Drosophila Survey of Hokkaido, XXXVI. Seasonal Changes in the Reproductive Condition of Wild and Domestic Species of *Drosophila*

By

Hide-aki Watabe

Zoological Institute, Hokkaido University

(With 4 Text-figures and 1 Table)

Seasonal changes in the reproductive condition have been investigated in wild populations of various drosophilids since the pioneer work of Dobzhansky and Epling (1944). The dynamic aspects of population and voltinism of species in a given district can be clarified by analyzing the ovarian condition of females throughout the active seasons (Begon, 1976; Watabe, 1977; Toda and Kimura, 1978). In cool and cold regions, the females of fall *Drosophila* populations are characterized as virgins with undeveloped ovaries and heavy sheets of fat in the abdomen. Such hibernal flies have been known to spend the winter in a state of reproductive diapause (Basden. 1954; Geyspits and Simonenko, 1970; Lakovaara, *et al.*, 1972; Lumme, *et al.*, 1974, 1975; Begon, 1976). Moreover photoperiodic control of the diapause has been ascertained in wild species overwintering as adults.

On the other hand, it seems reasonable that some domestic species of *Dorsophila* would be unable to survive outdoors during the winter in cool districts such as in Hokkaido (cf. Takada and Toyofuku, 1961; Chiang, *et al.*, 1962; Dobzhsanky, 1965; Watabe, unpubl.).

In the present paper, seasonal changes in the females' reproductive condition are shown in some wild and domestic *Dorsophila*, which are common near Sapporo. The effects of the photoperiodic reactions of these species on diapause determination are investigated, and the results obtained are discussed in relation to climatic adaptation to the northern environment.

The author is greatly indebted to Prof. Eizi Momma for his sincere encouragment and reading of the manuscript, and Messrs. M. J. Toda, M. T. Kimura, K. Beppu, N. Ichijo and N. Minami for their kind advice and help in collections.

Area Surveyed and Collection Methods

The University Botanical Garden at Sapporo (43°N) was selected to be the sruveyed area, because both wild and domestic *Drosophila* have been obtained in abundance (Momma, 1965). The vegetation and geography of this semi-natural area have also been descrived by Momma (1965). The flies have been collected in three successive years from 1975 to 1977, using "retainer" traps baited with fermenting banana (Toda, 1977). The samples were fixed with Kahle's solution and removed weekly. The reproductive condition of the females was examined under the stereoscopic binocular microscope. The developmental condition of ovaries was divided into four stages: Stage I, undeveloped; Stage II, developing; Stage III, mature; Stage IV, post-mature (Watabe and Beppu, 1977).

Methods of Experiments on Photoperiodism

Eggs taken from the wild-caught females and stocks were collected daily and treated with 70% alcohol to inhibit mold. About 40 eggs were placed in a culture vial containing the *Drosophila* medium, and incubated at 15±1°C and 18±1°C. Light cycles were administered by white fluorescent tubes. The newly emerged adults were transferred to a vial with a fresh medium. The diapause was investigated by the delay of ovarian development in a short daily light condition, and quantitatively estimated from the percentage of females with undeveloped ovaries within the total number of females dissected.

The experimental methods have been described in more detail elsewhere (cf. Watabe and Beppu, 1977).

Results and Remarks

1. Field-survey

The seasonal activity and age constitution of wild species were different from those of domestic. *Wild species*: The fall population of *D. bifasciata* consisted exculsively of females with undeveloped ovaries (Fig. 1). A heavy fat body was observed in the abdomens of flies caught in fall. The spring active peak, which consisted of the hibernated individuals, was recorded in mid April. In June, the increase in number was due to the emergence of the *first generation*. The new females soon developed their ovaries. The *second generation* adults continued to emerge from mid July to early August and performed the second breeding. The *third generation* flies began to emerge from mid August. The generation of this species would overlap during the summer months. The *fourth generation* flies collected in October and November did not develop ovaries and entered hibernation. In Sapporo, *D. bifasciata* had four, or partially three, generations per year. Nine common species, *D. confusa*, *D. auraria*, *D. biauraria*, *D. testacea*, *D. nigromaculata*, *D. brachynephros*, *D. unispina*, *D. histrio* and *D. multispina*, showed a similar pattern.

Though the number of generations per year was somewhat different from species to species, they had a multivoltine life cycle near Sapporo. Populations fluctuated in correspondence with the changes of generation (Watabe, 1977).

Domestic species: During the entire collecting season, the populations of *D. melanogaster*, *D. simulans* and *D. immigrans* (Fig. 2) always included representatives of all the developmental stages of ovaries. Even in late fall when the first snow was observed, females with developing and mature ovaries were collected but soon after seemed to die from the low temperatures. A conspicuous accumulation of fat in the abdomen was not observed during this time unlike the wild species. Four species, *D. busckii*, *D. melanogaster*, *D. simulans* and *D. immigrans*, showed the same pattern. They have rarely or never been collected from spring to early summer.

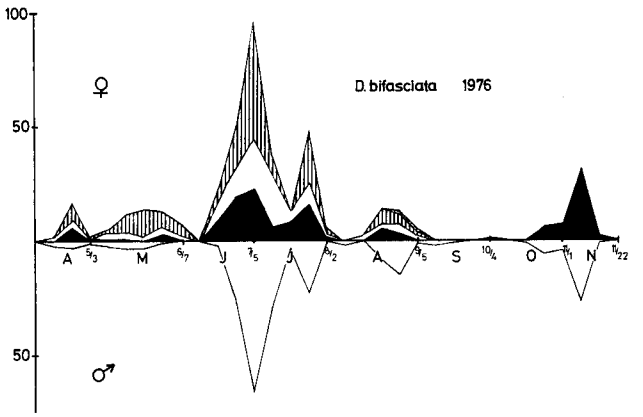

Fig. 1. Seasonal changes of female reproductive age structure and male individual numbers of *Drosophila bifasciata*. Black (Stage I), white (Stage II), vertical line (Stage III) and dot (Stage IV).

2. Experiment

In the females of *D. bifasciata*, a short daylength (LD 10:14) induced a delay in the development of ovaries (Fig. 3–A). Ovarian development proceeded without interruption when the flies were reared in a long-day photoperiod, LD 24:0. The critical daylength fell near 14 hours of light per day (Fig. 3-B). On the other hand, ovaries of *D. melanogaster* were not interrupted by a short-day photoperiod in their development and growth (Fig. 4-A).

Most ovaries matured at least within 8 days after eclosion at 15°C and 2 days at 18°C. *D. immigrans* was also a rapid breeder and the development of ovaries proceeded without any delay (Fig. 4-B). The length of time required for development was identical between a short and long photoperiodic condition in *D. melanogaster* and *D. immigrans* (Table 1).

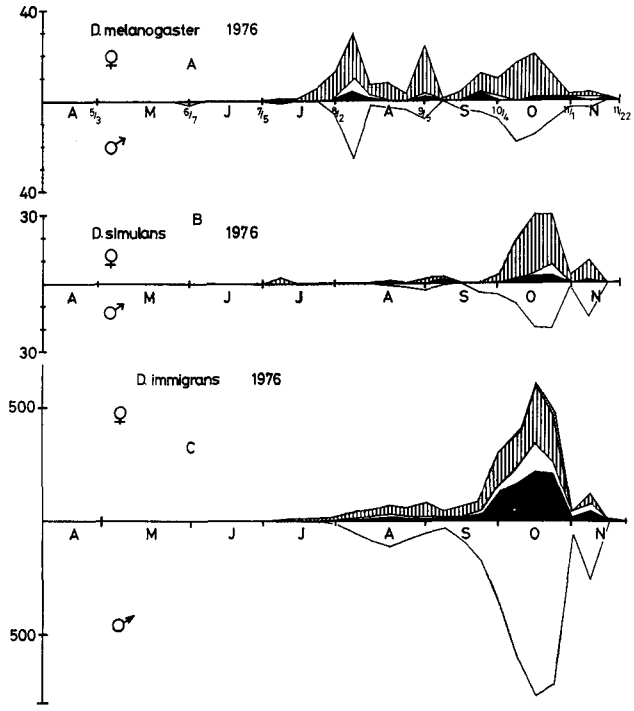

Fig. 2. Seasonal changes in female reproductive condition of *D. melanogaster* (A), *D. simulans* (B) and *D. immigrans* (C).

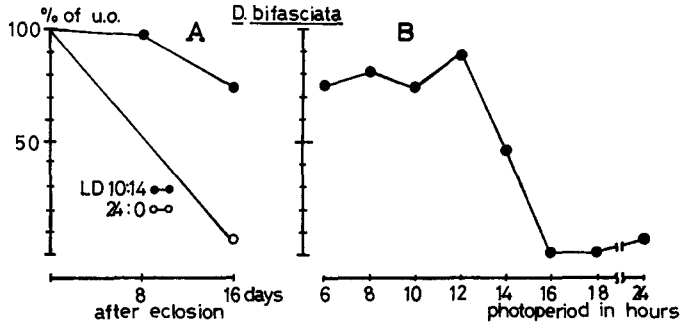

Fig. 3. A: The percentage of females with undeveloped ovaries. Flies were cultured at 18±1°C. B: Photoperiodic response curve for *D. bifasciata*. Flies were examined at the age of 16 days after eclosion.

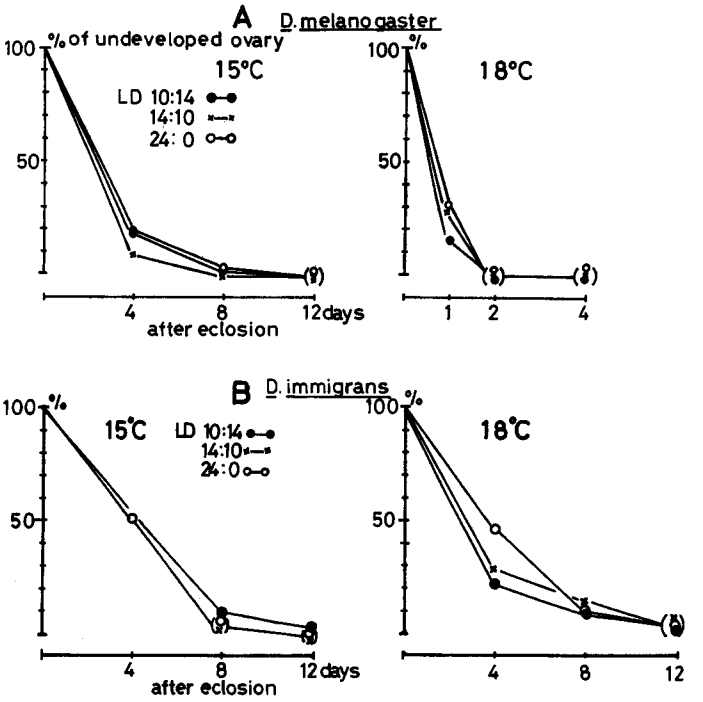

Fig. 4. The percentage of undeveloped ovaries within about 40 females dissected. Flies were reared in three photoperiodic regimes. A, *D. melanogaster*; B, *D. immigrans*.

Table 1. The duration required for development from egg to eclosion in a short and a long daily light regime

	D. melanogaster		*D. immigrans*	
	15±1°C		18±1°C	
LD 10:14	34.3±0.096	18.8±0.052	33.0±0.070	22.5±0.058
LD 14:10	34.2±0.083	18.2±0.091	31.8±0.087	22.5±0.051

Mean±S.E. (days).

Discussion

D. bifasciata, belonging to the *obscura* species group of the subgenus *Sophophora*, is distributed widely in the northern parts of the Holoarctic. Lakovaara, *et al.* (1972) has reported the adult diapause of the Finnish *D. bifasciata*. In the Sapporo population, the reproductive diapause under a short daylength was ascertained. The actual length of the critical photoperiods would vary with the ten

wild species mentioned above, and therefore the timing of the induction of the diapause might also differ. Field data suggst that they would spend the winter in the state of adult diapause. In fact some hibernating adults were found in the snowy season.

On the other hand, four species (*D. melanogaster, D. simulans, D. immigrans* and *D. busckii*) were very rare in occurrence during spring. No interruption of development of their ovaries was observed in the short daily light regimes.

Lumme (1978) reports that photoperiodism was not detected in *D. melanogaster*. Alpatov (1929) reported that early instars of *D. melanogaster* had undergone diapause, but MacKenzie (1975) considers that this might reflect genetic variation within a population. In the Sapporo population, no change in photoperiod influenced the developmental period from egg to adult. Therefore the overwinterings by these domestic species would not appear to involve the mechanism of a strict diapause (cf. Andrewartha, 1952; Mansingh, 1971; MacKenzie, 1975). They can hibernate only in manprotected warm places in Sapporo.

This seems to be related to the original distribution of domestic species. The present distribution is due to modern commerce and transportation. They are immigrants from tropical regions of the Old World. *D. melanogaster* and its sibling *D. simulans* belong to the *melanogaster* species group of the subgenus *Sophophora* (Bock and Wheeler, 1972). The group under discussion itself almost surely arose in tropical regions of the Old World (cf. Throckmorton, 1975). *D. immigrans* is a member of the *immigrans* group of the subgenus *Drosophila*, being regarded as originating in South-eastern Asia (cf. Throckmorton, 1975). Perhaps *D. busckii* is also originally from the tropical regions of the Old World.

The *hibernal diapause* may not be necessary for their survival in a tropical environment.

In conclusion, domestic species of *Drosophila* originating in tropical regions would not adapt to seasonal changes in the northern environment.

Summary

The seasonal changes of the females' reproductive condition of ten wild and four domestic species of *Drosophila* have been surveyed at the Botanical Garden in Sapporo. The photoperiodic responses of one wild and two domestic species were studied.

1. In ten wild species, the fall populations consisted of females having undeveloped ovaries and a heavy fat body in the abdomen.

2. The adult diapause of *D. bifasciata* was ascertained and occurred when night was 10 hours or longer.

3. In domestic species, the populations included females at all developmental stages of ovaries during the entire collecting season.

4. The development of ovaries of *D. melanogaster* and *D. immigrans* proceeded without any interruption in a short daily light condition.

References

Alpatov, W. W. 1929. Growth and variation of *Drosophila melanogaster* larvae. J. Exp. Zool. **52**: 407–437.

Andrewartha, H. C. 1952. Diapause in relation to the ecology of insects. Biol. Rev. **27**: 50–92.

Basden, E. B. 1954. Diapause in *Drosophila* (Diptera: Drosophilidae). Proc. R. Ent. Soc. Lond. (A) **29**: 114–118.

Begon, M. 1976. Temporal variations in the reproductive condition of *Drosophila obscura* Fallen and *D. subobscura* Collin. Oecologia **23**: 31–47.

Bock, I. R. and M.R. Wheeler 1972. The *melanogaster* species group. Univ. Texas Publ. **7213**: 1–102.

Chiang, H. C., Benoit, D. and J. Maki 1962. Tolerance of adult *Drosophila melanogaster* to sub-freezing temperatures. Can. Entmol. **94**: 722–727.

Dobzhansky, Th. 1965. "*Wild*" and "*domestic*" species of *Drosophila*. The Genetics and Colonizing Species (Edit. by Baker, H.G. and G.L. Stebbins). Acad. Press, New York, pp. 533–546.

——— and C. Epling 1944. Contribution to the genetics, taxonomy, and ecology of *Drosophila pseudoobscura* and its relatives. Carnegie Institute Washington Publ. **554**: 3–46.

Geyspits, K. F. and N. P. Simonenko 1970. An experimental analysis of seasonal changes in photoperiodic reaction of *Drosophila phalerata* Meig. (Diptera: Drosophilidae). Entmol. Rev. **49**: 46–54.

Lakovaara, S., Saura, A., Santibanz, S. and L. Ehrman 1972. Aspects of diapause and its genetics in northern drosophilids. Hereditas **70**: 89–96.

Lumme, J. 1978. Phenology and photoperiodic diapause in northern populations of *Drosophila*. Evolution of Insect Migration and Diapause (Edit. by H. Dingle). Spring-Verlag, New York, pp. 145–170.

———, Lakovaara, S., Oikarinen, A. and J. Lokki 1975 Genetics of the photoperiodic diapause in *Drosophila littoralis*. Herditas **79**: 143–148.

———, Oikarinen, A., Lakovaara, S. and R. Alataro 1974. The environmental regulation of adult diapause in *Drosophila littoralis*. J. Insect Physiol. **20**: 2023–2033.

Mansingh, A. 1971. Physiological classification of dormancy in insects. Can. Entmol. **103**: 983–1009.

MacKenzie, J. A. 1975. The influence of low temperature on survival and reproduction in populations of *Drosophila melanogaster*. Aust. J. Zool. **23**: 237–247.

Momma, E. 1965. The dynamic aspects of *Drosophila* populations in semi-natural area. I. Associations and relative numbers of species. Part 1: Results of trapping. Jap. J. Genet. **40**: 275–295.

Takada, H. and Y. Toyofuku 1960. Notes on hibernation of Drosophilidae in Hokkaido. Zool. Mag. **69**: 223–232 (In Japanese with English summary).

Throckmorton, L. H. 1975. The phylogeny, ecology and geography of *Drosophila*. Handbook of Genetics, III (Edit. by R.C. King). Plenum Press, New York, pp. 421–469.

Toda, M. J. 1977. Two new "retainer" bait traps. *Drosophila* Inform. Serv. **52**: 180.

——— and M. T. Kimura 1978. Bionomics of Drosophilidae (Diptera) in Hokkaido. I. *Scaptomyza pallida* and *Drosophila nipponica*. Kontyû **46**: 83–98.

Watabe, H. 1977. Drosophila Survey of Hokkaido, XXXIV. Seasonal variations of body color of *Drosophila testacea*. J. Fac. Sci. Hokkaido Univ. Ser. VI, Zool. **21**: 21–30.

——— and K. Beppu 1977. Drosophila Survey of Hokkaido, XXXIII. Ovarian development of *Drosophila* in relation to wild population. *Ibid.* **20**: 611–620.