SOME NEW PERSPECTIVES ON THE BREEDING ECOLOGY OF COMMON GRACKLES

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The Common Grackle (Quiscalus quiscula) is a conspicuous bird, abundant through much of eastern North America. Bent and Gross (in Bent, 1958) have described the general features of its ecology. Their account was necessarily based upon scattered observations and local studies. Recent standardized methods of data collection by volunteers, particularly roadside breeding-bird counts and nest record card programs, should permit fuller perspectives of some aspects of Grackle ecology. This paper is an attempt to explore some possibilities of data collected by these new methods, using chiefly material from Canada.

MATERIALS AND METHODS

The cooperative Breeding Bird Survey (Robbins and Van Velzen, 1967, 1969) was started in Maryland in 1965, and first included all of the continental United States in 1968. All Canadian provinces except Newfoundland were included in the 1968 and 1969 surveys (Erskine, 1970), but coverage was neither complete nor uniform in the four western provinces and in the northern parts of Ontario and Quebec. This survey uses a standard procedure and a random sampling plan to make roadside counts on a single day in June each year. I have examined the data for individual surveys in Canada; in the United States the mean numbers of birds per survey in each state as given by Robbins and Van Velzen (1967, Table 2; 1969, Tables 2-4) were used.

Data on individual bird nests are entered on nest record cards, which are assembled in central files at the end of each breeding season (Mayer-Gross, 1970). The cards vary somewhat in design between regions, but nearly all request data on precise location, habitat, nest site and construction, and the numbers of eggs or young present on each visit, with other pertinent information. Data from the Grackle cards in the files of the Maritimes, Ontario, and Prairie Nest Record Schemes were used in this study; the Newfoundland, Quebec, and Pacific Nest Record Schemes contained too few Grackle records to warrant analysis at this time. I had contributed all except five of the 199 Grackle records from Cape Breton Island, Nova Scotia, in the Maritimes file; these provided a convenient sample which could be compared with data from other areas.

DISTRIBUTION

The A.O.U. Check-list (1957) and Bent (1958) indicate that the breeding range of the Common Grackle includes most of North America east of the Rocky Mountains and south of the tundra. The distribution in Canada extends far into the boreal forest, particularly in the northwest where it reaches Great Slave Lake (Godfrey, 1966). These accounts are based upon specific breeding localities, but they do not attempt to suggest the relative importance of different parts of the range.
The cooperative Breeding Bird Survey does not provide actual proof of breeding, but it does provide standardized indices of grackle numbers during the breeding season through most of their range. The mean numbers of Common Grackles noted per survey in each state and province are plotted in Figure 1, using the data for 1968–70 obtained from the Migratory Bird Population Station. Figure 1 shows that the A.O.U. Check-list (1957) and Godfrey (1966) place far too much emphasis on the peripheral records. The vast northwestern extension of the range is very sparsely populated with Grackles, whose main range lies largely east of 100° W and south of 48° N. The highest densities are between 35° and 43° N, along the Atlantic and in the Mississippi valley. Numbers generally thin out towards the limits of the range, but there is a remarkable concentration of Grackles in the Maritimes, particularly on Prince Edward Island (Fig. 2).

Nest record cards contain the same kinds of data used in compiling the
Fig. 2. Common Grackle density indices in the Maritime Provinces, from breeding bird survey data, 1966-70.

ranges in the A.O.U. Check-list (1957) and Godfrey (1966). Future compilations of this kind will be based to a great extent on nest record cards, which are, for common species, much more numerous than published breeding records. Through 1969, the Canadian nest record files contained over 1,700 records of Common Grackle nests.

However, even a cursory plotting of the distribution of nest record cards for a species shows that they are less valuable for distributional studies than might be expected. Nest records are provided by volunteer observers working chiefly near their homes, and frequently revisiting the same areas—or even the same sites—each year. A concentration of nest records represents a concentration of effort by one or more observers much more faithfully than it does local abundance of the species involved. The numbers of Grackle nest record cards for the Maritimes are presented by counties (Fig. 3) for comparison with the Breeding Bird Survey results (Fig. 2). The high density in western and central Prince Edward Island, and the low density along all the
Atlantic slope of Nova Scotia show up in both kinds of data. But nest records for the St. John valley in New Brunswick are obviously absent because no one spent much time searching for nests there; the totals for southeastern New Brunswick and western Cape Breton Island are high because of enthusiastic nest hunting. Such efforts have inflated a rather average density and given a quite distorted picture.

On the prairies, where the Breeding Bird Survey coverage was incomplete, the Grackle nest records help to fill in the picture. But these too are scarce. Nest records suggest that Grackles are found west to Calgary and Stettler, Alberta, and north to Battleford, Saskatchewan. Only single records, from the Lesser Slave Lake region of Alberta and from near Fort Smith, Northwest Territories, confirm the existence of the extended ranges shown in distributional summaries. In this attempt to correlate Grackle distribution with environment and with ranges of potentially competing species, the peripheral ranges can be largely ignored, since the local situations on which they depend will not show up in a broad-scale study.

Fig. 3. Numbers of nest record cards of Common Grackles, by county, in the Maritime Provinces, 1960-68.
HABITAT AND NEST SITE SELECTION

Nest record cards are biased sources of information on habitats and nest sites, just as they are as sources for distributional data. Observers tend to return to the same locations, habitats, and nest sites each year. After finding a species in a particular situation, they tend to look for other nests in similar habitats or sites in the same area. The habitats and sites in which nests can most easily be found will always be over-represented in these nest samples: the bias may be illustrated with data from the Maritimes.

I observed over 190 Grackle nestings in eastern Nova Scotia from 1960 to 1968. More than 95 per cent of these were close to water; however, this was chiefly because they were found during work on mergansers and other ducks, which was necessarily done in riparian situations. Only 15 per cent of over 360 nests on Prince Edward Island, found in 1963 to 1968, were stated to be near water. The observers there had looked for nests chiefly in the farming country around their homes.

Actually, about 95 per cent of the Grackle nest sites on Cape Breton Island were within one-half mile of fields (often old or abandoned fields), and most were much closer than this. But this information is drawn from my knowledge of the surrounding areas. The entries on the nest record cards usually refer only to the habitat(s) within 200 yards of the nests: thus, farmland was mentioned on only about one-quarter of the cards from Cape Breton, appreciably less than on the Nova Scotia mainland, in New Brunswick, or on Prince Edward Island.

I have seen Grackles foraging, and occasionally nesting, near open areas other than farmland—in marshes and even sphagnum bogs. Gross (in Bent, 1958) gave many examples of them feeding along shores, and Wiens (1965) and Snelling (1968) studied a Grackle population nesting in a cattail marsh. Probably this adaptability to alternative feeding areas has permitted the Common Grackle to breed locally far into the boreal forest, but its low densities there suggest poorer feeding opportunities than in open, arable lands.

Although Grackles often nest in abandoned farm buildings, the species is not one that typically associates with man’s dwellings, as does the Starling (Sturnus vulgaris). On Cape Breton Island, only one nest could have been termed “in a farmyard.” Concentrations close to villages were always in poorly accessible or inconspicuous places, such as flooded alder swamps or the girders of railway bridges. Unlike the cavity nests of Starlings, the large, untidy nests of Grackles are obvious and vulnerable to small boys, so nesting in urban areas obviously depends on whether suitably inaccessible nest sites exist. Grackles which nest in city parks (cf. Petersen and Young, 1950) and
in city gardens usually build high in ornamental conifers or in vines on the sides of buildings.

My Cape Breton data on Grackle nest sites required editing to minimize duplication between years, as some areas were visited annually. I have summarized below the maximum number of nests found in any one year in a particular kind of site in a given locality, rather than the total of all nests found over the years. Such selective treatment of the data from nest record cards is seldom feasible (cf. von Haartman, 1969).

Nests: in shrubs or small trees (under 15 feet tall) 65
(alder 33, hawthorn 13, willow 9, others 10)
in trees or tree stubs 7
in abandoned buildings (mostly old barns) 13
in bridges (both road and railway) 32

The highest proportions of nest sites were in alder swamps (28 per cent) and in bridges (27 per cent), because my work was along rivers. The nests studied on Prince Edward Island by M. Thomas included a much larger proportion in old farm buildings, while those studied by B. and K. Pigot were largely in conifer windbreaks. We would need larger and more evenly distributed samples than are now available to use these cards to describe quantitatively Grackle habitats or nest sites. Anyone attempting to use the data on nest record cards for these purposes should especially note the sites visited in several successive years, as these can introduce serious bias when samples are contributed by a relatively small observer corps.

LAYING DATES OF GRACKLES

Published laying dates for Grackles are few. Bent (1958) gave egg dates only. If many records were available from one state, we might assume that the earliest and latest dates approached the actual span from earliest laying to latest hatching; however, with small samples this is not likely to be true. The safest thing one can do with such records is to assign them to the midpoint of the egg period (laying + incubation = ca. 16 days). Three detailed studies of Grackles have been made at the University of Wisconsin (Petersen and Young, 1950; Wiens, 1965; Snelling, 1968), but I was unable to derive accurate laying dates from the graphical presentation in the two later papers. Records from Bent (1958) and Petersen and Young (1950) are presented in Figure 4.

I have followed Myres' (1955) method, with some minor modifications set out by Snow (unpubl. outline, British Trust for Ornithology, 1967), to calculate laying dates from nest record cards. An important feature of their method is that each calculated laying date is assigned a degree of accuracy
Fig. 4. Laying dates of Common Grackles from literature and nest record cards, with median dates and interquartile ranges where available. Assumed second nestings excluded.
(a) Published records from Bent (1938) except as shown; all ± 8 days except Wisc. (± 0-2 days). (b) From nest record cards; all ± 0-2 days. Sample size in second column.

depending on the span of possible dates within which it falls. A nest found and revisited during laying can be back-dated to an accuracy of ± 1 day or better. Nests with apparently complete clutches or with unaged nestlings can only be back-dated to the mid-points of the incubation or nestling stages; these periods are each about 12 days long, so the calculated date has an accuracy of ± 6 days. In this study, only nests dated to an accuracy of ± 0-2 days were used, but in studies involving smaller numbers of nests it may be desirable to use less precise records as well. Composite laying dates for the Maritime Provinces, Ontario, Saskatchewan, and Alberta are presented in Figure 4, with those from the literature. The Maritimes nest records were
sufficiently numerous that they were subdivided for further examination into six groups, namely: eastern (E-NS) and western (W-NS) Nova Scotia, eastern (E-PEI) and western (W-PEI) Prince Edward Island, and northern (N-NB) and southern (S-NB) New Brunswick.

CLUTCH SIZE

There are few detailed accounts of Grackle clutch sizes. Bent and Gross (in Bent, 1958) stated that four and five egg sets were usual, and six not especially rare; three was apparently less common than six, since Bent did not mention it for the southern races. Petersen and Young (1950) gave exact data from a three-year study in Wisconsin: 3 (3), 4 (9), 5 (36), 6 (6), 7 (1), for a mean of 4.87. Wiens (1965) gave a mean of 4.4 eggs per clutch, with no details, from a different habitat in the same area of Wisconsin. It is not clear how many of these values involved clutches counted on more than one visit (cf. Snow, 1955a), but those of Petersen and Young and of Wiens presumably did.

A recent paper (Willson et al., 1971), presents additional data on clutch size from central Illinois, a high density part of the range (see Fig. 1). Their data confirm the larger clutch size (mean 4.9 eggs) reported from the middle of the continent by Petersen and Young (1950), and they cite further references (not examined) to large mean clutches (4.7 eggs) in Kentucky and Kansas. The data they cited from Long and Long (1968), refer to clutches examined on two dates late in the nesting season; these should not be considered comparable to other samples taken over the entire season.

In my samples all nests containing only one or two eggs were omitted as being incomplete, although three nests had checked counts of two egg sets. Two of these were not found until midway through incubation; the third was not checked for 10 days during incubation, and it also showed an abnormally long period between the start of laying and the hatching, a likely sign of disturbance. In these nests additional eggs could have been laid and subsequently lost.

Some of the nest record samples included too few checked counts (i.e. counted on two or more visits) to be very helpful. Checked clutches consistently averaged larger than unchecked but apparently complete (≥ 3 eggs) ones, the ratio of unchecked/checked being 0.98. The means and samples are given in Table 1.

In all Canadian samples of 10 or more clutches, except those from N-NB and checked clutches from S-NB, five was the most frequent clutch, four prevailing in the exceptions. But only in E-PEI (both checked and unchecked samples) was six the most frequent clutch after five and four; elsewhere three was commoner than six.
### Table 1

**Checked and Unchecked Clutch Sizes of Common Grackles, based on Nest Records in Canadian Programs**

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BREEDING SUCCESS

The only published data on breeding success of Grackles are those of the Wisconsin studies, and Snelling (1968) believed that his activities (study of food brought to nestlings) had had a markedly adverse effect on reproductive success. Only one-fifth (18–21 per cent) of the grackle cards recorded nests found before incubation began, and less than half of these (5–9 per cent of total) were followed through to success or failure (cf. Snow, 1955b). Mayfield's (1961) method would permit use of more records, but it is unlikely that a meaningful analysis of Grackle breeding success based on nest record cards can be attempted until more records are available.

DISCUSSION

Distribution and Habitat.—The distribution of Grackles in the Maritimes (Fig. 2) agrees fairly well with that of agriculture. The highest densities occur on Prince Edward Island, which has 55 per cent of its area in cleared agricultural land. The highest densities in New Brunswick are in the potato-growing areas along the St. John valley and in more localized farming areas on the east and north coasts. But the main agricultural area in Nova Scotia, the Annapolis valley, seems to support relatively low Grackle densities, certainly less than in poorer farming areas on the north shore and western Cape Breton Island. The low densities in the Annapolis valley may reflect the more prosperous farming, with larger fields, fewer hedgerows, and fewer abandoned buildings for nest sites; the Bobolink (Dolichonyx oryzivorus), whose distribution in the Maritimes closely parallels that of the grackle but which nests on the ground in grassy fields, reaches its highest densities in the Annapolis valley. Much of the Maritimes was apparently settled by grackles only during the past 50 to 100 years (Godfrey, 1954, 1958; Tufts, 1962; Ouellet, 1969). Present distribution and densities there are possibly the temporary result of formerly more extensive agricultural settlement; as the many farms abandoned since the early 1900's revert to forest, the habitat becomes at first favorable but ultimately unsuitable for grackles.

The correlation between the Grackle's range and that of agriculture probably holds elsewhere in eastern Canada. Densities of Grackles certainly decrease rapidly as one moves north from the main farming areas of southern Quebec and Ontario. However, grackles virtually disappear (Fig. 1) in the northern grain-growing regions and on the dry prairies along the eastern flank of the Rockies, presumably owing to scarcity of elevated nest sites in these treeless regions.

If we consider only the main ranges of each species (Fig. 5), we find that the birds at present divided among the genera Quiscalus, Euphagus, and Cas-
sidix are nearly exclusive. Furthermore, their main ranges (omitting peripheral records) coincide closely with those of the greatest concentrations of species in the bird faunas to which each belongs (Udvardy, 1963). The Rusty Blackbird (Euphagus carolinus), of the taiga group of the Boreal Forest Fauna, spans the northern conifer forests from Newfoundland to Alaska. The
Brewer’s Blackbird (*E. cyanocephalus*), of the Western Woodland-edge Fauna, occupies dry, open country from the Pacific to the eastern edge of the short-grass prairie. The Common Grackle, of the forest-edge group of the Deciduous Forest Fauna, extends from the less dry, eastern prairies to the Atlantic, south of the Boreal Forest. The larger grackles (*Cassidix major* and *C. mexicanus*), of the Tropical South American Fauna, occupy Mexico and Florida and coastal areas from Texas to New Jersey. All of these are basically species that forage in open country but nest in somewhat elevated sites, in woody or herbaceous vegetation. Although the Brewer’s Blackbird nests on the ground in some areas, I believe that this is a secondary adaptation in a more typically tree- or bush-nesting species. Selander (1965), merged *Cassidix* with *Quiscalus*. Any future revision of this genus should also consider the species now set apart in *Euphagus*, which are similar in morphology as well as complimentary in distribution. Between them, these species occupy most open country habitats in North America except for the tundra and the southwestern deserts.

Except for the Rusty Blackbird, the northernmost of the group, these blackbirds co-exist throughout most of their ranges with one or several other Icterid species. The other species are also open country foragers, but they nest characteristically in marshes or on the ground. The more adaptable species may also use the nesting habitats of other species, resulting in competition. The most common comparison involving the Common Grackle has been with the Red-winged Blackbird (*Agelaius phoeniceus*), the typical marsh-nesting Icterid of eastern North America. These two are the most common and familiar blackbirds throughout the east, but their nesting habitats are largely segregated.

Wiens (1965) and Snelling (1968) studied Grackles nesting in a cattail marsh with Redwings. They concluded that the Grackles adjusted their behavior to minimize conflict with the highly territorial Redwings, and that the two species had almost complete temporal nesting separation, the Grackles nesting nearly two weeks earlier. The latter may be the factor that permitted the Grackles to invade this, to them, atypical habitat. Marsh-nesting by Grackles is known, on a local scale, in other areas. On Cape Breton Island, I found a few Grackle nests in sweet gale bushes in a shrubby marsh largely occupied by Redwings, and Redwings also nest sparsely in sweet gale clumps along the edges and in openings in alder swamps where Grackles nest commonly.

Many studies of competition between blackbird species have centered on the marsh-nesting species, particularly the Red-winged vs. Yellow-headed (*X. xanthocephalus*) Blackbirds (e.g. Willson & Orians, 1963), and the Red-winged vs. Tricolored (*A. tricolor*) Blackbirds (e.g. Lack and Emlen, 1939).
The Yellowhead is the dominant blackbird where it occurs in western marshes, as it readily supplants the Redwing. The Breeding Bird Survey (Robbins and Van Velzen, 1969) suggests that the Yellowhead is nowhere nearly as common as the Redwing. While this is probably correct on any but a local scale, the density of the Yellowhead is likely to be underestimated, as its habitat—deep, permanent marshes (Willson, 1966)—is poorly sampled by this roadside survey technique. Orians (1966) has shown that the Yellowhead is largely confined to the more fertile marshes, while the Redwing occupies the marsh edges and the less fertile areas.

In the west, Redwings frequently nest in willows and other tall marsh shrubs, the kind of habitat where one expects Grackles in the northeast. This habitat is available in the west because the Brewer’s Blackbird, in other respects the western geographic replacement of the Common Grackle, usually prefers drier habitats (cf. Orians and Horn, 1969). The Brewer’s Blackbird also nests on the ground in treeless areas, something which is unknown in the Grackle. This ground-nesting adaptation apparently places the Brewer’s in competition with the Bobolink. The latter co-exists widely with the Grackle, but occurs very sparsely in the range of the Brewer’s Blackbird. Bent (1958) quoted Roberts and Schрогer on the (partial) replacement of Bobolinks by Brewer’s Blackbirds in Minnesota and Wisconsin in the early decades of this century, but the evidence of the Breeding Bird Survey is that the Bobolink is still much more numerous in these states. Habitats frequented by the Common Grackle and other Icterid species with which it comes in contact are diagrammed in Figure 6.

Habitats, food, and social systems all enter into blackbird competition. Broadly, the trend is from densely colonial, marsh-nesting species at one extreme, to solitary, scrub-nesting species at the other. The most highly colonial species (A. tricolor) is monogamous, as are the solitary species (E. carolinus and Q. quiscula) at the other extreme; in between there are various degrees of polygyny. Recent studies (e.g. Horn, 1968) have shown that colonial nesting is adaptive where food sources are unevenly distributed, whereas solitary nesting is favored where the food supply is stable and uniformly distributed. The latter is true especially if grouped nests become unusually vulnerable to predation, as with ground-nesting species in grassland. But it would also apply to species using infertile habitats such as the spruce bogs frequented by Rusty Blackbirds. The Common Grackle is at most loosely colonial (Lack, 1968) would term it “grouped nesting” rather than truly colonial behavior). There are no useful data on whether the Grackle is more or less colonial in the different parts of its range; in fact, there seem to be no major studies from the areas where it is most common! My own data from Cape Breton suggested that clumped nesting was the most common organization, but this
FIG. 6. Habitats used for nesting by grackles and other Icterids.

could be solely because clumped nests are much easier to find than solitary ones. Except in bridges, nests were usually more than 15 feet apart, particularly in the more extensive swamps where alternative nest supports were readily available.

The social organization of the Grackle involves minimal territorial defense (Ficken, 1963; Wiens, 1965), in contrast with the noisy and energetic defense of nest territories of marsh-nesting blackbirds. But the Brewer’s Blackbird (Williams, 1952) is not conspicuously territorial, and the promiscuous or polygynous Cassidix grackles defend only the nest rather than an area around it (Skutch, in Bent, 1958). I am left with the feeling that the Common Grackle differs rather little in social organization from the other scrub-nesting icterids, but that it is quite strictly monogamous in the northern parts of its range. Comparisons between Grackle and Rusty and between Grackle and Brewer’s Blackbirds, along the lines of those described by Wiens (1965) and Snelling (1968), would be extremely interesting. Although these species do exist in the same general areas, my own impression (Erskine, 1968) is that they never nest together in the same habitat. It is likely that their require-
ments are so similar that no two of these species can occur together without one gradually displacing the other. But we badly need comprehensive studies of the breeding biology of Common Grackles near the center of their range where they are most numerous.

Laying Dates.—The start of laying in the Maritimes is well correlated with local temperatures (Canada, Department of Transport, 1961–68) in any area and year. Within each year, the start of laying seems to follow a rise in daily mean temperature above 42° F (6° C) by five to seven days. This relationship (e.g. Fig. 7a) resembles that found by Nice (1937) for the Song Sparrow (*Melospiza melodia*), except that the usually earlier laying dates of the sparrow were accompanied by a considerably higher temperature threshold.

The only sample within which the relationship between temperature and laying date is anomalous is that from E-PEI (Fig. 7b). There the interval between temperature rise above 42° F and onset of laying was shorter than five days in all years for which nine or more accurate dates were available. This could be explained if the temperature around the nesting site was (say) 2–3° F higher than at the station (Charlottetown CDA) at which weather records were taken. There is no evidence that the nesting locality was actually warmer, but this nest sample was the only one in which nests in dense conifers predominated. The micro-habitat provided by this substrate may be sufficiently warmer and better insulated than other nesting sites that a lower temperature threshold is tolerable there (cf. Horvath, 1964).

There is no correlation between median laying dates and monthly mean temperatures, probably because in the Maritimes the critical period for the start of ovulation falls sometimes in late April and sometimes in early May. Probably one could demonstrate correlation of laying dates with 10-day or weekly means of daily temperatures, but the correlation with the daily temperatures is likely to be more useful.

Clutch Size.—The clutch size frequencies reported by Bent and Gross are too general to be very helpful. In combination with the data of Petersen and Young (1950) and those from the nest record cards (Table 1), they suggest that the clutch size decreases slightly from south to north, with five and six egg sets becoming scarcer and three and four more frequent. But we obviously need far more data from the center of the species’ range before this can be taken as proved. Present data are not sufficient to show whether clutch size differs between habitats in any one area, as occurs in some species (cf. Lack, 1966—Table 25).

Clutch size varied inversely with laying dates in most parts of the Maritimes. This could not be verified from data on individual clutches, since too few records gave both an accurate laying date and a checked clutch size. There was fair correlation (Fig. 8) between mean clutch size and median laying
CLUTCH INITIATION DATES KNOWN TO

Fig. 7. Comparison of daily mean temperatures and of clutch initiation dates for Common Grackles: (a) Baddeck, Nova Scotia, 1962; (b) Charlottetown, Prince Edward Island, 1964.
date in Nova Scotia, Prince Edward Island, and S-NB, but the relationship did not apply in N-NB. The very early laying dates found in E-PEI were accompanied by a high frequency of six egg sets and an overall high clutch size. But the early laying dates in N-NB, which were well correlated with temperatures in the warm springs of 1964 and 1968, were accompanied by the lowest mean clutch size of any area in the Maritimes. The N-NB sample is from about 100 miles farther north than any other Maritimes sample, but all of the Maritimes samples are about equally near to the limits of the species' distribution. I cannot at present explain this discrepancy.

**SUMMARY**

In this paper data collected in the cooperative Breeding Bird Survey and in nest record programs are used to obtain new perspectives on the breeding biology of the Common Grackle. Much of the range outlined in recent handbooks, especially in the north and west, is seen to be populated very sparsely—or perhaps very locally—by Grackles. The main range coincides well with agricultural areas and other open habitats where there are elevated sites (trees, bushes, buildings) for nests. The main range is mutually exclusive with those of the other blackbirds now placed in the genera *Euphagus* and *Cassidix*.

Nest record cards are shown to be quite biased as samples for data on distribution, breeding habitat, and nest site. Data on laying dates and clutch size are more satisfactory, provided they are interpreted carefully. The start of laying is generally well correlated with temperature, and the clutch size is usually (but not always) correlated with laying date. There is a suggestion that nests in dense conifers are started earlier and at lower temperatures than those in less protected sites. The clutch size may decrease slightly from south to north, but there are insufficient published data from the central and south-
ern parts of the main range to establish this at present. Data on reproductive success are generally meager, and this subject was not explored further.

ACKNOWLEDGMENTS

Thanks are due to all persons who collected the breeding bird survey and nest record data summarized in this paper. It is not possible to name all individually, but I particularly wish to mention the major contributors in the Maritime Provinces, whose data provided the framework around which the other data were arranged: Martin Thomas, Stanley Vass, Bruce Pigot, Keith Pigot, Ford Alward, Ronald Godin, Joseph Johnson, Cyril Coldwell, David Christie, Jean-Paul Lebel, Darrell Kitchen, and the late Gregory Hope. To these and to many others, my thanks are quite inadequate recognition of the time and enthusiasm represented by their contributions.

LITERATURE CITED


CANADIAN WILDLIFE SERVICE, OTTAWA, ONTARIO, CANADA. 10 MAY 1971.