CHLAENIUS CORDICOLLIS (COLEOPTERA: CARABIDAE) NOT A FREQUENT FLYER IN MANITOBA, CANADA

N. J. Holliday

Department of Entomology, University of Manitoba,Winnipeg, Manitoba, Canada R3T 2N2

Neil_Holliday@UManitoba.CA

ABSTRACT

Flight of *Chlaenius cordicollis* Kirby (Coleoptera: Carabidae) was studied on beaches of the south basin of Lake Winnipeg and in the laboratory. Window traps, deployed from early May until late September 1982, caught adult beetles only within a 20-day period in late June. In dissections of beetles collected from nearby beaches in the same year, females were developing eggs by the middle of the flight period and by the time of the last catch period all females were gravid. The period of catches largely preceded oviposition, timing that conforms to expectations from a broad interpretation of the oogenesis-flight syndrome. In June, in laboratory trials using newly collected beetles, beetles did not fly at 20 °C: females flew at ≥ 23–30 °C and males flew at 25–30 °C. At temperatures above the threshold for both sexes, 55% of females and 14% of males flew. In fall, no beetles were caught in window traps, but newly collected beetles flew in the laboratory at 25 °C and 30 °C, although their flight ability was less than in June. The discussion explores implications of the oogenesis-flight syndrome constraining migratory flight to be in June, a time when temperature thresholds for flight are infrequently exceeded in the beetles' habitat because of its proximity to the recently ice-covered lake. It is concluded that, under Manitoba conditions, migratory flight of adult *C. cordicollis* can occur on only a few days of the year, and in some years, there may be no days suitable for flight.

Key Words: oogenesis-flight syndrome, migration, flight, temperature threshold

INTRODUCTION

Insect flight may be for migration or dispersal (Kennedy 1961). Migratory flight here is used in the sense of Southwood (1962) to mean a flight that results in the insect leaving its natal habitat and is distinguished from "trivial" flight that is within a habitat. Migratory flight involves a distinct physiological state that, in female insects, is related to ovary development, a phenomenon known as the "oogenesis-flight syndrome" (Johnson 1969). The syndrome is hormonally regulated (Rankin *et al*. 1986; Dingle 2001) and is a characteristic of Insecta; in many insects migratory flight precedes reproductive maturity (Johnson 1969). Some authors (e.g. Desender 2000) consider that conformation to the syndrome requires inhibition of simultaneous development of ovaries and flight apparatus. However, Johnson (1969) provided examples of migration by gravid and sexually mature females and emphasized that there is much variation in the sequence of migration and reproductive development among insect species, but that in each there is a strong association of the two phenomena.

In carabids, trivial flight is restricted to a few genera: most flight is migratory (Southwood 1962). Based on flight-interception trapping in the Netherlands, many carabids conform to the oogenesis-flight syndrome; some species that live more than a year have a second migratory flight from summer reproductive habitat to winter habitat (Van Huizen 1977). Desender (2000) dissected ovaries and flight muscles of almost 3000 individuals of 25 European carabid species and applied a contingency table approach based on the expectation that in species conforming to the oogenesis-flight syndrome, developed ovaries would not occur concurrently with developed flight muscles. He concluded that 17 of the 25 species conformed to the oogenesis-flight syndrome. However, as many macropterous carabid species with fully-developed flight muscles have never been observed to fly (Venn 2016), it is difficult to interpret Desender's results in terms of actual flight. Migratory flight in carabids is seldom a response to overcrowding in the natal habitat, but rather is a mechanism for the colonization or recolonization of uninhabited suitable habitats (Den Boer 1971). Of 61 species caught in flight in window traps in the Netherlands, almost 80% had females that had mated; migratory flights of fertilized females have a higher chance of successful (re)colonization of a suitable habitat than do those of virgin females for which success would require a post-migratory encounter with a migrant male (Van Huizen 1990).

Chlaenius cordicollis Kirby (Coleoptera: Carabidae) is a monomorphically macropterous species, that inhabits stoney shores of lakes and large rivers (Bell 1960; Lindroth 1969; Larochelle and Larivière 2003). Its geographic range extends from Manitoba east to the Atlantic coast, and south to Arkansas and Mississippi (Bousquet 2012). Adults are mostly nocturnal and hide, often in groups, under stones during the day (Larochelle and Larivière 2003). In Manitoba, *C. cordicollis* is most common on lakeshore beaches with limestone slabs (Holliday 2025). *Chlaenius cordicollis* is a spring breeder: adults are the overwintering stage, and reproduction occurs in May–June in Quebec and Vermont (Bell 1960; Larochelle and Larivière 2003). In Manitoba, ovary development is initiated in response to photoperiods that first occur in early May, reproduction is from June to early August, and adults die after reproducing; teneral beetles of the new generation are observed in late July and August (Holliday 2025).

Bell (1960) kept adult *C. cordicollis* in finger bowls in the laboratory and noted that one individual escaped by flight. Flight was preceded by a period of metathoracic vibration and, following take-off, the beetle rose at about 30° to the horizontal. Larochelle and Larivière (2003) reported flight to artificial lights in the laboratory. Erwin (1981 p. 167) after referring to Bell (1960) asserted that *C. cordicollis* "are fully winged and fly", although it appears that in the context of the Plummer's Island study on which he was reporting, he saw no living specimens. In more than 40 years of studies of *C. cordicollis* in Manitoba, flight was never observed in the field (Holliday 2025) and there appear to be no published records of flight of *C. cordicollis* in the field. The objective of this study is to assess whether, and if so under what circumstances, *C. cordicollis* flies in the field in Manitoba.

METHODS

Field methods

On the east coast of Hecla Island, on a beach at 51.07079°N, 96.68545°W that was inhabited by a large number of *Chlaenius cordicollis*, double-sided window traps (Southwood and Henderson 2000) were erected in early May 1982. Each window trap (Figure 1) consisted of a 1 × 1 m pane of transparent polycarbonate plastic mounted in a wooden frame supported on two 10 × 10 cm vertical posts embedded in the beach so that the bottom of the pane was approximately 1 m above the beach surface. Galvanized steel troughs, 30 cm wide, were mounted below each side of the pane to collect the organisms that hit the pane and fell down. Troughs were filled with salt water with a few drops of detergent. Four traps were erected in two pairs; the pairs were about 50 m apart. One of each pair was about 1 m from the top of the beach and the other was about 4 m closer to the water's edge. All traps were oriented with the panes perpendicular to the water's edge, so that they would intercept organisms flying along the beach.

Window traps were operated from 14 May until 22 September 1982 and were serviced at approximately weekly intervals. Servicing involved scooping out organisms and debris in the troughs with a tea-strainer, transferring any carabid beetles to 70% ethanol for transport to the laboratory, and replenishing the salt solution.

As part of a multi-year assessment of seasonal patterns of *C. cordicollis* diet and physiology, (fully described in Holliday 2025), at intervals from 10 May–1 September 1982, adult *C. cordicollis* were hand collected from stoney beaches on Hecla Island. Beetles were killed and preserved in 70% ethanol and later dissected. The sex of each beetle, and the ovary development of dissected females was recorded. The sex ratio in the sample was compared with the expectation of equal numbers of males and females using a likelihood ratio χ^2 test (Sokal and Rohlf 2011).

Laboratory studies

Ability of adult *C. cordicollis* to fly was tested in two series of laboratory trials. A series in late June were conducted on beetles that had overwintered. A second series, in fall, was conducted on post-teneral new generation beetles.

Overwintered adult *C. cordicollis* for testing in the June series were hand collected from beaches on Hecla Island on 19 June 1984. Beetles were brought to the laboratory in 120 mL plastic screw-capped containers containing moistened beach gravel. In the laboratory, beetles were held in 20 × 9 × 7 cm acrylic plastic boxes (2–3 beetles per box) at 21 °C in an illuminated incubator (Precision Model 818, GCA/Precision Scientific Group, Chicago, Illinois) with a lighting regime of 16:8 h light:dark. Boxes were one quarter filled with beach gravel and supported at about 10° to the horizontal with a small amount of water at the lower end; finely-ground Tender Vittles cat food (Purina, St. Louis, Missouri) was provided as food.

Figure 1. Window trap installed on a beach on Hecla Island, Manitoba.

Flight ability trials were conducted from 20–27 June 1984 in an arena consisting of an open rectangular plastic tub, with interior basal dimensions of 53 × 41 cm, and walls 25 cm high (Stack and Nest Container S-10718GR, Uline Canada, Milton, Ontario, Canada). In each trial, one beetle was removed from a plastic box, its sex determined using the method of Holliday (1977), and it was then placed in the arena for 5 minutes, during which the number of flights (if any) and the time to the first flight were recorded. Trials were conducted at 20 °, 23 °, 25 ° and 30 °C; trials at 25 °C were conducted on the laboratory bench, and those at other temperatures were performed in controlled environment chambers. All trials were conducted between 9 AM and 5 PM under ambient fluorescent lighting. A minimum of 10 beetles of each sex were tested at each temperature; each individual was used in only one trial.

Flight ability trails on new generation beetles were conducted in fall 1984, on beetles collected from 8–25 September 1984. Collection methods and holding conditions were the same as for the first series of trials. Trials in the fall series were conducted 2–22 October in controlled environment chambers at 25 °and 30 °C; 20 trials were conducted at each temperature. The sex of beetles was not determined, but in all other aspects the protocols for the second series of trials were the same as for the first.

Relationships of series, temperature, and beetle’s sex with the frequency of trials in which flight occurred were analysed using log-linear modelling of contingency tables (Bishop *et al*. 2007) with probability values estimated by permutation tests where appropriate. Effects on the number of flights and time to the first flight were analysed using non-parametric statistics (Hollander and

Wolfe 1973). Statistical analyses were performed using Genstat Release 24 (VSN International 2024).

Voucher specimens from the study were deposited in the J. B. Wallis/R. E. Roughley Museum of Entomology, University of Manitoba.

RESULTS

The four window traps caught a total of seven *C. cordicollis* adults (Figure 2). Despite traps being operated from spring to fall, all catches were between 11 June and 30 June. Sex and egg-content of beetles caught in window traps were not recorded, as beetles decayed rapidly in the intervals between trap servicing.

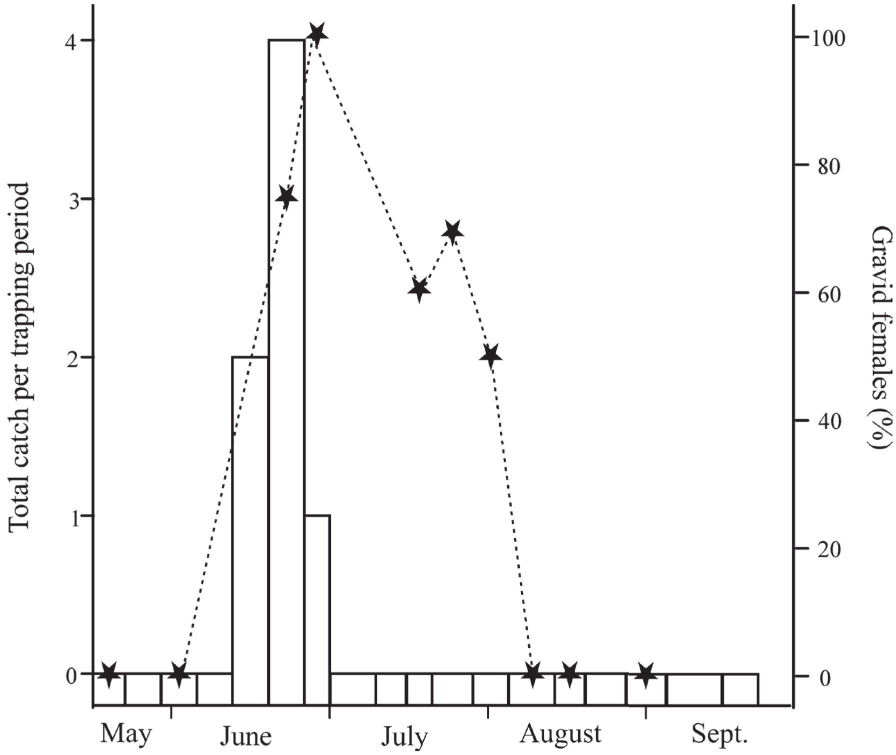

Figure 2. Total catch of *C. cordicollis* in four window traps and percentage of females with fully-developed eggs in trapping periods in 1982. The horizontal extent of bars indicates the duration of each trapping period and the height of the bar relative to the left-hand axis shows the total catch in the period. Trapping periods for which ovarian condition was assessed are indicated by stars, the height of stars relative to the right-hand axis indicates the percentage of females containing fully-developed eggs.

A total of 113 female and 97 male beetles were hand collected during the period of window trap operation and later dissected. The sex ratio in this sample did not differ from 1:1 (L.R. [Log ratio] $\chi^2 = 1.2$; d.f. = 1; $P = 0.3$). Females collected before there were catches in the window traps contained no fully-developed eggs. In the second trapping period with window trap catches, 75%

of females were gravid as were all females collected in the third period with catches. Thereafter, until early August, ≥ 50% of females were gravid.

In laboratory flight ability trials, beetles that flew buzzed audibly for some time before take-off. Not all beetles that made the buzzing noise successfully took flight. Most beetles that flew ascended at a shallow angle to the horizontal, hit the wall of the tub, and fell back to the bottom.

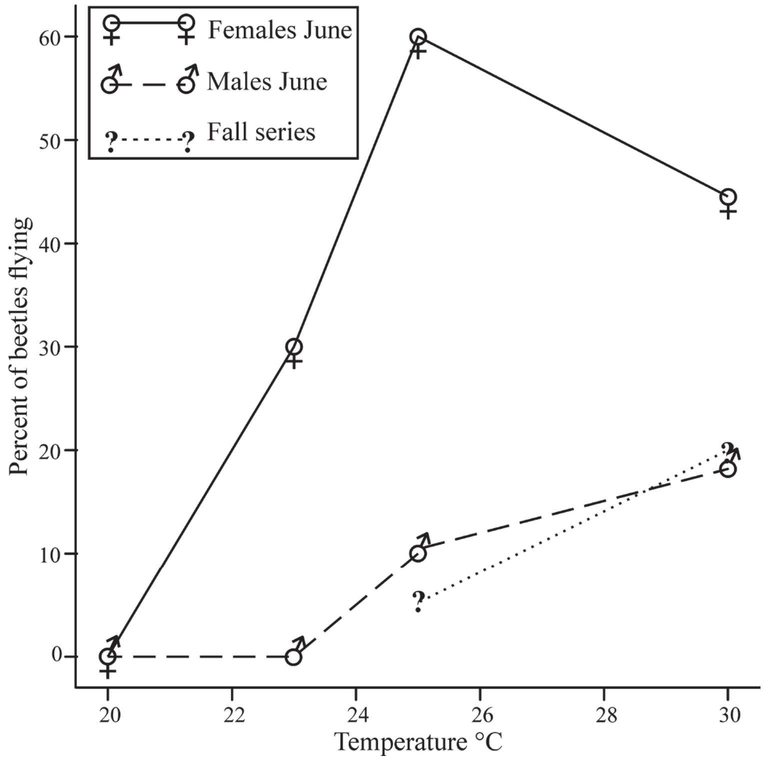

Figure 3. Percentage of *C. cordicollis* that flew in laboratory trials in relation to temperature for the June series, in which sex of beetles was determined, and the Fall series, in which sex was not determined.

In the June series of flight ability trials, the frequency of trials in which flight occurred (Figure 3) was significantly affected by temperature (L.R.χ^2 = 13.4; d.f. = 3; P = 0.01) because no flight occurred in trials at 20 °C. There was no significant effect of temperature (L.R.χ^2 = 2.5; d.f. = 2; P = 0.3) when the analysis was restricted to the temperatures 23 °, 25 ° and 30 °C. In this restricted analysis the frequency of trials with flight was affected by sex (L.R.χ^2 = 11.4; d.f. = 2; P = 0.002); flight occurred in 45% of trials (n = 31) with females and 10% of trials with males (n = 31). In trials at 23 °C, females flew but males did not. Even when analysis was further restricted to 25 ° and 30 °C, temperatures at which both sexes flew, the frequency of trials with flight was significantly higher for females (55%, n = 21)) than for males (14%, n = 21) (L.R.χ^2 = 7.2; d.f. = 1; P = 0.007). The interaction of beetle sex with temperature did not significantly affect the frequency of trials in which flight occurred (L.R.χ^2 = 1.7; d.f. = 2; P = 0.4).

In the June series, a total of 94 flights involving 21 beetles were observed, of these, 85 flights terminated when the beetle hit the end of the plastic tub and fell back to the bottom. Four beetles flew out of the tub; three did so once, and one flew out of the tub six times. The time to the first flight was 1.6 ± 0.9 minutes (mean ± SD) and was affected neither by the sex of the beetle (Mann-Whitney U = 19.5; $P = 1.0$) nor by the temperature of the trial (Kruskal-Wallis H = 1.95; d.f. = 2; $P = 0.38$). In trials where beetles flew, the number of flights was 5.5 ± 3.0 (mean ± SD) and was independent of beetle sex (Mann-Whitney U = 20; $P = 0.9$) and temperature (Kruskal-Wallis H = 2.96; d.f. = 2; $P = 0.23$). On the final date of the June series, five of the females were gravid and two of these gravid females flew, each of them making nine flights.

In the fall series with new generation beetles, sexes were not distinguished. The frequency of trials in which beetles flew was similar to that for males in the June trials (Figure 3), and there was no significant effect of temperature on this frequency ($\chi^2 = 2.06$; d.f. = 1; $P = 0.3$ [permutation test]). Comparisons of the fall series with equivalent trials in the June series (Table 1) show that, relative to beetles in June, those in October flew in a lower proportion of trials, took longer before their first flight, and made fewer flights.

Table 1. Comparison of results of flight trials in the June and Fall series. In the Fall series, sex of beetles was not determined, and trials were carried out at 25 ° and 30 °C. Tabulated data for the June series are for the same two temperatures and are pooled over males and females.

Series	Trials (n)	Trials in which flight occurred (%)	Beetles that flew (n)	Time to first flight (minutes) (mean ± SE)	Number of flights (mean ± SE)
June	42	33	14	1.7 ± 0.3	4.9 ± 0.8
Fall	40	13	5	3.6 ± 0.4	2.0 ± 0.6
Comparisons		L.R.$\chi^2 = 5.1$; d.f. = 1 $P = 0.02$		Mann-Whitney U = 4.5 $P = 0.003$	Mann-Whitney U = 13 $P = 0.04$

DISCUSSION

Window traps are effective methods of catching flying carabid beetles of many species (Den Boer 1971, 1977). Catches during 1982 clearly demonstrated a peak of flight activity in a 20-day period in late June. It had been intended that window traps be operated again in years subsequent to 1982, but the traps were destroyed by wind-driven ice during winter 1982–1983, and resources were not available for their replacement. In 1982, gravid females were first detected during the period when window traps were catching beetles, and gravid females were collected until about one month after the last catch in window traps.

Laboratory flight trials in June 1984 were conducted on dates corresponding to those in 1982 when *C. cordicollis* were collected in window traps and so are expected to characterize capabilities at the time of migratory flights. At temperatures at which flight occurred, numbers of flights and time to the first flight did not differ between males and females; however, many beetles did not fly, and the proportion of "flyers" was higher for females than males. Higher proportions of flyers in females than males also occur in the milkweed bug *Oncopelptus* *fasciatus* (Dallas) (Heteroptera: Lygaeidae) (Dingle 1966) and in leaf beetles (*Trirhabda* spp. (Coleoptera: Chrysomelidae) (Messina 1982). Dingle (1966) hypothesized that, following migratory flight, male colonizers could fertilize the eggs of several colonizing females, so females have greater value as colonizers than males. If females mate before migration, (Van Huizen 1990), migrating males have even less value as colonizers, and males may be able to fertilize more females if they do not divert resources to flight. In either circumstance, there would be stronger selection for female flyers than for male flyers. Non-flyers in a population remain at a natal habitat that has proven to be favourable, and so selection may favour maintenance of two behavioural morphs: flyers and non-flyers, with higher equilibrium frequencies of flyers for females than males.

Flight trials in the fall series demonstrated that new generation *C. cordicollis* can fly, albeit all measures showed less flight ability than in June. No beetles of the new generation were caught in window traps, and it is unlikely that migratory flight would occur at this time as it is far removed from the reproductive season, and beetles can walk to the winter habitat at the top of the beaches they inhabit in summer (Holliday 2025). Absence of trap catches does not disprove the occurrence of trivial flight at heights other than the traps or at such low frequency as to be undetected. Trivial flights, possibly in response to inundation (Venn 2016: Holliday 2025) or a predator threat may occur, although the need for a warm-up period may limit flight as a response to these rapidly developing threats.

The laboratory arena may provide flight-inducing stimuli that are absent in the field. Adult *C. cordicollis* are positively thigmotactic (Holliday 2025) and, in light, hide under any available object in the laboratory (Holliday unpublished) and in the field (Larochelle and Larivière 2003). Deprivation of all cover, as beetles experienced in Bell (1960) and in arenas in this study, may provide a flight-inducing stimulus that *C. cordicollis* would not encounter on the stoney beaches it normally inhabits.

The buzzing noise heard before take-off in laboratory trials is no doubt a consequence of thoracic muscle activity to warm the muscles prior to flight, as occurs in many insects (Johnson 1969; Dingle 1972). Despite this thoracic warming, low temperatures are evidently a constraint on flight of *C. cordicollis* and the timing of the flight period makes this particularly so. Lake Winnipeg is ice-covered in winter and the south basin becomes 50% ice free in late April or May (McCullough 2005). While there is ice on the lake, lakeside temperatures in spring are well below those in other areas of southern Manitoba (Segal and Kubesh 1996). A comparison of daily temperatures at the lakeside climate station at Gimli Harbour (Environment Canada 2024a) with an inland station 16 km from the lake at Arborg (Environment Canada 2024b) for the 11 years in which both stations operated showed that lakeside daily maxima averaged 2.4 ± 0.2 °C lower in May than those inland, but that there was wild variation with lakeside maxima on individual days ranging from 12.8 °C below to 8.7 °C above those at Arborg. In June, temperatures were more similar between the stations, with the lakeside maxima 1.3 ± 0.1 °C lower than inland maxima and daily lakeside maxima ranging from 6.0 °C below to 2.7 °C above those at Arborg.

Chlaenius cordicollis in Manitoba does not conform to the interpretation of the oogenesis–flight syndrome that requires nonconcurrent development of ovaries and flight apparatus. The observation of flight in gravid females in the laboratory trials, together with the co-occurrence of catches in window traps and gravid females in hand collections demonstrate that oogenesis is not delayed until after the period of migratory flight. However, laboratory studies (Holliday 2025) suggest that, even in the presence of males, females do not begin to oviposit until a more-or less complete complement of eggs is matured. Consequently, female gravidity at the time of flight does not negate the hypothesis that migration precedes oviposition. As female gravidity persisted for about a month after the last catch in window traps, much egg laying had to occur following the period of flight. Thus, the flight can be considered a migration in that egg deposition follows flight and can result in colonization of new habitats—an identical outcome in life history strategy to that in which migration precedes oogenesis.

An expectation of the oogenesis-flight syndrome is that the timing of migration and reproduction are strongly associated (Johnson 1969), and as ovary development is in response to photoperiod cues in *C. cordicollis* (Holliday 2025), it follows that the timing of the migratory flight is also seasonally constrained. That constraint dictates that flight activity be at a time when temperatures in the beach habitats are strongly influenced by the recently ice-covered lake, and daily maxima may be below the temperature thresholds for flight. Temperatures experienced by beetles caught in window trap catches in 1982 are unknown, as the nearest meteorological records for 1982 are for Arborg. Gimli Harbour Climate Station (Environment Canada 2024a) has operated from 2000–2024 and, like the window trap sites, is within a few metres of the water's edge on the west side of the south basin of Lake Winnipeg and so are expected to have similar temperature regimes.

Observations from Gimli Harbour and temperature thresholds from the laboratory flight trials (23 °C for females and 25 °C for males) predicts the frequency of years with a given number of days within the 20-day flight period that are too cool for flight (Figure 4). For the period when window traps caught beetles in 1982 (Figure 4A), 50% of years would have 16 or more days that were too cool for male flight and 12 or more days would be too cool for female flight. In two of the 22 years used to generate the predictions, 19 of 20 days were too cool for male flight and in one year 18 of 20 days were too cool for female flight. The date when 50% of females were gravid in 1982 was 12 days later than the date predicted from laboratory studies of photoperiodic cues and the observed values from dissections in 1981 (Holliday 2025). This was probably associated with late break-up of ice in 1982 preventing beetles buried in wintering sites from receiving photoperiodic cues for oogenesis induction. Hence, flight before reproductive maturity in 1982 was probably about 12 days later than in years when beetles can perceive the critical photoperiod when it first occurs on 5 May (Holliday 2025). Figure 4B depicts predictions for number of days out of 20 that are unsuitable for flight in years when the flight period is 12 days earlier than in 1982. In 50% of such years, temperatures on 18 or more days would be too cool for male flight and 16 or more days would be too cool for female flight. Within the 18 years used for the predictions, there were three years with no days suitable for male flight and one year with no days suitable for female flight. These predictions cannot readily be fine tuned to specific years with early or late dates of ice break-up. The number of days suitable for flight may be greater than the predictions if beetles behaviourally thermoregulate by finding microhabitats that are warmer than air temperatures or by basking. Numbers of days suitable for flight my be lower than predicted because temperatures from the weather station are daily maxima that may occur for a brief period during which factors such as high wind prevent take-off,

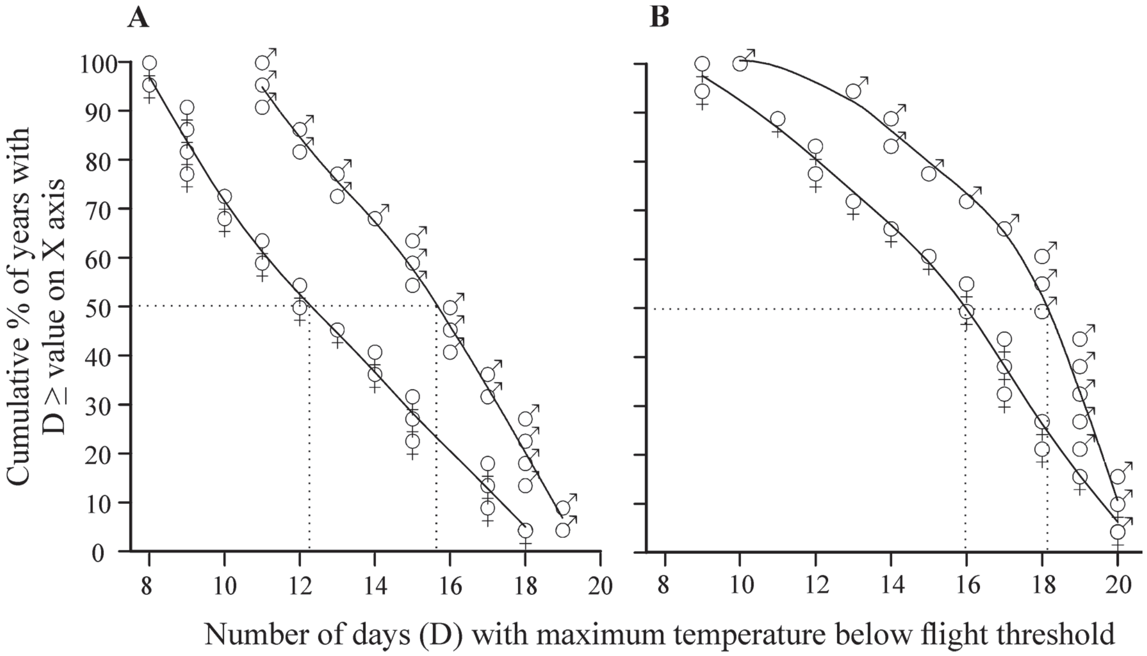

Figure 4. Predicted percentage of years in which the maximum temperature is < than the threshold for flight on a particular number of days out of a possible total of 20 days. A) Predictions based upon the observed period when beetles were caught in 1982, B) Predictions based upon the hypothesized "average" 20-day period during which pre-oogenesis flight would occur. Maximum temperature data are from 18 years of daily maxima from Gimli Harbour Climate Station (Environment Canada 2024a). See text for more details.

For flight that is constrained to be before an early summer oviposition period and to be close to a cold lake migration may be possible on few or no days (Figure 4). Further, at temperatures between the flight threshold for males and females, the migrant population will be entirely female, thereby lowering the proportion of colonizing males even further than expected from the sex-specific frequency of flyer morphs. Manitoba represents the extreme northwestern limit of the geographic range of *C. cordicollis* (Bousquet 2012). One reason for the western and northern limits on the range may be the need for deep snow to insulate overwintering sites (Holliday 2025). A second reason may be limits on the number of days on which colonization or recolonization of habitats can occur. The limitations described in this study are localized and certainly do not apply in the southern part of the insect's range.

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