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Seasonal and spatial distributions in relation to reproduction of blowflies (Diptera, Calliphoridae) in Hokkaido, Japan

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Abstract: Seasonal and spatial distributions of blowflies in relation to reproduction were investigated by baited traps in eight sites from lowland to high mountainous areas in Hokkaido, Japan. A total of 6,571 blowflies consisting of seven species in three genera was collected. The most predominant species was *Calliphora vomitoria* (Linnaeus) (5,946 flies, 90.5%), followed by *C. nigribarbis* Vollenhoven (537 flies, 8.2%). The remaining five species (*Triceratopyga calliphoroides* Rohdendorf, *C. vicina* Robineau-Desvoidy, *C. loewi* Enderlein, *C. subalpina* (Ringdahl), and *Aldrichina grahami* (Aldrich) were few in numbers. *Calliphora vomitoria* had the highest peak in autumn (October) in lowland to upland areas (70 m, 400 m, and 500 m), and it was also abundant from July to September in highlands (1,000–1,150 m). *Calliphora nigribarbis* was present in low numbers, but it was comparatively abundant in summer in highland areas (1,000–1,150 m). Emergence traps yielded 1,441 individuals from four species (*C. vomitoria*, *C. nigribarbis*, *C. vicina*, and *T. calliphoroides*), showing their reproductive potential in each site. Of these, *C. vomitoria* and *C. nigribarbis* emerged at 500 m (Nissho Pass) and 1,850 m (Mt. Kurodake) in August, indicating that they have reproductive cycles at upland to high mountainous areas. Further, adult emergence of *C. vomitoria* in 2009 from traps placed in the preceding autumn at Mt. Kurodake showed that this species can hibernate at high altitudes. For *C. vomitoria*, 62.7–84.1% of females had matured follicles (stages IV–V), and mating rates were very high (99.5–100%) in lowland and uplands in October. At Mt. Kurodake, high percentages of females of *C. vomitoria* and *C. nigribarbis* had mature follicles from July to October, with high mating rates. Life histories and reproduction of blowflies in Hokkaido were discussed.

Key words: blowflies, distribution, emergence, Hokkaido, life history, reproduction

Introduction

Blowflies play an important role as scavengers which decompose animal materials; on the other hand, some species transmit diseases by carrying various pathogens (Melnick and Penner, 1947; Hall, 1948; Greenberg, 1971). Recently, highly pathogenic H5N1 avian influenza viruses were isolated from the blowflies collected in the vicinity of poultry houses in Japan (Sawabe et al., 2006). It is worth noting on synanthropy, movement, and reproductive potential of blowflies in various environments surrounding human settlements. Up to now, there have been many reports on the species composition, distribution, seasonal and spatial distribution, and movement of blowflies (Wardle, 1927, 1930; Dicke and Eastwood, 1952; Siverley and Schoof, 1955; MacLeod, 1956; MacLeod and Donnelly, 1957, 1958, 1960, 1962; Nuorteva, 1966; Davies, 1990, 1999, 2006; Hwang and Turners, 2005), but these studies are virtually restricted to the high latitudes of north Europe and North America. Extensive work on the bionomics of blowflies in the

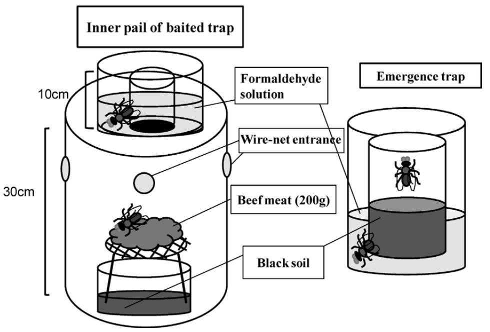

Fig. 1. Inner pail of baited trap and emergence trap.

world was reviewed by Norris (1965). In the western part of Russia, seasonal and diurnal changes of synanthropic flies including blowflies were presented by Sychevskaya (1957, 1962). These results show that the bionomics and characteristics of blowflies vary geographically and locally.

In eastern Asia, the studies of distribution, abundance, life histories, and migration of blowflies have been done in Honshu and Kyushu, Japan (Buei, 1959; Kano et al., 1965; Kurahashi et al., 1984, 1991, 1994; Kawai et al., 1985; Kurahashi, 1991; Arakawa et al., 1991; Tachibana and Numata, 2006). However, little is known of the bionomics and characteristics of blowflies in Hokkaido, the northernmost island of Japan. The purpose of this study is to clarify the species composition, seasonal and spatial distributions, and reproduction of blowflies in Hokkaido, Japan by using bait and emergence traps

Materials and Methods

Baited trap for collecting of flies and emergence trap

For collection of blowflies, the improved Yoken-style baited traps using beef (Suenaga and Kurahashi, 1994) were used. This trap consists of outer large square container (60 liters) and inner small pail (Fig. 1; 12 liters). Most of the wall from the 4 lateral sides of the outer box is cut away to allow entry to the inner trap box. The lid of the outer container protects the trap from rain. The inner round pail (bottom diameter 23 cm) is composing the main part of the trap and has four funnel-shaped wire-net entrances for attracted flies on the sides (Fig. 1). A smaller plastic tray (bottom diameter 19 cm) with black soil (2 cm in depth) for pupation is set in the pail. Inside the pail there is also a tripod stand attached with a wire-net on the top for placing beef meat (200 g). The pail cover has a hole with a plastic pipe leading out to an upper plastic container (diameter 15 cm) with a solution of 3% formaldehyde (5 cm in depth). Flies attracted to the meat enter the trap through the wire-net entrance holes, and after feeding or oviposition on the meat they move up to the upper plastic container through the pipe, and soon drop in the formaldehyde solution. The mature fly larvae grown on the meat will drop on the black soil through the wire-net on the top of the tripod stand. The baited traps were left throughout the seasons and when the flies were collected, new beef (150 g) was added to the trap. Fully grown larvae and pupae that had dropped in the black soil were transferred to an emergence trap. The emergence trap consists of two plastic containers with lids, outer large one (2 liters; height 25 cm × length 15 cm × width 7.5 cm) and inner one (Fig. 1; 1 liter; height 18 cm × length 12 cm × width 7.5 cm). The outer large container was filled with 3% formaldehyde solution (about one-third the height of the container). The inner small container contained black soil 5 cm deep, and pupae and mature larvae removed from the main trap were put in this small container. Flies newly emerged from the inner container will drop into the solution of the outer container, be fixed and stored. Emergence traps were buried under the ground by the side of the main trap.

Surveyed areas

During three years from 2007 to 2009, the survey was conducted at seven sites with different altitudes from 70 m to 1,150 m in the Tokachi District (No. 1–7 sites), surrounding Obihiro-city (42°55′N, 143°11′E), and one site at Mt. Kurodake (1,850 m) in the Kamikawa District (No. 8 site) (Table 1). Baited traps were set at No. 1–7 sites from June 2007 to November 2009 and at No. 8 site from July to October 2008 and 2009. Collection of flies

Table 1. A list of trap sites for blowfly surveys by using baited traps from 2007 to 2009 in Hokkaido, Japan

Site	Year	Name of city or town	Distance* (km)	Altitude (m)	Description
1. Poutry house	2008–2009	Shimizu-town	22	160	Rural wood area surrounded by cultivated field
2. Urikari riverside	2007–2008	Obihiro-city	5	70	Riparian wood lowland in rural area in Obihiro-city
3. Nissho Pass	2007–2008	Shimizu-town	33	500	Mid-slope of Nissho Pass
4. Nissho Pass	2007–2008	Shimizu-town	38	1,000	Near top of Nissho Pass
5. Mt. Tsurugi	2009	Shimizu-town	27	400	Foot of Mt. Tsurugi
6. Mt. Tsurugi	2009	Shimizu-town	29	850	Near mid-slope of Mt. Tsurugi
7. Mt. Tsurugi	2009	Shimizu-town	32	1,150	Near top of Mt. Tsurugi
8. Mt. Kurodake	2008–2009	Kamikawa-town	90	1,850	Near top of Mt. Kurodake, Daisetsuzan National Park

* From center of Obihiro-city

was conducted at intervals of two weeks at No. 1–7 sites and once at a month at Mt. Kurodake. Materials obtained were brought to the laboratory and identified and counted, but *Lucilia*, *Phormia*, and *Protophormia* spp. were excluded in the present study.

Follicle development and mating rate

Abdomens of females collected were dissected to examine the growth of ovarian follicles using a stereoscopic microscope. The stages of follicular development described in *Lucilia cuprina* by Vogt et al. (1974) were applied here, and they were classified into six stages (0, I, II, III, IV, and V). During in this observation, the spermathecae were removed, placed on a slide glass and covered with a cover glass, and the slide was examined under a light microscope for the presence of sperm.

Data analysis

Differences between percent frequencies of follicle stages and mating rates were analyzed by Excel Statistics Ver. 6

Results

Species composition, and seasonal and spatial distributions

A total of 6,571 blowflies consisting of seven species in three genera (*Calliphora vomitoria* (Linnaeus), *C. nigribarbis* Vollenhoven, *C. loewi* Enderlein, *C. vicina* Robineau-Desvoidy, *C. subalpina* (Ringdahl), *Aldrichina grahami* (Aldrich), and *Triceratopyga calliphoroides* Rohdendorf) was trapped in eight sites throughout a three-year survey (Table 2). Among them, *C. vomitoria* was the most predominant species (5,946 flies, 90.5%), followed by *C. nigribarbis* (537 flies, 8.2%), *T. calliphoroides* (35 flies, 0.5%), and *C. vicina* (28 flies, 0.4%). Very few other species were recovered throughout the survey. *Calliphora vomitoria* dominated in lowland to mountainous areas, with an extremely large number at the high altitude of Mt. Kurodake (1,850 m). *Calliphora nigribarbis* was captured at all sites, but its numbers were not large. Seasonal distributions of these two predominant species in Urikari riverside (70 m) and Nissho Pass (500 m and 1,000 m) are shown in Fig. 2. In 2007, female *C. vomitoria* were extremely abundant at 70 m and 500 m sites in October, but in 2008 there was a small peak in October in each site. At 1,000 m of the Nissho Pass, *C. vomitoria* was fewer in numbers than those at 70 m and 500 m, but its numbers were high overall from July to September in both years. On Mt. Tsurugi, *C. vomitoria* was abundant at 400 m in October, but it was present in much lower numbers at 850 m and 1,150 m with a peak in July at 1,150 m (Fig. 3). On the other hand, there were few *C. nigribarbis* throughout the seasons, but it showed a tendency to be abundant in July and August at 400 m of Mt. Tsu-

Table 2. Number of blowflies collected at each site in Tokachi and Kamikawa Districts, Hokkaido from 2007 to 2009.

Species	Site	Poultry house*	Urikari riverside**	Nissho Pass**		Mt. Tsurugi***			Mt. Kuro-dake*	Total
	Altitudes	160 m	70 m	500 m	1,000 m	400 m	850 m	1,150 m	1,850 m	
Calliphora vomitoria		84	729	414	322	627	19	11	3,740	5,946
Calliphora nigribarbis		65	36	40	141	33	21	26	175	537
Calliphora loewi		0	0	0	3	1	4	5	0	13
Calliphora vicina		2	8	0	1	1	2	1	13	28
Calliphora subalpina		0	0	0	0	0	1	0	6	7
Aldrichina grahami		0	0	1	0	0	0	0	4	5
Triceratopyga calliphoroides		0	0	2	2	0	1	0	30	35
Total		151	773	457	469	662	48	43	3,968	6,571

* 2008–2009; ** 2007–2008; *** 2009

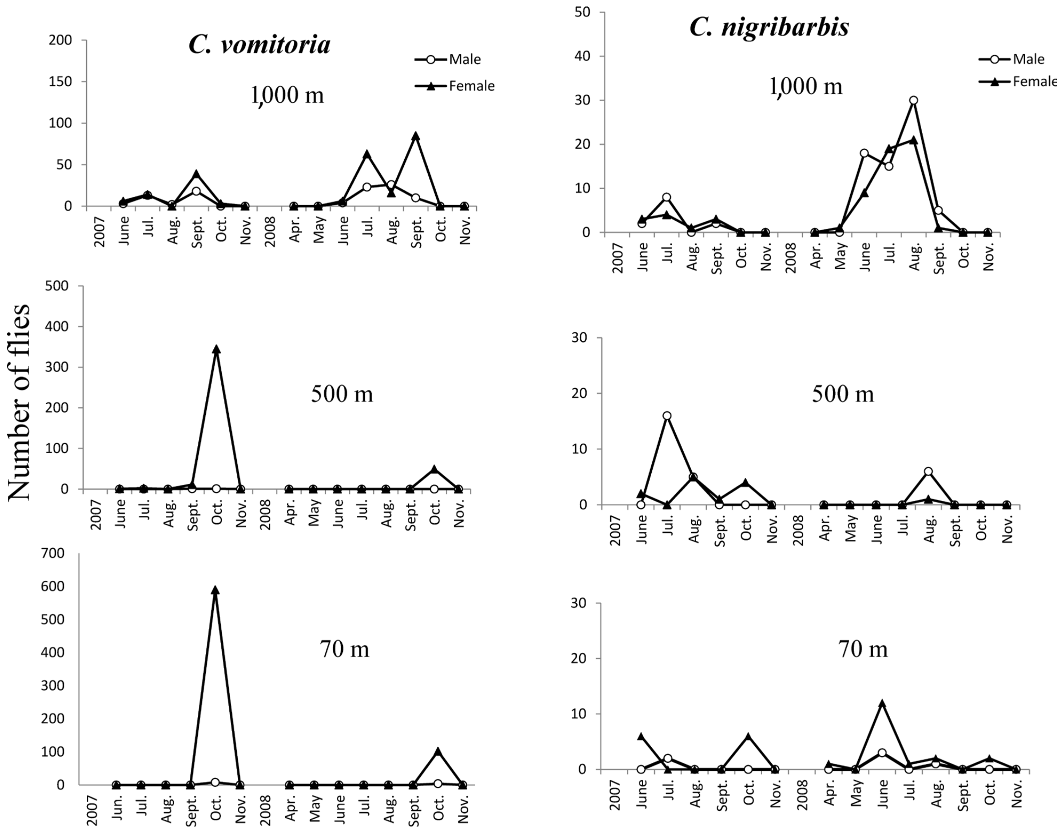

Fig. 2. Seasonal distribution of *Calliphora vomitoria* and *C. nigribarbis* on Urikari riverside (70 m), Nissho Pass (500 m, 1,000 m) from June 2007 to November 2008.

rugi, and at 500 m and 1,000 m of the Nissho Pass.

Adult emergence from emergence traps

A total of 1,441 flies consisting of four species in two genera emerged from emergence

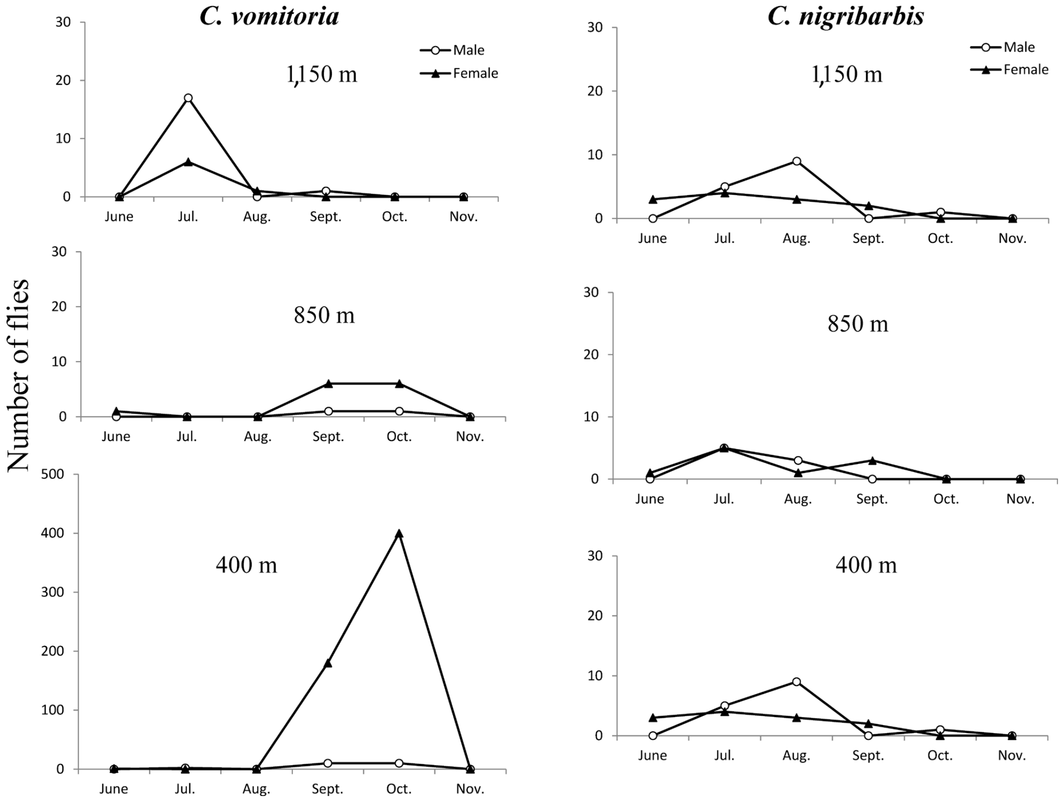

Fig. 3. Seasonal distribution of *Calliphora vomitoria* and *C. nigribarbis* on Mt. Tsurugi (400 m, 850 m, and 1,150 m) from June to November 2009.

traps at three sites (Table 3). *Calliphora vomitoria* was found in emergence traps at Nissho Pass (500 m; 2007) and Mt. Kurodake (1,850 m; 2008) in August. Furthermore, in June 2009 three flies emerged from a trap placed in the preceding autumn at Mt. Kurodake (1,850 m), showing that this species hibernated during winter from 2008 to 2009 at this site. For *C. nigribarbis*, 21 and 4 flies emerged at Nissho Pass (500 m; 2007) and Mt. Kurodake (1,850 m; 2008), respectively. Only one *C. vicina* emerged at 500 m at the Nissho Pass in August 2007. Emergence trap contained *T. calliphoroides* at the Nissho Pass (500 m; 2007), Mt. Tsurugi (1,150 m; 2009), and Mt. Kurodake (1,850 m; 2008), especially with high numbers at Mt. Kurodake.

Follicle development and mating rates

States of follicle development and mating rates of female *C. vomitoria* trapped at four sites (2–5) are shown in Table 4. Sixty-two to eighty-four percent of females at 70, 400, and 500 m in October 2007 had matured follicles (Stages IV–V). Especially in 400 m, percentage of individuals with matured follicles greatly increased in October than that of September. At 1,000 m, 81.5% and 100% of females had matured follicles in September and October, respectively, although the numbers were few. Mating rates were very high at all lowland (70 m), upland (500 m), and highland (1,000 m) sites in October 2007. On Mt. Kurodake (1,850 m), high percentages of *C. vomitoria* (75.0%–85.9%) had matured follicles from July to October, and *C. nigribarbis* also had matured follicles with high percentages (75.0%–75.9%) in August and September (Table 5). From July to September at Mt. Kurodake, mating rates for *C. vomitoria* and *C. nigribarbis* were 91.7%–97.5% and 80.9%–96.9%, respectively.

Table 3. Number of blowflies emerged from emergence traps at three sites from 2007 to 2009.

Species	Nissho Pass 500 m	Mt. Tsurugi 1,150 m	Mt. Kurodake 1,850 m		Total
	Aug. 2007	July 2009	Aug. 2008	Jun. 2009	
Calliphora vomitoria	17	0	64	3	84
Calliphora nigribarbis	21	0	4	0	25
Calliphora vicina	1	0	0	0	1
Triceratopyga calliphoroides	24	18	1,289	0	1,331
Total	63	18	1,357	3	1,441

Table 4. Percent frequency of follicle stages and mating rates of females *Calliphora vomitoria* at Urikari riverside, Mt. Tsurugi, and Nissho Pass from 2007 and 2009.

Site	Urikari riverside 70 m				Mt. Tsurugi 400 m				Nissho Pass 500 m				Nissho Pass 1,000 m			
	% of follicle stages			% mate	% of follicle stages			% mate	% of follicle stages			% mate	% of follicle stages			% mate
Month	0–I	II–III	IV–V		0–I	II–III	IV–V		0–I	II–III	IV–V		0–I	II–III	IV–V	
September	—	—	—		61.2[a]	59.0[a]	9.6[b]	35 (31)	—	—	—	—	5.2[a]	13.2[a]	81.6[a]	89.5 (38)
October	4.5	32.7	62.7	99.5 (590)	25.0[b]	5.0[b]	70.0[a]	100 (60)	0.3	15.5	84.1	100 (341)	0[a]	0[a]	100[a]	100 (3)

Values in parentheses are numbers of females examined. Values followed by different letters within the columns are significantly different (P<0.01: Z test).

Discussion

At high latitudes in northern Europe, it is well known that *C. vicina* and *C. vomitoria* are the representative species, followed by *C. loewi* Enderlein and *C. subalpina* (Ringdahl) in surveys using bait traps (Nuorteva, 1966; Davies, 1990; Hwang and Turner, 2005). In Honshu, Japan, *C. nigribarbis* and *A. grahami* are the predominant species in lowlands (Kano et al., 1965; Kurahashi et al., 1991), and *C. nigribarbis*, *C. vomitoria*, *C. vicina*, and *A. grahami* coexist in high altitudes (Shinonaga, 1965; Arakawa et al., 1991). From the present results, in Hokkaido, whose latitude is lower than northern Europe and higher than Honshu (Japan), *C. vomitoria* predominated from lowlands to high altitude areas. *C. nigribarbis*, which is endemic to East Asia, is commonly found in Honshu and Kyushu (Kano and Shinonaga, 1968), but the population density is low in Hokkaido, suggesting that Hokkaido is a northern limit for the geographic distribution of this species.

Nuorteva (1966) reported that *C. vicina* is widely distributed from urban to mountain areas. In Japan, *C. vicina*, which was first discovered in Hokkaido in 1956 (Kano and Shinonaga, 1968), is probably a recent immigrant introduced by human activity in Japan. This species has now also invaded Honshu, where it gathers on garbage and dead animals (Kano and Shinonaga, 1968; Kurahashi et al., 1976), but its population density is low in Hokkaido.

Triceratopyga calliphoroides hibernates in larval, prepupal and pupal stages, and it is collected in high mountains of about 1,500 m (Kano and Shinonaga, 1968). The results of emergence of this species show that this species can reproduce in a wide range of altitudinal habitats in Hokkaido with decaying animal materials as larval media, but it is never attracted to poultry houses.

Three remaining species, *C. loewi*, *C. subalpina*, and *Aldrichina grahami* are also present in much lower numbers in Hokkaido, and these species including *C. vicina* and *T. calliphoroides* are of less value for epidemiological significance. In poultry houses, blowflies

Table 5. Percent frequency of follicle stages and mating rates (%) of females *Calliphora vomitoria* and *C. nigribarbis* collected at Mt. Kurodake (1,850 m) in 2008.

Month	*Calliphora vomitoria*				*Calliphora nigribarbis*			
	% follicle stages			% mate	% follicle stages			% mate
	0–I	II–III	IV–V		0–I	II–III	IV–V	
July	9.2[a]	14.3[a]	76.6[a]	91.7 (40)	52.4[a]	0[b]	47.6[b]	80.9 (21)
August	2.4[b]	13.9[a]	83.8[a]	97.5 (40)	6.3[b]	18.7[a]	75.0[a]	96.9 (32)
September	0[c]	14.1[a]	85.9[a]	92.5 (40)	0[b]	24.1[a]	75.9[a]	92.3 (29)
October	0[c]	25.0[a]	75.0[a]	100 (4)	—	—	—	—

Values in parentheses are numbers of examined.Values followed by different letters within the columns are significantly different ($P<0.05$: Z test).

were not abundant, but we should still pay attention to *C. vomitoria* and *C. nigribarbis* as important species enable to invade the poultry houses in Hokkaido.

It is known that many factors affect the attractiveness of baited traps, such as recent feeding history and reproductive maturity, weather, height of traps and microgeographical variability (MacLeod, 1956; MacLeod and Donnelly, 1962). Small catches of *C. vomitoria* in October 2008 may be the result of a yearly change of population due to weather and other factors. Wardle (1927) reported that *C. vomitoria* appear in large numbers in spring and autumn in sheltered situations, but in open environment it is abundant in summer. On the other hand, this species exhibits a unimodal occurrence with the highest numbers in summer (Hwang and Turner, 2005). From the results of seasonal distribution (Fig. 2), *C. vomitoria* is expected to show a unimodal curve with a peak in October in lowland (70 m) to upland areas (500 m), and to show a summer appearance from July to September in high altitudes in Hokkaido. As Sychevskaya (1962) pointed out in the study of synathropic flies, *C. vomitoria* probably has different population curves in different parts of its geographic ranges. *Calliphora vomitoria* is known to overwinter in larval stage (Green, 1951). According to Nuorteva (1966), this species prefers forests and migrates from forests to human settlements in autumn. In Honshu, Japan, Arakawa et al. (1991) showed that adult *C. vomitoria* migrates to mountains in summer and suggested the possibility that they descend to lowland in autumn. Results of high percentages of mature follicles and high mating rates in females of *C. vomitoria* collected at 70, 400, and 500 m in October show that they can oviposit in lowland to upland areas in autumn. At Mt. Kurodake, high percentages of mature follicles and high mating rates in females from July to October also may indicate that this species reproduces at high altitudes in summer and autumn. These observations are supported by confirmation of adult emergences from emergence traps at 500 m (Nissho Pass) and 1,850 m (Mt. Kurodake). Further, we confirmed that overwintering larvae emerged from pupae in spring (May) in the rearing room where the temperature is close to that of the outside air (unpubl. data). From these results, it is felt that in Hokkaido *C. vomitoria* emerges from pupa derived from overwintering larva in spring and reproduces in a wide range from upland to high mountains at least with two generations per year, and may descend to lowland in autumn (October) for oviposition. However, adult emergence at Mt. Kurodake in spring of 2009 from an emergence trap which was left in autumn of 2008 (Table 3) suggests that this species has another population which hibernates at high mountainous areas. MacLeod and Donnelly (1963) postulated that there exist two types of dispersal in liberated flies, "a rapid exodus flight" and "a random process of multidirectional short flight". Though the dispersal pattern of *C. vomitoria* emerging naturally in the field is unclear, it is conceivable that there are two populations with different movement and dispersal in the same locality. According to Wardle (1927), British *Calliphora* species are multivoltine, with four generations through the year. The number of generations of *C. vomitoria* may vary according to altitudes in Hokkaido.

Green (1951) reported that *C. vomitoria* infests slaughterhouses and referred on its economic importance. From a hygienic point of view the season when *C. vomitoria* is important in houses of domestic animals and surroundings is autumn (October) in Hokkaido.

Kano et al. (1965) reported that *C. nigribarbis* had a bimodal seasonal distribution with peaks in April and November, and it was never collected in summer in Honshu, Japan. The present result suggests that this species has a tendency to appear in June and October in lowlands, but it is unimodal in upland to highland areas with a peak in summer in Hokkaido. In Honshu, Japan, adult *C. nigribarbis* migrates to mountainous areas for estivation with reproductive diapause in highlands in summer and return to lowlands for oviposition in autumn (Arakawa et al., 1991; Kurahashi et al., 1991, 1994; Kurahashi, 1993). From the results of seasonal distribution (Figs. 2, 3), we speculate that *C. nigribarbis* may also migrate among lowland, upland, and highland areas from spring to autumn in Hokkaido. However, confirmation of adult emergence of *C. nigribarbis* from emergence trap at 500 m in August shows that this species reproduces at uplands in summer in Hokkaido. Furthermore, from the results of follicle development and high mating rates from August to September, and confirmation of adult emergence of 4 individuals from emergence trap at Mt. Kurodake (Table 3 and 5), we suggest that *C. nigribarbis* is able to reproduce in high mountains in summer. It is possible that populations of *C. nigribarbis* in Hokkaido have a different life history from that of Honshu and Kyushu, because of different day-length and cool temperatures in summer. In Honshu, *C. nigribarbis* reproduces in winter and hibernates in all stages of adult, larva, and pupa, and it was suggested to be a univoltine insect (Kurahashi et al., 1994). However, Kurahashi and Tsuda (2007) also found that six adult specimens of *C. nigribarbis* labelled as 28 June 2003 from Hokkaido are teneral, which suggests *C. nigribarbis* might be multivoltine. Further in recent examination of this species deposited in our laboratory, we found many specimens with perfect wings collected in middle and late June; these are estimated as newly-emerged in June from Hokkaido (Unpubl. data). Though life history and overwintering stage of *C. nigribarbis* in Hokkaido are unclear, it is probably multivoltine in all parts of Japan including Hokkaido.

Williams et al. (1956) made an observation that indicates migratory flights of *C. vomitoria* and *C. vicina* in the Pyrenees, southern Europe. *Calliphora nigribarbis* and *A. grahami* with damaged wings were captured on ships which sailed on the Pacific Ocean and East China Sea, suggesting the possibility that they are transoceanic migratory insects (Kurahashi, 1991). Further, Kurahashi and Suenaga (1997) suspected a migratory flight of *C. nigribarbis* from Korean Peninsula to Kyushu Island over Tsushima Strait in autumn. It is worth notice whether this species is able to migrate over the strait between Hokkaido and Honshu or not.

Calliphora nigribarbis occurrs from carrion or human excrement (Kano and Shinonaga, 1968) and chicken dung (Niko and Ogata, 1958). Recently, avian influenza viruses were detected from *C. nigribarbis* and *A. grahami* collected in poultry houses (Sawabe et al., 2006), indicating a greater significance of these species from an epidemiological point of view. Further research is needed on local movements and transoceanic migratory flights of synanthropic blowflies by mark-release and recapture method.

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