia and southwestern Puerto Rico. Condor 92: 461-469.

Post, W., and J.W. Wiley. 1977. Reproductive interactions of the Shiny Cowbird and the Yellow-shouldered Blackbird. Condor 79: 176-184.

Preston, F.W. 1948. The cowbird (*M. ater*) and the Cuckoo (*C. canorus*). Ecology 29: 115-116.

Robbins, C.S., D. Bystrak, and P.H. Geissler. 1986. The breeding bird survey: its first fifteen years, 1965 - 1979. U.S. Fish Wildl. Serv., Resour. Publ. 157.

Robertson, R.J., and R.F. Norman. 1977. The function and evolution of aggressive host behavior towards the Brown-headed Cowbird (*Molothrus ater*). Can. J. Zool. 55: 508-518.

Rothstein, S.I. 1975. An experimental and teleonomic investigation of avian brood parasitism. Condor 77: 250-271.

Rothstein, S.I. 1976. Cowbird parasitism of the Cedar Waxwing and its evolutionary implications. Auk 93:498-509.

Rothstein, S.I. 1990. A model system for coevolution: avian brood parasitism. Ann. Rev. Ecol. Syst. 21: 481-508.

Rothstein, S.I. 1994. The cowbird's invasion of the far west: history, causes and consequences experienced by host species. Pp. 301-315 *in* J.R. Jehl, Jr., and N.K. Johnson (eds.), A Century of Avifaunal Change in Western North America. Stud. Avian Biol. No. 15. Cooper Ornithological Society, Sacramento.

Sauer, J.R., S. Schwartz, B.G. Peterjohn, and J.E. Hines. 1996. The North American Breeding Bird Survey Home Page. Version 95.1. Patuxent Wildlife Research Center, Laurel, MD.

Schluter, D., and J.D. McPhail. 1992. Ecological character displacement and speciation in sticklebacks. Am. Nat. 140: 85-108.

Scott, D.M., and C.D. Ankney. 1980. Fecundity of the Brown-headed Cowbird in southern Ontario. Auk 97: 677-683.

Scott, D.M., and R.E. Lemon. 1996. Differential reproductive success of Brown-headed Cowbirds with Northern Cardinals and three other hosts. Condor 98: 259-271.

Seltman, S. 1989. Spring and summer bird summary, March through July 89. Horned Lark 17: 1-3.

Soler, M., J.J. Soler, J.G. Martinez, and A.P. Møller. 1995. Magpie host manipulation by Great Spotted Cuckoos: evidence for an avian mafia? Evolution 49: 770-775.

Wauer, R.H. 1964. Ecological distribution of the birds of the Panamint Mountains, California. Condor 66: 287-301.

Weir, R.D. 1985. The spring migration. Ontario region. Amer. Birds 39: 291-296.

Wiley, J.W. 1985. Shiny Cowbird parasitism in two avian communities in Puerto Rico. Condor 87: 165-176.

Wiley, J.W. 1988. Host selection by the Shiny Cowbird. Condor 90: 289-303.

Woodward, P.W. 1983. Behavioral ecology of fledgling Brown-headed Cowbirds and their hosts. Condor 85: 151-163.

Wootton, J.T. 1986. Clutch-size differences in western and introduced eastern populations of House Finches: patterns and hypotheses. Wilson Bull. 98: 459-462.

6

Summary

This study has examined interactions between Brown-headed Cowbirds (*Molothrus ater*) and House Finches (*Carpodacus mexicanus*) in parts of North America. Colonization of eastern North America by House Finches has provided an opportunity to observe a parasite's response to a "new" host and the consequences of parasitism on both species. The results of parasite-host interactions have been used to predict change in frequency of parasitism with time in sympatry. Work was focused on four areas: 1) the assessment of frequency of parasitism on recently colonized populations of House Finches and the impact of parasitism on this host; 2) the availability of House Finches as hosts of cowbirds and their potential influence on cowbird reproductive success; 3) the suitabiliity of the House Finch as a host of the cowbird and its implications for host choice; 4) the relationship between duration of sympatry and frequency of cowbird parasitism on House Finches.

Cowbird Parasitism of House Finches

The effect of Brown-headed Cowbird parasitism on the reproductive success of a recently established population of House Finches was studied at St. Catharines, Ontario during 1983 - 1985. House Finches began to colonize Ontario in 1972 and breeding was first observed there in 1978. Cowbirds laid in 40.2% of finch nests and parasitism was most prevalent during the peak of House Finch nesting. Clutches initiated early in the season were free of cowbird eggs. Frequency of multiple parasitism was 24.2% and the number of cowbird eggs per nest was not significantly different from a Poisson distribution. Cowbirds depressed House Finch clutch size, number of young that hatched and left the nest, but the proportion of surviving eggs in parasitized nests that yielded hatchlings and fledglings was not influenced by parasitism. Overall growth of finch nestlings did not differ significantly between parasitized and unparasitized nests. Thus, House Finches were able to successfully rear most of their young irrespective of parasitism. Decreased reproductive output of House Finches was mainly due to egg removal by cowbirds. House Finches accept cowbird eggs but appear to recognize the adult parasites as a threat.

House Finch Abundance

The composition of Brown-headed Cowbird host communities was studied at four urban sites in southern Ontario and compared with those of non urban areas nearby in order to determine the frequency of House Finches in both types of habitat. Urban habitat contained fewer cowbird host species than non urban habitat. Most (≥ 83%) host species found in urban situations were also common to non urban environments, but fewer (≤ 42%) non urban species of other potential cowbird hosts were present at the urban sites. House Finches were the most common host (19 - 53%) species in all urban habitats and one non urban site, St. Catharines. The species comprised only a small (< 2%) proportion of the avian community in the other non urban sites.

House Finch abundance varied significantly among the urban study sites, which may be attributed to the time of their colonization there as well as available suitable habitat at each site. There was no significant difference in numbers of cowbirds among urban sites, and cowbirds occurred at about the same frequency in both urban and non urban habitats. Cowbirds that frequent developed areas are exposed to large numbers of House Finches. High frequency of parasitism on House Finches reported in Ontario suggests that this host may play an important role in determining cowbird reproductive success.

Failure of Parasitism

Brown-headed Cowbirds parasitized 99 (24.4%) of 406 House Finch nests observed at Barrie, Guelph, Orillia, and St. Catharines, Ontario, during 1983-85 and 1990-93. Hatching rate of cowbird eggs was 84.8%, but not a single cowbird was ever reared successfully. Cowbird growth was severely retarded in House Finch nests; nestlings required about twice as much time to accomplish the same amount of growth observed in nests of other hosts. Estimated final body mass of nestling cowbirds was about 22% lower than normal. Cowbird nestlings survived on average only 3.2 days. Only one cowbird left the nest but died within one day. Lack of cowbird survival in nests of the House Finch appears to be the result of an inappropriate diet (seeds versus the necessary arthropod nestling food). Nestling diet, therefore, may be important in determining cowbird choice of host.

Parasite-Host Coevolution

Frequency of Brown-headed Cowbird parasitism on House Finches varied with their time in sympatry. No parasitism was detected at Goleta, Santa Barbara County, CA, which represents an area of long-standing sympatry in the native western range; however, parasitism has been high in eastern North America where House Finches are recently established. In the east, frequency of parasitism was highest (30 - 87%) in areas of initial contact between host and parasite and became nonexistent at these sites after 20 years of sympatry. Intermediate durations of sympatry yielded intermediate frequencies of parasitism. This pattern was observed both locally and throughout the eastern colonized range indicating a widespread phenomenon. In addition, the number of cowbird eggs laid per nest also decreased with duration of sympatry.

House Finches represent a new host for cowbirds in the east and appear to be parasitized opportunistically when first encountered by the parasite. Decrease in parasitism over time suggests response of cowbirds to an unsuitable host. Because House Finches are abundant and heavily parasitized, yet rear no cowbirds, suggests that there may be strong selection on cowbirds to avoid them. Differential reproductive success as well as learning by cowbirds may contribute to the observed decrease in parasitism. Results suggest host discrimination by a generalist parasite and that changes in host preference may develop rapidly.

Concluding Remarks

This study has provided some insight into factors that may influence host choice in a generalist brood parasite. Decrease of frequency of parasitism over time noted in this study seems to be the result of parasite-host interaction. Cowbirds appear to recognize and respond to House Finches and I have proposed several mechanisms that could explain the observed change in host preference.

The notion of evolution of host discrimination in cowbirds assumes that variation in host choice among parasites results in their natural selection. Compared to cowbirds that parasitize House Finches, those that avoid the host may be at selective advantage because they will experience relatively greater fitness. Failure of cowbird parasitism in finch nests found in this study provides strong circumstantial evidence in support of cowbird differential reproductive success among hosts. However, a detailed investigation of reproductive success of cowbirds in populations that are allopatric and sympatric with House Finches is necessary in order to corroborate the results of this study.

This study has identified a relatively long-term directional trend in decrease of frequency of parasitism in eastern North America. Replicate study sites in Ontario showed a decrease in frequency of parasitism, which remained very low at St. Catharines for three consecutive years. Not only was the null model (no trend) rejected but, more importantly, a decrease in frequency of parasitism over time was predicted based on knowledge of cowbird-House Finch interactions in areas of long-standing sympatry (western range of both species) and host suitability. Long-term directional change in this trait suggests that it is not at a selective equilibrium. Thus, continued monitoring of parasitism in areas of recent sympatry should reveal a decrease in frequency of parasitism with time in those areas, and frequency of parasitism should remain low in eastern North America if cowbird-House Finch associations persist.

Despite the many existing studies of parasitism by Brown-headed Cowbirds, little is known about how they select their hosts. Detailed studies of the movements of individual birds are required in order to determine if females demonstrate host preferences. Host choice experiments may prove fruitful in this regard and may help to resolve the role of learning by cowbirds.

RÉSUMÉ

J'ai fait des recherches sur les intéractions entre le vacher à tête brune (*Molothrus ater*) famille parasitique et l'hôte roselin familier (*Carpodacus mexicanus*) durant 1983 - 1993. Les roselins familier sont natifs de l'Amerique du Nord occidentale où ils coexistent avec les vachers à tête brune. L'introduction récente du roselin familier en Amerique du Nord orientale y résultât en l'association des deux espèces. La fréquence du parasitisme sur les roselins familier parrait être en rapport avec la durée de coexistence; l'espèce est rarement parasitée dans son domaine indigène mais l'est frequemment dans celui de naturalisation. Pour determiner le mécanisme responsable de cette différence dans l'exploitation de l'hôte, j'ai étudié les conséquences du parasitisme sur les deux espèces en Californie et en Ontario où les vachers à tête brune ont très récemment affrontés le roselin familier.

Les roselins familier sont sévèrement parasités peu après leurs contact avec les vachers à tête brune mais subissent relativement peu de perte de reproduction dû aux activités des vachers à tête brune. Les roselins familier représentent l'hôte le plus commun dans l'habitat urbain et dans certain environmants rureaux. Un grand nombre de roselins familier en concert avec le parasitisme fréquent suggeste que cet hôte pourrait exercer un rôle important en influençant le succès reproductif des vachers à tête brune.

Les vachers à tête brune n'ont pas été élevés avec succès dans les nids de roselins familier. Ceci est apparemment le resultat d'une diète inadéquate (graines) nourrie aux jeunes vachers à tête brune par leurs parents adoptifs. En conséquence le roselin familier est un hôte inopportun. L'échec du parasitisme dans les nids de roselins familier indique que la diète de l'hôte peut être importante dans la détermination du choix de l'hôte par les vachers à tête brune.

Le parasitisme n'a pas été détecté à Goleta, Californie. La fréquence du parasitisme des vachers à tête brune sur les roselins familier en Amerique du Nord orientale varie avec leurs durée de coexistence. La fréquence du parasitisme était la plus élevée dans la région du contact initial entre espèces et non-existente aprés 20 ans de coexistence. La décroissance du parasitisme à travers le temps suggère la réaction des vachers à tête brune envers l'hôte inopportun. Le succès reproductif différentiel aussi bien que le savoir des vachers à tête brune peuvent contribuer à la décroissance observée dans le parasitisme. Il est suggéré que la discrimination d'hôte par le parasite général aboutissant aux changes de préférence d'hôte puisse se développer rapidement.

APPENDICES

Appendix 1. Brown-headed Cowbird sightings in urban habitats during the breeding season at Barrie, Guelph, Orillia and St. Catharines, Ontario.

Location d / m / y	Time	Gender	Observations[a]	Street
Barrie				
06/05/92	09:20	1♂	Perched; song	Royal Oak
	10:00	1♀	Chatter-call	Lover's Ct.
	10:35	1♂	Perched; song	Deborah
	10:50	1♂	Perched; song	Warnica
	10:55	1♂, 1♀	♂: perched; ♀: chatter-call	Coxmill
	11:15	1♂	Perched; song	Mary Ann
	13:20	1♂	Perched; song	Montgomerie
	13:45	2♂	Perched together; visual display; song	Pine
	13:47	1♂, 1♀	Flying together	Pine
	14:30	1♂	Perched; song	Spruce Dr.
08/05/92	07:40	2♂, 1♀	Flying together	Springhome
	07:50	1♂	Perched; song	Tower Ct.
	08:30	1♂, 1♀	Perched together; ♂: visual display; song; ♀: chatter-call	Meadowland
	09:00	3♂, 1♀	Perched together; ♂: visual display; song	Armstrong
13/05/92	11:15	1♂	Song	Pine
	11:36	1♂	Song	Poplar Dr.
	11:42	1♂, 1♀	Flying together	Walnut
	13:30	1♂	Flying; whistle-call	Royal Oak
15/05/92	08:57	1♂	Flying; whistle-call	Briar
	09:40	1♀	Chatter-call	Tower Ct.

(Appendix 1 continued)

	10:37	2♂, 1♀	Flying together	Thorncrest
	11:57	1♂	Perched; song	Libra
17/05/92	12:55	2♂, 2♀	Flying together	Royal Oak
20/05/92	09:25	1♂	Perched; song	Spruce Cr.
	09:40	1♂, 1♀	Flying together	Pine
	10:32	1♂	Perched; song	Warnica
	11:12	2♂, 1♀	Flying together	Royal Oak
21/05/92	08:20	1♂	Flying; whistle-call	Hillcrest
	08:50	1♂	Perched; song	Broadmoor
	08:58	2♂, 1♀	Foraging together	Tower Ct.
	11:02	1♂	Song	Glenridge
	13:35	2♂, 1♀	Perched together; ♂: visual display; song	Grand Pl.
24/05/92	07:45	1♀	Foraging on ground	Minet's Pt.
	08:00	1♂, 1♀	Foraging together on ground	Minet's Pt.
	10:10	2♂	Perched together; visual display; song	Adelaide
27/05/92	09:57	1♂, 1♀	♂: perched; song; ♀: chatter-call	Pine
	10:35	1♀	Flying	Cedar Cr.
	11:35	1♂	Foraging on ground	Royal Oak
	13:15	1♂, 1♀	Foraging together on ground	Minet's Pt.
28/05/92	09:07	1♂	Flying; whistle-call	Hambly Ct.
03/06/92	10:05	1♂	Flying; whistle-call	Thorncroft
	10:10	1♂	Perched; song	Chieftain
04/06/92	08:30	1♂	Song	Warnica
	09:10	1♂	Perched	Spruce

(Appendix 1 continued)

	10:33	1♂	Flying	Royal Oak
	13:30	1♂, 1♀	Perched	Springhome
11/06/92	10:30	1♂	Flying; whistle-call	Baldwin
18/06/92	08:00	1♀	Chatter-call	Marshall
	08:45	1♂	Song	Dodson
	09:25	1♂	Perched; song	Cedar
	10:30	1♂	Song	Forestwood
24/06/92	10:05	2♂	Perched together; visual display; song	Walnut Cr.
	10:07	1♀	Flying; chatter-call	Cedar
	11:20	1♂	Perched; song	Royal Oak
	13:13	1♂	Perched; song	Woodcrest
25/06/92	08:30	1♀	Chatter-call	Jane
	11:33	3♂, 1♀	Flying together	Cedar
01/07/92	08:20	1♀	Chatter-call	Marshall
	08:35	1♀	Flying	Carol
	09:20	1♀	Chatter-call	Springhome
	10:00	1♀	Foraging on ground; chatter-call	Springhome
	12:56	1♂	Perched	Deborah
08/07/92	11:25	1♂	Flying	Spruce
	11:43	1♀	Chatter-call	Cedar
	14:30	1♂	Perched; song	Minet's Pt.
09/07/92	09:07	1♂	Song	Chieftain
		1♀	Perched	Chieftain
	10:00	1♂	Song	Clover
		1♀	Perched	Clover

(Appendix 1 continued)

15/07/92	10:55	1♂	Whistle-call	Walnut
16/07/92	08:45	1♂	Perched	Marshall
	09:50	1♂	Perched; song	Tower
30/07/92	08:40	1♂	Song	Springhome
11/06/93	08:00	2♂, 1♀	Foraging together on ground	Minet's Pt.
	08:10	2♂, 1♀	Perched together; ♂: visual display; song	Royal Oak
	08:20	1♂	Song	Forestwood
	08:55	1♂, 1♀	Flying together; ♀: chatter-call	Warnica
	09:05	1♀	Chatter-call	Dodson
	09:25	1♀	Flying; chatter-call	Spruce
	09:55	2♂, 1♀	Flying together; ♂: whistle-call; ♀: chatter-call	Cedar
	13:50	1♂	Song	Brennan
	14:20	1♂	Song	Greenfield
	14:35	1♀	Foraging on ground	Woodcrest
18/06/93	08:00	1♂	Perched; song	Royal Oak
	08:40	1♂	Perched; song	Bertha
	09:35	2♂	Perched together; visual display; song	Hambly
	09:40	2♀	Chatter-call	Greenfield
	09:50	3♂	Perched together; visual display; song	Greenfield
	10:20	1♂	Flying; whistle-call	Highcroft
24/06/93	08:40	1♂	Song	Mary Ann
	08:45	1♂	Flying; whistle-call	Dodson
	09:05	1♂	Perched; song	Nina

(Appendix 1 continued)

	09:40	1♀	Chatter-call	Kenneth
	10:00	1♀	Chatter-call	Spruce
	10:02	1♂	Flying; whistle-call	Spruce
30/06/93	06:43	1♂	Flying; whistle-call	Broadmoor
	08:10	1♀	Chatter-call	Royal Oak
	09:35	1♂	Perched; song	Deborah
	09:40	1♂	Perched; song	Walnut
	09:45	1♂, 1♀	Perched together; ♂: visual display; song; ♀: chatter-call	Walnut
	09:50	1♂	Perched; song	Big Bay Pt.
	10:45	1♂	Song	Libra
	13:45	1♂	Song	Greenfield
	14:10	1♂	Perched; song	Greenfield
09/07/93	06:50	2♀	Flying together	Walnut
	08:25	1♂	Song	Lover's Ct.
	09:35	1♂	Flying, whistle-call	Gloscester
	10:25	1♂	Song	Walnut
16/07/93	08:40	1♂	Song	Chieftain
	09:00	1♂	Perched; song	Libra
Guelph				
10/06/93	09:45	1♂, 1♀	Perched together	Dean
	10:00	1♂	Song	Harvard
	10:40	1♂	Perched; song	Dimson
	11:40	1♂	Flying; whistle-call	Rickson
16/06/93	10:00	1♂	Perched; song	Colborne
	10:07	1♂	Perched; song	Evergreen

(Appendix 1 continued)

	10:35	1♂	Song	Harvard
	13:50	1♀	Chatter-call	Keats
	16:07	1♂	Song	College
	19:30	2♂	Flying together	Kron
23/06/93	07:30	1♂	Song	Hanlon
	07:42	1♀	Flying; chatter-call	Hanlon
	08:25	1♂	Song	Kortright
	09:50	1♂	Perched; song	Harvard
	10:33	1♂	Flying; song	Harrow
	14:10	1♂	Song	Cole
	14:25	1♀	Chatter-call	Briarlea
29/06/93	08:20	1♀	Chatter-call	Hanlon
	09:12	1♂	Song	Hands
	09:25	1♂, 1♀	Foraging together on ground	Forester
	09:30	1♂	Perched; song	Dimson
	11:15	1♂	Song	Birch
07/07/93	06:20	1♂	Flying	Shadybrook
	06:50	1♂	Flying	Kortright
	08:45	1♂	Flying; whistle-call	Monticello
	08:50	1♂	Perched; song	Stone
	09:35	1♂	Perched; song	Harrow
15/07/93	09:25	1♂	Song	Cole
	10:07	1 juv.	Fed by Chipping Sparrow	Evergreen
	10:45	1♂	Perched; song	Forester

(Appendix 1 continued)

Orillia

05/05/92	11:20	2♂	Perched together; visual display; song	Murray
	11:45	1♂	Song	Grace
	12:30	1♂	Song	Jarvis
		1♀	Chatter-call	Jarvis
	13:30	1♂	Song	Skyline
	13:35	1♂	Song	Leonard
07/05/92	07:45	1♂	Perched; whistle-call	Drinkwater
	07:57	1♀	Chatter-call	Drinkwater
	08:06	1♂	Perched; song	Bridget
	08:25	1♀	Flying	Lahay
	08:30	1♂	Whistle-call	Fourth
	08:32	2♂, 1♀	Perched together; ♂: visual display; song	Fourth
	09:15	1♂	Perched; song	First
	09:17	3♂	Flying together	Goldie
	09:50	1♂	Song	Orma
	10:10	1♂	Perched; song	Jameson
	10:25	1♀	Foraging on ground	Jameson
	11:10	1♂	Flying; whistle-call	Stanton
	13:42	1♂	Perched; song	Tallwood
	13:55	1♂	Perched; song	Highland
14/05/92	09:05	1♂	Perched; song	Second
	09:15	1♂	Perched; song	Goldie
	10:20	1♂	Perched; song	Bay

(Appendix 1 continued)

	10:55	1♀	Leaving tree that supports nest of House Finch	Highland
	11:30	1♂	Perched; song	Stanton
	14:50	1♂	Flying; whistle-call	Lawson
	15:45	1♂	Perched; song	Harmon
16/05/92	08:15	1♂	Perched; song	June
	08:37	1♂	Perched; song	North
	08:55	1♂	Flying; whistle-call	Lawrence
	08:57	1♂	Perched; song	Gerald
	11:05	1♂	Perched; song	Highland
	13:02	1♂	Perched; song	Drinkwater
	13:05	1♂	Flying; whistle-call	Francis
	13:07	1♀	Roaming through branches of tree	Maple
	13:11	1♂	Perched; song	Hughes
22/05/92	08:07	2♂, 1♀	Flying together	Hughes
	08:45	5♂, 1♀	On ground together; ♂: visual display; song; ♀: foraging	Boundary
	10:11	1♂	Perched; song	Jameson
	10:31	1♂	Perched	Free
	11:30	1♂	Perched	Highland
23/05/92	07:55	1♂	Perched; song	Dalton
29/05/92	08:05	1♂	Perched; song	Fourth
	09:15	1♂	Perched; song	Bay
	10:15	1♂	Song	Galley
	10:50	1♂	Perched; song	Orma
	11:10	1♂	Perched; song	Jameson

(Appendix 1 continued)

30/05/92	08:40	2♂	Flying	Dalton
	09:12	1♂	Perched; song	Collegiate
	13:30	1♂, 1♀	Flying together	Galley
05/06/92	09:02	1♂	Perched; song	Bridget
	09:30	1♂	Flying; whistle-call	Goldie
	10:55	1♂	Perched; song	Fittons
	14:35	1♂	Song	Highland
06/06/92	08:50	1♂	Perched; song	Park
	09:07	1♂, 1♀	Perched together	Gerald
	09:20	1♂	Perched; song	Borland
	09:35	1♀	Foraging on ground	Dalton
12/06/92	09:10	2♂, 1♀	Perched together; ♂: visual display; song	Belmoral
	10:00	1♂	Flying; whistle-call	Orma
	10:35	1♂	Perched; song	Goldie
13/06/92	08:10	3♂, 1♀	Perched together	Stanton
19/06/92	08:32	1♂, 1♀	Foraging together on ground	June
	08:55	2♂	Perched; visual display; song	Dalton
26/06/92	08:25	1♂	Song	Stanton
	08:35	1♂	Song	Free
	08:37	2♂, 2♀	Perched together; ♂: visual display; song	Sundial
	09:55	1♂	Perched; song	Lahay
	10:45	1♀	Perched	Jameson
	13:13	1♂	Song	Belmoral
	13:40	2♂	Perched together; visual display; song	Dalton

(Appendix 1 continued)

02/07/92	08:07	1♂	Perched; song	Rosslyn
	08:30	1♂	Perched; song	Collegiate
	09:40	1♂, 1♀	Perched together	Orma
	11:00	2♂	Perched together	Sundial
10/07/92	08:40	1♂	Song	Third
	08:45	3♂, 1♀	Perched together; ♂: visual display; song	Goldie
	09:18	1♂	Song	Stanton
	09:32	1♀	Chatter-call	Sundial
	10:17	1♂	Song	Martin
	10:30	1♂, 1♀	♂: song; ♀: chatter-call	Collegiate
	11:25	1♂	Perched; song	Harmon
18/07/92	09:10	1♂	Song	Martin
14/06/93	08:00	1♂	Perched; song	Third
	08:15	1♂	Perched; song	Boundary
	09:40	1♂	Song	Highland
	10:45	1♀	Foraging on ground	Stanton
	10:55	1♂	Song	Sundial
	11:28	1♂	Song	Francis
	11:30	1♂	Perched; song	Francis
	11:35	1♂, 1♀	♂: song; ♀: chatter-call	Bridget
	13:30	1♀	Flying; chatter-call	Jameson
	13:50	1♂	Flying	Belmoral
	13:55	1♂	Song	Rosslyn
		1♂	Flying	Rosslyn
22/06/93	07:58	2♂, 1♀	Perched together; ♂: visual display; song; ♀: chatter-call	Jarvis

(Appendix 1 continued)

	08:50	1♂, 1♀	♂: song; ♀: chatter-call	Third
	09:05	1♂	Flying	Second
	09:45	1♂	Song	Orma
		1♂, 1♀	Perched together; ♂: song; ♀: chatter-call	Orma
	10:10	2♂, 1♀	Perched together; ♂: visual display; song; ♀: chatter-call	Drinkwater
	10:50	4♂, 1♀	On ground together	Maple
	11:10	1♂	Perched; song	Stanton
	11:30	1♂	Perched; song	Sundial
	14:15	1♂	Song	Delta
	16:05	1♂	Perched; song	Alexander
28/06/93	06:29	1♂	Flying	Jameson
	06:40	1♀	Flying; chatter-call	Orma
	06:45	1♂	Song	Orma
		1♂	Flying	Orma
	06:50	1♀	Perched; chatter-call	Jameson
	07:02	1♂, 1♀	♂: song; ♀: chatter-call	Tallwood
	08:45	1♀	Chatter-call	Lawrence
	08:52	1♂	Song	Martin
	09:15	1♂	Song	Dalton
	11:45	1♂	Foraging on ground	Jameson
	13:45	1♂	Song	Bridget
	13:55	1♂	Perched; song	Francis
	14:37	1♀	Chatter-call	Tallwood
05/07/93	06:45	1♂	Flying	Highland
	07:05	2♀	Chatter-call	Lahay

(Appendix I continued)

	07:20	1♂	Flying; whistle-call	Boundary
	08:20	1♀	Chatter-call	Second
	08:40	1♂	Song	Second
	09:15	2♂	Song	Drinkwater
	10:25	1♂, 1♀	♂: song; ♀: chatter-call	Tallwood
	11:05	1♂	Song	Orma
	12:10	1♂	Perched; song	Borland
12/07/93	06:30	1♂	Flying	North
	08:07	1♀	Chatter-call	Murray
	08:37	2♀	Foraging together on ground	Second
		2♂	Perched together; visual display; song	Second
	09:10	1♂	Song	Bay
	11:10	1♂	Song	Tallwood
	14:00	1♂	Song	Dalton
St. Catharines				
06/05/90	13:00	6♂	Perched together; visual display; song	Bogart
07/05/90	13:20	1♂	Perched	Castlemere
12/05/90	07:20	1♂	Song	Village Green
	07:35	1♂	Perched	Village Green
	13:50	1♂	Song	Longford
	14:35	1♂	Perched; song	Village Green
15/05/90	07:30	1♂	Song	Shore
19/05/90	08:33	1♂	Perched	Westgate
20/05/90	13:50	1♂	Flying	Village Green

(Appendix 1 continued)

22/05/90	07:45	2♂	Perched together	Shore
	08:30	1♂	Perched	Farrington
23/05/90	09:20	2♂, 1♀	Perched together; ♂: visual display; song	Westgate
27/05/90	09:40	1♂	Perched	Royal York
28/05/90	08:10	1♂	Flying	Westgate
	09:45	1♂	Flying; song	Royal York
29/05/90	10:10	1♂	Perched	Castlemere
	15:00	1♂	Song	Royal York
30/05/90	08:30	2♂	Flying together	Village Green
	09:30	1♀	Perched	Shore
		1♂	Song	Shore
		1♂	Flying	Shore
	11:45	5♂, 1♀	Perched together; ♂: visual display; song	Royal York
31/05/90	08:00	1♂	Perched	Ziraldo
	09:15	2♂	Perched together	Village Green
	11:15	1♂	Perched	Royal York
01/06/90	11:35	1♀	Foraging on hedge	Royal York
		2♂	Perched together	Royal York
02/06/90	07:25	1♂	Perched	Shore
	08:35	1♂	Song	Westgate
	10:05	2♂, 1♀	Perched together	Royal York
03/06/90	07:35	1♂, 1♀	Perched together	Ziraldo
	10:00	1♂	Perched	Royal York
06/06/90	10:00	1♂	Perched	Beachview
07/06/90	09:50	1♂	Perched	Royal York

(Appendix 1 continued)

	15:05	1♂	Perched	Village Green
09/06/90	07:05	6♂	Perched together	Ziraldo
11/06/90	08:00	1♂	Perched	Royal York
13/06/90	10:30	2♂	Perched together	Royal York
14/06/90	11:20	2♂	Song	Royal York
15/06/90	07:30	1♂	Song	Ziraldo
17/06/90	07:30	1♂	Perched	Village Green
	07:40	1♂	Perched	Castlemere
	14:00	1♂	Song	Ziraldo
18/06/90	13:40	1♂	Perched	Ziraldo
19/06/90	09:25	1♂	Perched	Castlemere
	10:55	1♂	Perched	Castlemere
20/06/90	10:15	1♂	Perched	Beachview
21/06/90	07:30	1♂	Perched	Ziraldo
25/06/90	09:45	2♂	Perched together	Castlemere
05/07/90	09:00	1♂	Song	Castlemere
07/07/90	07:45	3♂	Perched together	Ziraldo
	09:00	1♂	Song	Westgate
16/07/90	11:00	1♂	Song	Ziraldo
08/05/91	07:10	1♂	Song	Village Green
	07:25	1♀	Foraging on ground	Royal Henley
12/06/91	12:00	2♂	Flying together	Bogart
13/05/91	09:30	1♂, 1♀		Bogart
	11:15	2♂	Perched together	Royal York
14/05/91	08:45	1♂	Flying	Royal Henley
	13:00	1♂	Song	Lantana

(Appendix 1 continued)

		2♂	Perched together	Lantana
18/05/91	09:50	1♂	Song	Longford
	09:55	1♂	Perched	Longford
19/05/91	09:10	1♂	Flying	Royal Henley
	09:40	1♂	Flying	Royal Henley
	14:20	1♂	Flying	Lafayette
21/05/91	08:50	4♂	Perched together; visual display; song	Jaycee Pk.
	09:50	1♀	Roaming through branches of tree	Jaycee Pk.
	09:55	1♂	Flying	Ziraldo
	10:10	1♂	Perched	Castlemere
	14:45	2♂	Perched	Village Green
22/05/91	07:15	5♂	Perched together; visual display; song	Royal York
	14:30	1♂	Song	Village Green
		1♂	Song	Royal Henley
23/05/91	08:45	2♂		Jaycee Park
	09:05	2♂		Ziraldo
24/05/91	14:00	1♀	Foraging on ground	Nickerson
25/05/91	08:25	1♂		Spring Grdn.
	08:32	1♂, 1♀	On ground together; ♀: foraging	Spring Grdn.
25/05/91	08:40	1♂	Flying	Spring Grdn.
	13:50	1♂, 1♀	Foraging together on ground	Royal Henley
27/05/91	09:15	1♂	Flying	October
	14:25	1♂	Perched	Ziraldo
28/05/91	08:20	1♂, 1♀		Bayshore

(Appendix 1 continued)

	13:30	2♂		Spring Grdn.
29/05/91	08:00	1♂	Song	Spring Grdn.
	09:40	1♂	Flying	Castlemere
30/05/91	09:55	1♂	Song	Village Green
	10:10	3♂	Perched together; visual display; song	Castlemere
	10:40	1♂	Flying	Aquadale
02/06/91	09:24	1♂	Song	October
	13:40	1♂	Song	Village Green
03/06/91	11:05	1♂		October
04/06/91	10:10	1♀	Roaming through branches of tree	Westgate
05/06/91	14:50	1♂		Village Green
06/06/91	07:00	1♂	Flying	Royal Henley
	10:45	1♂	Perched	Castlemere
	12:00	1♂		Spring Grdn.
07/06/91	10:15	1♂		Westgate
	11:00	1♂	Song	Westgate
08/06/91	09:00	1♂	Song	Royal Oak
	09:50	1♂		Westgate
09/06/91	10:30	1♂		October
10/06/91	09:10	1♂	Song	Village Green
11/06/91	08:10	1♂, 1♀	Foraging together on ground	Aquadale
	08:45	1♂		Trinidad
12/06/91	12:30	1♀	Foraging on ground	Spring Grdn.
13/06/91	07:10	1♂	Foraging on ground	Aquadale
	07:35	3♂	Flying together	Mississauga

(Appendix I continued)

	09:35	2♂		Shore
	09:50	1♂		Castlemere
14/06/91	10:00	1♂	Flying	Village Green
17/06/91	08:30	1♂	Song	Ziraldo
	10:15	1♂		Boese
18/06/91	08:00	1♂	Perched together	Kimbermount
	09:30	1♂	Perched	Kimbermount
	11:45	1♂	Perched	Spring Grdn.
20/06/91	08:35	1♂	Perched	Rexleigh
	08:40	1♀	Foraging on ground	Rexleigh
21/06/91	09:20	2♂	Perched together	Boese
23/06/91	09:40	1♂	Perched	Kimbermount
24/06/91	09:00	1♂	Perched	Prince Chas.
25/06/91	09:00	3♂	Perched together	Shore
	10:10	1♂	Flying	Castlemere
26/06/91	06:00	3♂		Castlemere
30/06/91	06:00	2♂		Shore
02/07/91	09:20	3♂	Perched together	Kimbermount
		1♂	Flying	October
09/07/91	13:55	1♂		Prince Andy
10/07/91	08:35	3♂	Flying together	October
30/07/91	15:10	1♀	Foraging on ground	Royal York
11/05/92	08:20	1♂	Perched; song	Shore
	08:35	1♂	Whistle-call	Farrington
	09:34	1♂	Flying; whistle-call	Castlemere
12/05/92	08:55	1♂	Perched; song	Shore

(Appendix 1 continued)

	10:05	1♂	Perched	Westgate
18/05/92	08:37	1♂	Whistle-call	Ziraldo
	08:45	1♂, 1♀	Foraging together on ground	Ziraldo
	14:10	1♂	Song	Westgate
	14:20	1♂	Perched; song	Carn Castle
19/05/92	10:22	1♀	Chatter-call	Royal York
	10:40	1♂	Whistle-call	Spring Grdn.
25/05/92	11:30	1♀	Foraging on ground	Ziraldo
26/05/92	08:50	2♂	Perched together; visual display; song	Westgate
01/06/92	13:35	1♂	Perched; song	Bayshore
	13:40	2♂, 1♀	Flying together	Bayshore
02/06/92	09:50	1♂	Song	Duncan
09/06/92	14:00	1♂	Whistle-call	October
10/06/92	09:50	2♂	Flying together	Vine
	10:05	1♂	Whistle-call	Royal York
16/06/92	10:00	2♂	Perched together; visual display; song	Ameer
23/06/92	08:55	1♂	Perched; song	Royal York
	10:10	1♂	Song	Shore
	10:20	1♂	Whistle-call	Kilkenny
30/06/92	08:28	1♂	Flying	Beachview
	09:15	1♀	Foraging on ground	Bayshore
	12:40	1♂	Song	Guildwood
06/07/92	10:20	1♂	Song	Vanier
	10:55	1♂	Song	Shore
07/07/92	09:30	1♂	Whistle-call	Royal York

(Appendix 1 continued)

13/07/92	10:10	1♂, 1♀	Foraging together on ground	Royal Oak
	11:25	1♂	Whistle-call	Kimbermount
14/07/92	10:20	1♂	Flying	Vine
20/07/92	10:45	1♂	Foraging on ground	Royal Henley
	10:47	1♂	Perched; song	Wedgewood
21/07/92	07:50	1♂	Song	Farrington

[a] Cowbird behaviour terms described in Stokes and Stokes (1983). Visual display includes bill-tilt, song given during topple-over display.

LITERATURE CITED

Stokes, D.W., and L.Q. Stokes. 1983. A Guide to Bird Behavior. Volume II. Little, Brown and Co., Boston.

Appendix 2. Frequency of breeding species of avian and Brown-headed Cowbird host communities in urban habitat at Barrie, Guelph, Orillia and St. Catharines, Ontario. Species acronyms are as follows: AMCR, American Crow (*Corvus brachyrhychos*); AMGO, American Goldfinch (*Carduelis tristis*); AMRO, American Robin (*Turdus migratorius*); AMWO, American Woodcock (*Scolopax minor*); BAOR, Baltimore Oriole (*Icterus galbula*); BARS, Barn Swallow (*Hirundo rustica*); BAWW, Black-and-white Warbler (*Mniotilta varia*); BCCH, Black-capped Chickadee (*Parus atricapillus*); BHCO, Brown-headed Cowbird (*Molothrus ater*); BLJA, Blue Jay (*Cyanocitta cristata*); BRTH, Brown Thrasher (*Toxostoma rufum*); CEDW, Cedar Waxwing (*Bombycilla cedrorum*); CHSP, Chipping Sparrow (*Spizella passerina*); COGR, Common Grackle (*Quiscalus quiscula*); CSWA, Chestnut-sided Warbler (*Dendroica pensylvanica*); DOWO, Downy Woodpecker (*Picoides pubescens*); EAKI, Eastern Kingbird (*Tyrannus tyrannus*); EAWP, Eastern Wood-Pewee (*Contopus virens*); EUST, European Starling (*Sturnus vulgaris*); GCFL, Great Crested Flycathcher (*Myiarchus crinitus*); GRCA, Gray Catbird (*Dumetella carolinensis*); HAWO, Hairy Woodpecker (*Picoides villosus*); HOFI, House Finch (*Carpodacus mexicanus*); HOSP, House Sparrow (*Passer domesticus*); HOWR, House Wren (*Troglodytes aedon*); KILL, Killdeer (*Charadrius vociferus*); LEFL, Least Flycatcher (*Empidonax minimus*); MALL, Mallard (*Anas platyrhynchos*); MODO, Mourning Dove (*Zenaida macroura*); NOCA, Northern Cardinal (*Cardinalis cardinalis*); NOFL, Northern Flicker (*Colaptes auratus*); NOMO, Northern Mockingbird (*Mimus polyglottos*); Northern Parula (*Parula americana*); PISI, Pine Siskin (*Carduelis pinus*); PUMA, Purple Martin (*Progne subis*); RBGR, Rose-breasted Grosbeak (*Pheucticus ludovicianus*); RBNU, Red-breasted Nuthatch (*Sitta canadensis*); RCKI, Ruby-crowned Kinglet (*Regulus calendula*); REVI, Red-eyed Vireo (*Vireo olivaceus*); RODO, Rock Dove (*Columba livia*); RWBL, Red-winged Blackbird (*Agelaius phoeniceus*); SCTA, Scarlet Tanager (*Piranga olivacea*); SOSP, Song Sparrow (*Melospiza melodia*); SWSP, Swamp Sparrow (*Melospiza georgiana*); TEWA, Tennessee Warbler (*Dendroica peregrina*); TRES, Tree Swallow (*Tachycineta bicolor*); WAVI, Warbling Vireo (*Vireo gilvus*); WBNU, White-breasted Nuthatch (*Sitta carolinensis*); YWAR, Yellow Warbler (*Dendroica petechia*).

(Appendix 2 continued)

				Community			
				Avian		Host	
Location	Year	N^a	Species	N	Freq.	N	Freq.
Barrie	1992	16	AMCR	3	0.0054	.	.
			AMGO	39	0.0707	39	0.0899
			AMRO	75	0.1359	75	0.1728
			BAOR	5	0.0091	5	0.0115
			BARS	10	0.0181	10	0.0230
			BAWW	1	0.0018	1	0.0023
			BCCH	11	0.0199	.	.
			BHCO	13	0.0236	.	.
			BLJA	10	0.0181	.	.
			BRTH	2	0.0036	2	0.0046
			CEDW	34	0.0616	34	0.0783
			CHSP	33	0.0598	33	0.0760
			COGR	88	0.1594	88	0.2028
			DOWO	4	0.0072	.	.
			EAKI	4	0.0072	4	0.0092
			EUST	12	0.0217	.	.
			HAWO	1	0.0018	.	.
			HOFI	94	0.1703	94	0.2166
			HOSP	31	0.0562	.	.
			HOWR	2	0.0036	.	.
			KILL	1	0.0018	.	.
			MODO	28	0.0507	.	.
			NOCA	3	0.0054	3	0.0069
			PISI	4	0.0072	4	0.0092
			RBGR	1	0.0018	1	0.0023

(Appendix 2 continued)

			RCKI	1	0.0018	1	0.0023
			REVI	2	0.0036	2	0.0046
			SCTA	1	0.0018	1	0.0023
			SOSP	35	0.0634	35	0.0806
			TEWA	1	0.0018	1	0.0023
			TRES	2	0.0036	.	.
			WAVI	1	0.0018	1	0.0023
			TOTAL	552	1.0000	434	1.0000
Barrie	1993	15	AMCR	8	0.0143	.	.
			AMGO	21	0.0376	21	0.0625
			AMRO	75	0.1342	75	0.2232
			BAOR	2	0.0036	2	0.0060
			BARS	2	0.0036	2	0.0060
			BCCH	31	0.0555	.	.
			BHCO	6	0.0107	.	.
			BLJA	8	0.0143	.	.
			CEDW	9	0.0161	9	0.0268
			CHSP	22	0.0394	22	0.0655
			COGR	70	0.1252	70	0.2083
			DOWO	3	0.0054	.	.
			EUST	43	0.0769	.	.
			HOFI	102	0.1825	102	0.3036
			HOSP	75	0.1342	.	.
			MODO	48	0.0859	.	.
			NOCA	6	0.0107	6	0.0179
			PISI	5	0.0089	5	0.0149
			SOSP	19	0.0340	19	0.0565
			WAVI	2	0.0036	2	0.0060
			WBNU	1	0.0018	.	.
			YWAR	1	0.0018	1	0.0030
			TOTAL	559	1.0000	336	1.0000

(Appendix 2 continued)

Guelph	1993	15	AMCR	8	0.0146	.	.
			AMGO	16	0.0291	16	0.0567
			AMRO	53	0.0965	53	0.1879
			BCCH	3	0.0055	.	.
			BHCO	12	0.0219	.	.
			BLJA	2	0.0036	.	.
			CEDW	8	0.0146	8	0.0284
			CHSP	41	0.0747	41	0.1454
			COGR	57	0.1038	57	0.2021
			EUST	62	0.1129	.	.
			GRCA	2	0.0036	2	0.0071
			HOFI	80	0.1457	80	0.2837
			HOSP	145	0.2641	.	.
			MODO	34	0.0619	.	.
			NOCA	9	0.0164	9	0.0319
			REVI	4	0.0073	4	0.0142
			RWBL	1	0.0018	1	0.0035
			SOSP	11	0.0200	11	0.0390
			WBNU	1	0.0018	.	.
			TOTAL	549	1.0000	282	1.0000
Orillia	1992	17	AMCR	6	0.0099	.	.
			AMGO	21	0.0348	21	0.0493
			AMRO	97	0.1606	97	0.2277
			BAOR	9	0.0149	9	0.0211
			BAWW	1	0.0017	1	0.0023
			BCCH	15	0.0248	.	.
			BHCO	11	0.0182	.	.
			BLJA	10	0.0166	.	.
			CEDW	6	0.0099	6	0.0141
			CHSP	29	0.0480	29	0.0681
			COGR	98	0.1623	98	0.2300

(Appendix 2 continued)

			DOWO	2	0.0033	.	.
			EAKI	2	0.0033	2	0.0047
			EAWP	2	0.0033	2	0.0047
			EUST	54	0.0894	.	.
			GRCA	1	0.0017	1	0.0023
			HAWO	1	0.0017	.	.
			HOFI	89	0.1474	89	0.2089
			HOSP	14	0.0232	.	.
			HOWR	7	0.0116	.	.
			MALL	2	0.0033	.	.
			MODO	31	0.0513	.	.
			NOCA	8	0.0132	8	0.0188
			NOPA	1	0.0017	1	0.0023
			PISI	2	0.0033	2	0.0047
			RCKI	2	0.0033	2	0.0047
			REVI	6	0.0099	6	0.0141
			RODO	9	0.0149	.	.
			RWBL	5	0.0083	5	0.0117
			SOSP	39	0.0646	39	0.0915
			TRES	16	0.0265	.	.
			WAVI	6	0.0099	6	0.0141
			YWAR	2	0.0033	2	0.0047
			TOTAL	604	1.0000	426	1.0000
Orillia	1993	12	AMCR	4	0.0100	.	.
			AMGO	23	0.0572	23	0.0816
			AMRO	52	0.1294	52	0.1844
			BAOR	4	0.0100	4	0.0142
			BCCH	12	0.0299	.	.
			BHCO	11	0.0274	.	.
			BLJA	1	0.0025	.	.
			CEDW	6	0.0149	6	0.0213

(Appendix 2 continued)

			CHSP	11	0.0274	11	0.0390
			COGR	48	0.1194	48	0.1702
			DOWO	1	0.0025	.	.
			EAKI	2	0.0050	2	0.0071
			EAWP	1	0.0025	1	0.0035
			EUST	39	0.0970	.	.
			GRCA	1	0.0025	1	0.0035
			HOFI	89	0.2214	89	0.3156
			HOSP	8	0.0199	.	.
			HOWR	7	0.0174	.	.
			MODO	12	0.0299	.	.
			NOCA	6	0.0149	6	0.0213
			NOFL	3	0.0075	.	.
			REVI	3	0.0075	3	0.0106
			RODO	1	0.0025	.	.
			SOSP	30	0.0746	30	0.1064
			TRES	18	0.0448	.	.
			WAVI	5	0.0124	5	0.0177
			WBNU	3	0.0075	.	.
			YWAR	1	0.0025	1	0.0035
			TOTAL	402	1.0000	282	1.0000
St. Catharines	1990	50	AMCR	11	0.0035	.	.
			AMGO	24	0.0077	24	0.0216
			AMRO	190	0.0611	190	0.1710
			BAOR	2	0.0006	2	0.0018
			BCCH	6	0.0019	.	.
			BHCO	31	0.0100	.	.
			BLJA	23	0.0074	.	.
			CEDW	30	0.0096	30	0.0270
			CHSP	6	0.0019	6	0.0054
			COGR	169	0.0543	169	0.1521

(Appendix 2 continued)

			CSWA	1	0.0003	1	0.0009
			DOWO	6	0.0019	.	.
			EAWP	1	0.0003	1	0.0009
			EUST	192	0.0617	.	.
			HOFI	611	0.1964	611	0.5500
			HOSP	1611	0.5178	.	.
			HOWR	1	0.0003	.	.
			MALL	2	0.0006	.	.
			MODO	108	0.0347	.	.
			NOCA	51	0.0164	51	0.0459
			NOFL	5	0.0016	.	.
			NOMO	3	0.0010	3	0.0027
			PUMA	3	0.0010	.	.
			RBGR	1	0.0003	1	0.0009
			RBNU	1	0.0003	.	.
			REVI	4	0.0013	4	0.0036
			RWBL	1	0.0003	1	0.0009
			SOSP	12	0.0039	12	0.0108
			SWSP	1	0.0003	1	0.0009
			YWAR	4	0.0013	4	0.0036
			TOTAL	3111	1.0000	1111	1.0000
St. Catharines	1991	40	AMCR	10	0.0037	.	.
			AMGO	21	0.0078	21	0.0200
			AMRO	173	0.0643	173	0.1644
			AMWO	1	0.0004	.	.
			BAOR	4	0.0015	4	0.0038
			BCCH	3	0.0011	.	.
			BHCO	38	0.0141	.	.
			BLJA	16	0.0059	.	.
			CEDW	21	0.0078	21	0.0200
			CHSP	10	0.0037	10	0.0095

(Appendix 2 continued)

			COGR	168	0.0624	168	0.1597
			DOWO	4	0.0015	.	.
			EUST	129	0.0479	.	.
			GCFL	1	0.0004	.	.
			HOFI	538	0.1999	538	0.5114
			HOSP	1301	0.4835	.	.
			LEFL	2	0.0007	2	0.0019
			MODO	96	0.0357	.	.
			NOCA	82	0.0305	82	0.0779
			NOFL	4	0.0015	.	.
			NOMO	8	0.0030	8	0.0076
			PUMA	23	0.0085	.	.
			RBGR	1	0.0004	1	0.0010
			REVI	6	0.0022	6	0.0057
			RODO	13	0.0048	.	.
			RWBL	3	0.0011	3	0.0029
			SOSP	15	0.0056	15	0.0143
			TOTAL	2691	1.0000	1052	1.0000
St. Catharines	1992	15	AMCR	3	0.0029	.	.
			AMGO	11	0.0108	11	0.0273
			AMRO	73	0.0717	73	0.1811
			BAOR	2	0.0020	2	0.0050
			BCCH	4	0.0039	.	.
			BHCO	10	0.0098	.	.
			BLJA	5	0.0049	.	.
			CEDW	4	0.0039	4	0.0099
			CHSP	5	0.0049	5	0.0124
			COGR	55	0.0540	55	0.1365
			CSWA	1	0.0010	1	0.0025
			DOWO	3	0.0029	.	.
			EUST	46	0.0452	.	.

(Appendix 2 continued)

HOFI	203	0.1994	203	0.5037
HOSP	488	0.4794	.	.
LEFL	2	0.0020	2	0.0050
MALL	1	0.0010	.	.
MODO	46	0.0452	.	.
NOCA	28	0.0275	28	0.0695
NOFL	3	0.0029	.	.
NOMO	7	0.0069	7	0.0174
PUMA	6	0.0059	.	.
RWBL	2	0.0020	2	0.0050
SOSP	9	0.0088	9	0.0223
YWAR	1	0.0010	1	0.0025
TOTAL	1018	1.0000	403	1.0000

[a] Number of transects.

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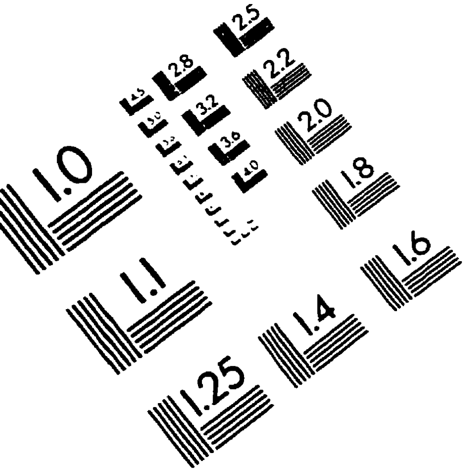

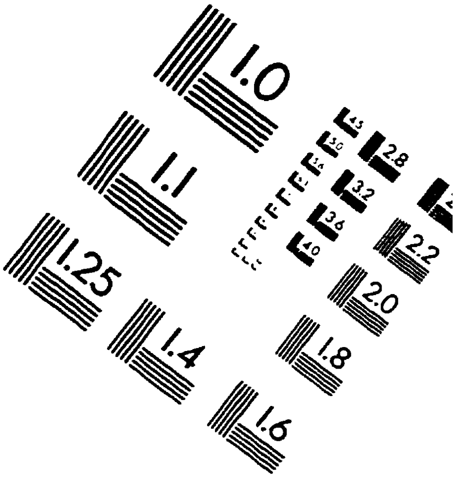

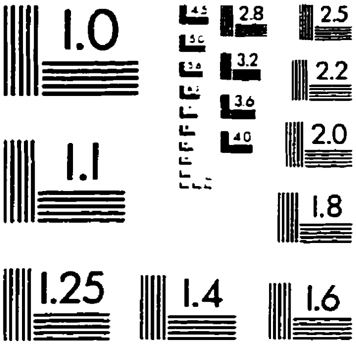

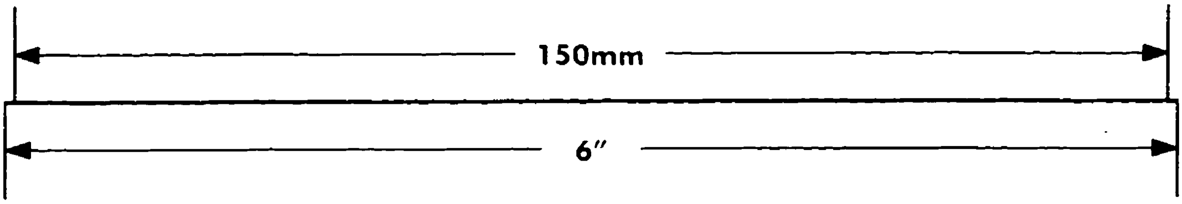

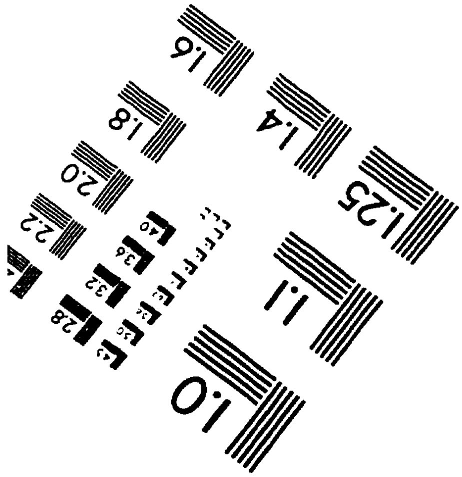

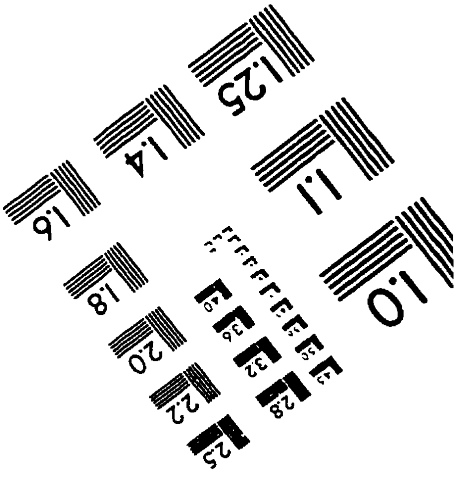

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