Condor, 80:401–406

THE ANNUAL CYCLE OF THE AMERICAN GOLDFINCH

ALEX L. A. MIDDLETON

The American Goldfinch (*Carduelis tristis*) is noteworthy for its unusually late breeding season (Tyler 1968, Immelman 1971, Middleton 1972, Mundinger 1972, Newton 1972, von Haartman 1972), and for its prenuptial (prealternate) body molt, which is unique among cardueline finches (Newton 1972, Middleton 1977). Although late nesting was at one time thought to result from the need for thistle down (Forbush and May 1939), it was more recently suggested that some environmental factor such as photoperiod may regulate the timing of gonadal development, the flowering and seeding of certain Compositae serving as the ultimate factor which stimulates nesting from year to year (Holcomb 1969, Newton 1972). No one has thus far suggested that late gonadal development may be regulated by some other annual event.

In this paper, details of the major events of the annual cycle of the American Goldfinch at Guelph, Ontario, are outlined. The scheduling of these events, within the annual cycle, suggests that the prenuptial molt may serve as the main physiological factor which precludes early breeding by this species.

METHODS AND MATERIALS

Between May 1967, and November 1970, 118 male and 82 female goldfinches were shot within an 8 km radius of Guelph, for gonadal examination. At collection each bird was sexed, and the males were aged (Middleton 1974a). From June until September, birds were collected at bi-weekly intervals, and at monthly intervals between September and May.

Immediately after death, the left testis and seminal sac, or ovaries and oviducts were dissected and placed in Allen's fluid for 24 h. The right testis and right seminal sac were placed in 10% formalin. After fixation for 24 h all excess tissues were removed, the organs blotted dry and weighed to the nearest 0.1 mg on an Oertling R-20 balance. Wherever possible, diameters of the largest ovarian follicles were measured to the nearest 0.1 mm with a vernier caliper. Materials fixed in Allen's fluid were embedded in wax and sections cut at 6μ. Ovaries in which the follicular diameters could not be measured macroscopically were serially sectioned to permit microscopic measurement of the largest follicle. Materials fixed in formalin were embedded in gelatin and frozen sections were cut at 10μ. Sections were mounted and either stained with Weigert's haematoxylin and eosin (Allen's fixed material) or with lipophyllic Sudan IV and Weigert's haematoxylin (Formalin fixed materials).

The histological condition of left testes was determined using techniques of Scott and Middleton (1968) while lipid distribution within right testes was used to determine hormonal condition (Marshall and Coombs 1957) and the phases of the testicular cycle (Marshall 1959). Due to the small sample sizes obtained from any collection period, gonadal data were pooled in the analysis of the annual gonadal cycle.

In addition to birds collected for gonadal study, molt data were also obtained from an additional 3,433 individuals banded at Guelph between mid-November and mid-May, 1970 to 1975, and from 371 birds trapped at nests during July and August, 1968 to 1975. Details of molt are given in Middleton (1977).

RESULTS

THE GONADAL CYCLE

Testicular cycle. Unwittingly I carried out my study at approximately the same time as Mundinger (1972). With a few notable differences, the size (Fig. 1) and histology of the testes were similar to those in New York State (Mundinger 1972). However, I give the results of my study here as they can be related directly to the other events of the annual cycle at Guelph.

At Guelph old males (birds in at least their second breeding season) come into breeding condition (stage 6 testes, Scott and Middleton 1968) approximately two weeks in advance of first-year birds; testes of first-year birds were generally lighter, though nonsignificantly so ($P > 0.05$; students' t-test), than those of old birds (Table 1); and old males lost breeding condition (testes at stage 8) slightly in advance of first-year birds.

The seasonal development of seminal sacs was reflected in development of the cloacal protuberance. Basically, the weight cycle of seminal sacs was similar to that of testes, but peak weight of the former was reached slightly later than in testes (Table 2). The histological cycle of seminal sacs has been described elsewhere (Middleton 1972).

The ovarian cycle. No attempt was made to study detailed histology of ovaries, and the ovarian cycle was assessed on follicular size (Fig. 2). Based upon a follicular diameter of > 1.0 mm (Middleton 1971), breeding condition was reached by the population in mid-July and lasted until mid-August. However, first follicles of > 1.0 mm were collected from individuals on 6 July 1967, 28 June 1968, and 12 May 1969, respectively. Maximum ovarian development occurred in the latter half of July when all the female birds were in breeding condition. Thereafter, ovarian activity waned

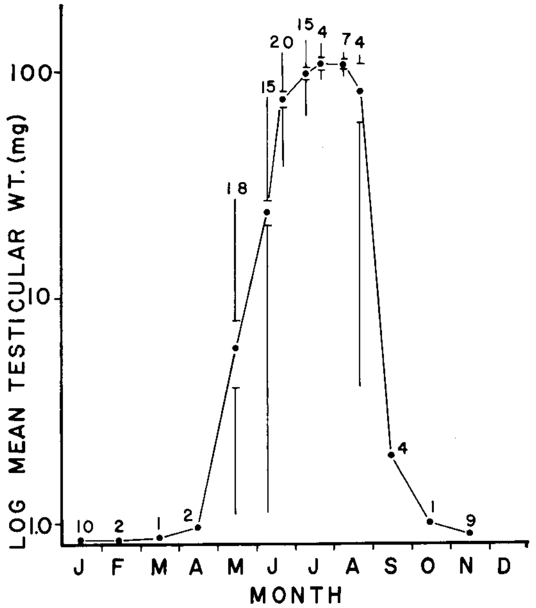

FIGURE 1. Testicular cycle of the American Goldfinch at Guelph, Ontario, based on weight of left testis. Vertical bars = range; horizontal bars = 2 SE; numbers give sample size.

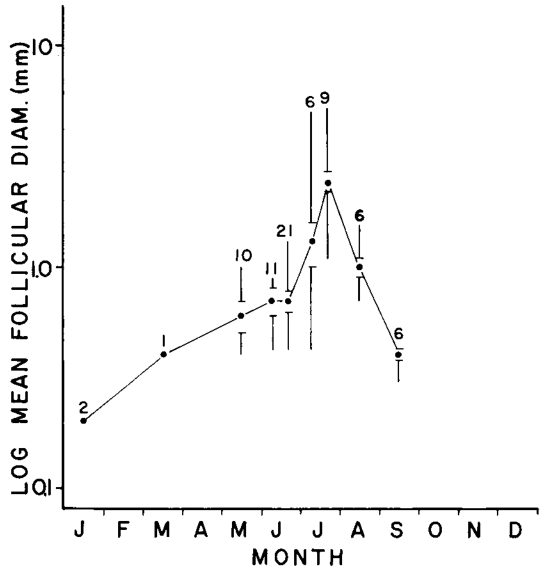

FIGURE 2. Ovarian cycle of the American Goldfinch at Guelph, Ontario, based on size of largest follicle. See Figure 1 for interpretation of symbols.

and by September no females had ovaries in breeding condition (Fig. 2).

The seasonal development of oviducts paralleled that of ovaries (Table 2). Oviducts were minute between October and May, enlarged slowly during June, then rapidly reached maximum development in the second half of July at the height of the egg-laying period (Middleton 1978). During August oviduct weight dropped markedly and regressed rapidly in September with the termination of breeding activity (Table 2).

MOLT

Although the molt cycle of the goldfinch has been described elsewhere (Middleton 1977) certain aspects emerge as being important to this discussion. Both postnuptial and prenuptial molts are prolonged, and it is difficult

TABLE 1. Weights of left testes of old and first-year goldfinches collected May–August, at Guelph, Ontario, 1967–70.

Collecting period	Age	N	Weight (mg) Mean ± SE	Range
*May	Old	5	7.8 ± 5.2	0.7 – 28.5
	1st-year	11	4.9 ± 4.4	0.3 – 14.9
June 1–15	Old	9	25.9 ± 10.3	0.3 – 78.5
	1st-year	6	21.0 ± 9.6	0.3 – 57.4
June 16–30	Old	7	85.3 ± 9.7	41.5 – 115.2
	1st-year	13	71.7 ± 7.8	38.7 – 123.2
July 1–15	Old	5	96.9 ± 8.5	71.2 – 119.7
	1st-year	10	99.3 ± 9.2	64.2 – 143.4
July 16–31	Old	2	114.3 ± 24.1	90.2 – 138.4
	1st-year	2	108.4 ± 0.6	107.8 – 108.9
*August 1–15	Old	3	115.7 ± 9.0	98.1 – 128.0
	1st-year	3	104.4 ± 8.9	93.7 – 122.0
August 16–31	Old	2	110.2 ± 11.0	99.1 – 121.3
	1st-year	2	58.8 ± 50.5	8.3 – 109.3

* Discrepancy in sample size with Figure 1 arose through loss of age identity of samples.

to determine exactly when one ends and the other begins (Fig. 3). However, there are peaks of molting activity which are similar to those of the other temperate zone species (Middleton 1977). Also, in the prenuptial molt, body molt begins with marked regularity in the second week of March (Middleton 1977). Molt ends abruptly at about the time nesting starts. The nesting season is the only time of the year when no molt was found within the goldfinch population (Fig. 3).

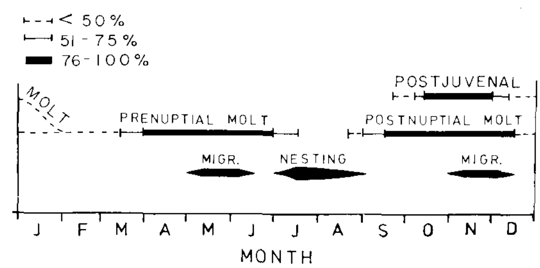

FIGURE 3. Chronology of the major events of the annual cycle of the American Goldfinch at Guelph, Ontario.

MIGRATION

Although Wiseman (1975) found no evidence for migration by goldfinches at Cincinnati, Ohio, banding results at Guelph indicate that the breeding population leaves the area during winter and is replaced by a distinct wintering population. In addition, recovery in Louisiana of a goldfinch banded in Guelph, and the recovery records of the North American Bird Banding Scheme (courtesy of Canadian Wildlife Service) prove that some goldfinches do undertake lengthy migrations. The disappearance and reappearance of color-banded summer birds, coincident with the reappearance and disappearance of winter banded individuals, indicate that migration of the Guelph goldfinch populations occurs between early May to mid-June and between late October to mid-December (Fig. 3).

DISCUSSION

In addition to corroborating the histophysiological details of the testicular cycle given by Mundinger (1972), my study shows that male goldfinches apparently reach breeding condition about two weeks before those in New York. However, this may have been a function of Mundinger's small samples and irregular collecting schedule. At Guelph, old males reach breeding condition before first-year males and apparently lose breeding condition slightly before first-year birds. Although Mundinger separated birds according to age he did not comment on the effect of age on the testicular cycle.

The details of the testicular cycle fit nesting data at Guelph which showed that old birds (those in at least their second breeding season) tend to build the earliest nest and produce the first clutches, while presumed first-year birds build most of the late August nests (Middleton in press). Also, the testes of old birds were generally heavier than those of first-year birds as with some other avian species (Scott and Middleton 1968, Payne

TABLE 2. Weights (mg) of left seminal sacs, and oviducts from goldfinches collected May–August, at Guelph, Ontario, 1967–70.*

	Seminal sacs			Oviducts		
Month	N	Mean ± SE	Range	N	Mean ± SE	Range
May	–	–	–	4	3.8 ± 0.8	1.7 – 5.3
June 1–15	2	5.1 ± 1.9	3.2 – 6.9	7	7.6 ± 1.6	2.8 – 15.1
June 16–30	12	8.4 ± 1.8	1.8 – 16.7	17	15.8 ± 2.7	4.4 – 46.9
July 1–15	9	13.5 ± 2.2	8.2 – 25.6	10	154.0 ± 63.5	10.6 – 465.6
July 16–31	5	19.6 ± 2.4	15.0 – 28.6	8	186.9 ± 117.6	1.9 – 949.3
August 1–15	4	24.0 ± 2.6	18.7 – 30.8	4	45.9 ± 15.3	13.9 – 87.6
August 16–31	3	26.4 ± 7.1	13.1 – 37.1	–	–	–
September	4	3.0 ± 0.5	1.7 – 4.2	6	12.0 ± 1.4	8.6 – 17.0

* Age classes not considered in these analyses.

1969, Erskine 1971). Although testicular size cannot be equated precisely with gonadal condition (Middleton 1971, Mundinger 1972) it may have a bearing on the apparent high fertility of old males (Middleton in press).

Because the seminal sacs function as storage organs (Middleton 1972, 1974b) it was not surprising that their development should follow the testes. The attainment of peak weight in late August was probably due to the accumulation of fluids and debris concomitant with the onset of testicular regeneration (Middleton 1974b).

The ovarian cycle closely follows the testicular cycle, though the majority of males reach breeding condition earlier than the females, as in most avian species (Lofts and Murton 1973). However, females vary more than males in the time at which they first reach breeding condition, because the date on which the first ovarian follicles of > 1.0 mm diameter were collected varied by almost two months. Such variability may help to explain the reports of abnormally early nesting by goldfinches (Nice 1939, Trautman 1940, Stokes 1950, Sutton 1959).

The stages of the ovarian cycle of the American Goldfinch at Guelph bore a similar relationship to the testicular cycle as that in the European Goldfinch (*Carduelis carduelis*) in Australia (Middleton 1971). The oviduct cycle closely follows the ovarian cycle, with peak oviduct weight coinciding with the peak of egg-laying in the nesting population (Middleton in press).

The most striking feature of the annual cycle of the goldfinch at Guelph is the amount of time devoted to molt (Fig. 3). Although this is mainly due to the gradual nature of the molt in the head region, associated with the emergence of a sexually dimorphic plumage in both first-year birds and old birds (Middleton 1977), the peak period of both prenuptial and postnuptial molts lasts longer than is characteristic of temperate zone passerines (Middleton 1977). The absence of molting during the height of the nesting season agrees with most temperate zone species in which breeding and molt are usually mutually exclusive events (Davis 1971, Payne 1972, Morton and Welton 1973). By contrast, molt apparently overlaps with migration in both spring and fall. Usually molt is either completed before, or is suspended during, migration in most temperate zone species (Haukioja 1971, Payne 1972, Pearson 1973) because the energetic demands of the two processes are incompatible (Evans 1969). However, as molt of the flight feathers is completed in the goldfinch before migration occurs, capability for flight is not impaired. Because different food constituents are needed for molt and deposition of fat, there is little overlap in the demands of molt and migratory preparation (Evans 1969). Therefore, the overlap of molt and migration probably does not impose an undue energetic strain on the goldfinch.

Also noteworthy in the annual cycle are the markedly regular timing of sperm production, prenuptial body molt (Middleton 1977), and migration from year to year (Middleton, unpubl. data). Little doubt remains that seasonal variations of physiological and behavioral phenomena are partly controlled by endogenous rhythms in various animal groups (Gwinner 1973, 1975). In birds, the cycles of reproduction, molt, and migration depend upon such circannual rhythms (Gwinner 1973). However, if such circannual rhythms are deprived of the appropriate environmental periodicities, they show periods which differ from the environmental cycles which they normally match (Payne 1972). Circannual rhythms in some species can be affected by day-length, which strongly suggests that it is the annual fluctuations of the photoperiod that maintain the timing of the rhythm (Gwinner 1973, 1975). For the goldfinch the precise relationship that exists between events of the annual cycle implies that some internal rhythm is present; while the precision with which events occur each year at Guelph suggests a response to a very predictable environmental timer, the most likely being photoperiod (Lofts and Murton 1968, Morrison and Wilson 1972, Immelman 1973, Follett and Davies 1975, Lofts 1975). In these respects the goldfinch appears typical of temperate zone passerines, but this does not explain what regulates its late gonadal development.

Mundinger (1972) showed that the duration of the regeneration, acceleration and culmination phases of the testicular cycle of the goldfinch resembled that in four other species, but the goldfinch differed in the late timing of all its phases. Mundinger noted the prolonged prenuptial molt but made no further reference to it. In two incomplete experiments with goldfinches (most birds died from coccidiosis early in the experiments), I adjusted the photoperiod in an attempt to gain some insight into the proximate factor that controls the gonadal cycle (Middleton, unpubl. data). All birds that survived the experiments molted before showing a gonadal response (assessed by laparotomy and bill pigmentation; see Middleton 1971, Mundinger 1972). These tentative results suggest that molt was initiated by a changing photoperiod and that once it had reached a certain stage, gonadal recrudescence began. Thus, molt, rather than the gonadal cycle, may be the process that is initially triggered by a photoperiodic response in the goldfinch. This may also be true for some other temperate zone passerines (Snow 1969, Dolnik 1975).

Although the exact nature of the interaction between molt and reproduction is poorly understood, the hormones associated with each process usually inhibit each other in temperate zone species (Lofts and Murton 1968, Payne 1972). The hormonal balance is probably different during the prenuptial and postnuptial molts in species that molt twice a year (Payne 1972). In the goldfinch, rapid gonadal growth does not occur until May, when the prenuptial molt is well advanced (Middleton 1977). Thus the incorporation of the prenuptial molt into the annual cycle may prevent early gonadal recrudescence, and may be the factor which ensures the late timing of the constituent phases of the gonadal cycle discussed by Mundinger (1972).

Clearly, molt is the most time consuming event in the annual cycle of the goldfinch at Guelph. It may therefore be the basic event which anchors the timing of the other major events. If so, the annual cycle of the American Goldfinch is apparently similar in its physiological timing to that proposed for some tropical species (Miller 1962, Snow and Snow 1964, Lofts and Murton 1968, Snow 1976), and may be unusual for a temperate zone species. Although Mayr and Short (1970) suggested that this species has no obvious close relatives, my results suggest that it may have tropical affinities as suggested for the other North American "goldfinches," *C. psaltria* and *C. lawrencei* (Mayr and Short 1970).

SUMMARY

The gonadal and molt cycles of the American Goldfinch were studied at Guelph, Ontario between 1968 and 1975. The gonads of 200 birds were examined while molt data were obtained from an additional 3,804 individuals trapped throughout the year.

Reproductive condition was first reached by mid-June, and all birds were in breeding condition by mid-July. Breeding condition persisted until late August. Old male goldfinches had heavier testes, and reached breeding condition earlier, than first-year birds. The cycles of the seminal sacs and oviducts closely followed those of the gonads.

Both prenuptial and postnuptial molts were prolonged and occupied most of the year. The nesting season was the only time when molt was not observed.

Based on banding data, migration occurred in early May to mid-June and between late October and mid-December.

The timing of all events in the annual cycle is assessed. Precision in the timing of the gonadal development, molt and migration is noted, which suggests a response to a predictable proximate factor, the most likely being photoperiod. As molt occupies the greater part of the year, the timing of events within the annual cycle of the goldfinch appears to be controlled by molt and not by the gonadal cycle.

ACKNOWLEDGMENTS

Thanks are offered to Murray Pengelley, Glen Fox, Mary and Mike Dyer, Richard Hamilton, and Alex Derry, for their assistance in the field. E. D. Bailey and D. E. Joyner provided valuable criticisms of earlier drafts of the paper, while the comments of P. Mundinger and an anonymous referee further strengthened it. The research was financially supported by the National Research Council of Canada, through grant #A3911 to the author.

LITERATURE CITED

DAVIS, J. 1971. Breeding and molt schedules of the Rufous-collared Sparrow in coastal Peru. Condor 73:127–146.

DOLNIK, V. R. 1975. Photoperiodic control of seasonal cycles of the body weight, moult and sexual activity in Chaffinches (*Fringilla coelebs*). Zool. Zh. 54:1048–1056.

ERSKINE, A. J. 1971. Growth, and annual cycles in weights, plumages and reproductive organs of Goosanders in eastern Canada. Ibis 113:42–58.

EVANS, P. R. 1969. Ecological aspects of migration, and pre-migratory fat deposition in the Lesser Redpoll *Carduelis flammea cabaret*. Condor 71:316–330.

FOLLETT, B. K. AND D. T. DAVIES. 1975. Photoperiodicity and the neuroendocrine control of reproduction in birds. Pp. 199–224. *In* M. Peaker [ed.], Avian physiology. Academic Press, London.

FORBUSH, E. H. AND J. B. MAY. 1939. Natural history of the birds of eastern and central North America. Houghton Mifflin Co., Boston.

GWINNER, E. 1973. Circannual rhythms in birds: Their interaction with circadian rhythms and environmental photoperiod. J. Reprod. Fertil. 19: Suppl., 51–65.

GWINNER, E. 1975. Circadian and circannual rhythms in birds. Pp. 221–285. *In* D. S. Farner and J. R. King [eds.], Avian biology. Vol. 5. Academic Press, New York.

HAUKIOJA, E. 1971. Summer schedule of some subarctic passerine birds with reference to postnuptial moult. Kevo. Subarctic Res. 7:60–69.

HOLCOMB, L. C. 1969. Breeding biology of the American Goldfinch in Ohio. Bird-Banding 40: 26–44.

IMMELMAN, K. 1971. Ecological aspects of periodic reproduction. Pp. 341–389. *In* D. S. Farner and J. R. King [eds.], Avian biology. Vol. 1. Academic Press, New York.

IMMELMAN, K. 1973. Role of the environment in reproduction as source of "predictive" information. Pp. 121–147. *In* D. S. Farner [ed.], Breeding biology of birds. Natl. Acad. Sci., Washington, D.C.

LOFTS, B. 1975. Environmental control of reproduction. Pp. 177–197. *In* M. Peaker [ed.], Avian physiology. Academic Press, London.

LOFTS, B. AND R. K. MURTON. 1968. Photoperiodic and physiological adaptations regulating avian breeding cycles and their ecological significance. J. Zool. Lond. 155:327–394.

LOFTS, B. AND R. K. MURTON. 1973. Reproduction in birds. Pp. 1–107. *In* D. S Farner and J R. King [eds.], Avian biology. Vol. 3. Academic Press, New York.

MARSHALL, A. J. 1959. Internal and environmental control of breeding. Ibis 101:456–478.

MARSHALL, A. J. AND C. J. F. COOMBS. 1957. The interaction of environmental, internal and behavioral factors in the Rook, *Corvus f. frugilegus* Linnaeus. Proc. Zool. Soc. London 128:545–589.

MAYR, E. AND L. L. SHORT. 1970. Species taxa of North American birds. Nuttall Ornithol. Club. Publ. No. 9.

MILLER, A. H. 1962. Bimodal occurrence of breeding in an equatorial sparrow. Proc. Natl. Acad. Sci. 48:396–400.

MIDDLETON, A. L. A. 1971. The gonadal cycle of the Goldfinch in south-eastern Australia. Emu 71:159–166.

MIDDLETON, A. L. A. 1972. The structure and possible function of the avian seminal sac. Condor 74:185–190.

MIDDLETON, A. L. A. 1974a. Age determination in the American Goldfinch. Bird-Banding 45:293–296.

MIDDLETON, A. L. A. 1974b. Spermiation and sperm transport in passerine birds. J. Reprod. Fertil. 40:31–37.

MIDDLETON, A. L. A. 1977. The molt of the American Goldfinch. Condor 79:440–444.

MIDDLETON, A. L. A. Influence of age and habitat on reproduction by the American Goldfinch. Ecology. In press.

MUNDINGER, P. C. 1972. Annual testicular cycle and bill color change in the Eastern American Goldfinch. Auk 89:403–419.

MORRISON, J. V. AND F. E. WILSON. 1972. Ovarian growth in Tree Sparrows (*Spizella arborea*). Auk 89:146–155.

MORTON, M. L., AND D. E. WELTON. 1973. Postnuptial molt and its relation to reproductive cycle and body weight in Mountain White-crowned Sparrows (*Zonotrichia leucophrys oriantha*). Condor 75:184–189.

NEWTON, I. 1972. Finches. Collins, London.

NICE, M. M. 1939. Territorial song and non-territorial behavior of Goldfinches in Ohio. Wilson Bull. 51:123.

PAYNE, R. B. 1969. Breeding seasons and reproductive physiology of Tricolored Blackbirds and Redwinged Blackbirds. Univ. Calif. Publ. Zool. 90:1–115.

PAYNE, R. B. 1972. Mechanisms and control of molt. Pp. 103–155. *In* D. S. Farner and J. R. King [eds.], Avian biology. Vol. 2. Academic Press, New York.

PEARSON, D. J. 1973. Moult of some palaearctic warblers wintering in Uganda. Bird Study 20: 24–36.

SCOTT, D. M. AND A. L. A. MIDDLETON. 1968. The annual testicular cycle of the Brown-headed Cowbird (*Molothrus ater*). Can. J. Zool. 46:77–87.

SNOW, D. W. 1969. The moult of British thrushes and chats. Bird Study 16:115–129.

SNOW, D. W. 1976. The relationship between climate and annual cycles in the Cotingidae. Ibis 118:366–401.

SNOW, D. W. AND B. K. SNOW. 1964. Breeding seasons and annual cycles of Trinidad land birds. Zoologica 49:1–39.

STOKES, A. W. 1950. Breeding behavior of the Goldfinch. Wilson Bull. 62:107–127.

SUTTON, G. M. 1959. The nesting fringillids of the Edwin S. George reserve, southeastern Michigan (Part 2). Jack-pine Warbler 37:37–50.

TRAUTMAN, M. B. 1940. The birds of Buckeye Lake, Ohio. Univ. Mich. Mus. Zool. Misc. Publ. 44.

TYLER, W. M. 1968. *Spinus tristis tristis* (Linnaeus) Eastern American Goldfinch. Pp. 447–466. *In* O. L. Austin Jr. [ed.], Life histories of North American cardinals, grosbeaks, buntings, towhees, finches, sparrows and allies. U.S. Natl. Mus. Nat. Hist. Bull. 237, Part 1.

VON HAARTMAN, L. 1972. Further observations on late nesting in cardueline finches. Ornis Fenn. 49:15.

WISEMAN, A. J. 1975. Changes in body weight of American goldfinches. Wilson Bull. 87:390–411.

Department of Zoology, University of Guelph, Guelph, Ontario, Canada N1G 2W1. Accepted for publication 13 February 1978.