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Niche Analysis of Three Closely Related Species of the Genus *Drosophila*

By

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(With 4 Text-figures and 3 Tables)

The *auraria* species complex (the *montium* species subgroup of the *melanogaster* species group of *Drosophila*) consists of four species, *D. auraria*, *D. biauraria*, *D. triauraria*, and *D. quadraria*. The first three are distributed in Japan and Korea, and the last is known only from Formosa. Some authors have studied these species from the view of genetics of speciation, e.g., heredity of bristle number of the sixth sternite and body color (Okada, 1954; Kurokawa, 1956a, 1962, 1967b; Lee, 1964; Lee and Choo, 1969), isozyme variation (Triantaphyllidis *et al.*, 1978), and the sexual isolation (Kurokawa, 1956b, 1959, 1960, 1963; Lee, 1970, 1974; Grossfield, 1977). However, few data exist on their ecology (Takada, 1954; Kurokawa, 1967a; Toda, 1973a, b, 1974). This paper reports some ecological characteristics of three species, *D. auraria*, *D. biauraria*, and *D. triauraria*, on the basis of study in an area where these three species are coexisting.

Before going further, I wish to express my sincere thanks to Dr. Eizi Momma for pertinent guidance in the course of the present study, and also to Messrs M.J. Toda, M.T. Kimura, K. Beppu, and H. Watabe for their advice. Cordial thanks are also due to Dr. Kenkichi Ishigaki, Tomakomai Experiment Forest, Hokkaido University, who gave me many facilities for the present study.

Study Area and Collecting Methods

The survey was made at Tomakomai Experiment Forest of Hokkaido University, about 50 km south of Sapporo City. In total eight traps were set linearly at intervals of about 25 m along a line running through three different vegetations: Trap A, B at secondary broad-leaved forest (main plant species: *Quercus crispula*, *Fraxinus mandshurica*, *Pterocarya rhoifolia*, *Acer mono*, *Syringa reticulata*, *Pachysandra terminalis*, and *Dryopteris crassirhizoma*), D, E at grassland

(*Trifolium repens*, and *Taraxacum officinale*), G, H at reforestation area of conifers (*Pinus strobus*, *P. koraiensis*, *Maianthemum dilatatum*, and *Schizandra chinensis*), and C, F, at forest edges (Fig. 1).

All traps but D, which was set on the ground, were suspended from branches or trunks of trees, kept at the height of about 1 m above the ground. The

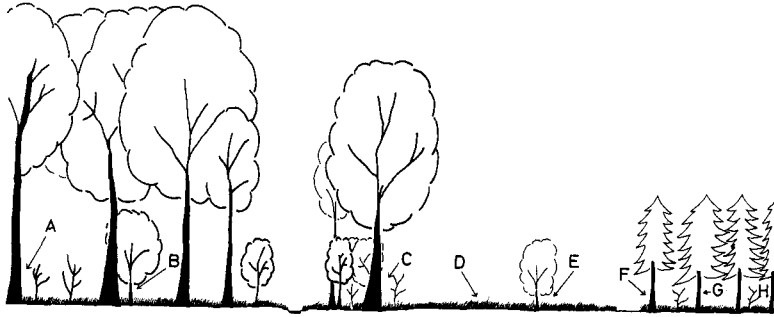


Fig. 1. Schema of trap spot environments.

collections were made for two days in the middle of each month from April to October, 1977. Flies were collected at 1 hr. interval from sunrise to sunset. The trap used was a dry-milk tin (13 cm in diameter, 19 cm in depth), baited with banana fermented by Baker's yeast. The attracted flies were captured by covering the trap quickly with a polyethylene sack and were transferred into a glass vial containing 70% alcohol.

Recording of air temperature, relative humidity, and light intensity was carried out at two sites, B and D, at interval of 1 hr..

Results and Discussion

In total, 2,143 individuals consisting of 29 drosophilid species, which correspond to about 43% of a total of 67 species so far recorded in Tomakomai Experiment Forest (Minami *et al.*, 1979), were obtained. The numerical data of the total sample are presented in Table 1. *D. biawraria* was top ranked (occupying 58.66% of a total of 2,143 individuals), *D. auraria* the third (5.18%), and *D. triawraria* the fifth (4.29%). The combined percentage of these three species was 68.1% of the total sample. Other relatively frequent species were *D. suzukii*, *D. bifasciata*, *D. brachynephros*, *D. histrio*, *D. testacea*, and *D. lacertosa*. The ecological structure of the whole drosophilid assemblage in Tomakomai Experiment Forest was described in another paper (Minami *et al.*, 1979).

Microdistribution

In Fig. 2 the microdistributions of the three species are shown with absolute

numbers of specimens collected at each trap. *D. auraria* and *D. triauraria* were strongly restricted to grassland, while *D. biauraria* was rather eurytopic with two peaks at forest edges.

In Fig. 3 the relationship of habitat separations among these three species is shown with the measure of geometric distance,

$$D_{ij} = \sum_h (p_{ih} - p_{jh})^2,$$

Table 1. Total sample of drosophilid flies collected at four different vegetations.

Vegetation	Secondary forest	Forest edges	Grassland	Conifer reforestation area	Total	%
<i>D. biauraria</i>	345	499	200	213	1,257	58.66
<i>D. suzukii</i>	21	50	17	56	144	6.72
<i>D. auraria</i>	3	16	86	6	111	5.18
<i>D. bifasciata</i>	40	39	17	12	108	5.04
<i>D. triauraria</i>	2	9	77	4	92	4.29
<i>D. brachynephros</i>	40	18	1	27	86	4.01
<i>D. histrio</i>	61	13	—	10	84	3.92
<i>D. testacea</i>	27	27	4	11	69	3.22
<i>D. lacertosa</i>	26	30	5	—	61	2.85
<i>D. unispina</i>	11	9	1	4	25	1.17
<i>D. confusa</i>	13	6	—	2	21	0.98
<i>D. nigromaculata</i>	5	6	1	5	17	0.79
<i>Amiota conifera takadai</i>	10	5	—	2	17	0.79
<i>D. coracina</i>	1	4	3	—	8	0.37
<i>D. moriwakii</i>	1	—	2	4	7	0.32
<i>D. pseudosordidula</i>	5	2	—	—	7	0.32
<i>D. kanekoi</i>	—	1	5	—	6	0.28
<i>D. immigrans</i>	2	3	—	—	5	0.23
<i>Scaptomyza pallida</i>	—	1	3	—	4	0.19
<i>D. melanogaster</i>	—	—	2	1	3	0.14
<i>Leucophenga</i>						
<i>quinquemaculipennis</i>	1	1	—	—	2	0.09
<i>Amiota okadai</i>	1	—	1	—	2	0.09
<i>D. imaii</i>	1	—	—	—	1	0.05
<i>D. sordidula</i>	1	—	—	—	1	0.05
<i>D. ezoana</i>	—	1	—	—	1	0.05
<i>D. alboralis</i>	—	—	—	1	1	0.05
<i>D. nokogiri</i>	1	—	—	—	1	0.05
<i>D. busckii</i>	—	—	—	1	1	0.05
<i>Scaptomyza consimilis</i>	—	—	—	1	1	0.05
Total	618	740	425	360	2,143	

where p_{ij} is the frequency of species i in environment h (Levins, 1968). *D. biauraria* is far distant from the other two species, *D. auraria* and *D. triauraria*.

The general pattern observed in the present study coincides with the results obtained by Toda (1974), Kimura and Toda (1976), and Minami *et al.* (1979). However, Kurokawa (1967a) observed in Honshû that *D. triauraria* exhibited an

intermediate distribution pattern between *D. auraria* and *D. biauraria*. Further, Kurokawa (1967a) and Minami *et al.* (1979) observed that *D. auraria* occurred in human habitations, which were not involved within the trapping area in the present study. Considering also such information in other cases, habitat preferences of the these species can be summarized as follows: *D. triauraria* stenotopic, restricted to grassland at least in Hokkaido, *D. auraria* inhabiting not only grassland but also human habitations, and *D. biauraria* eurytopic, preferring forests

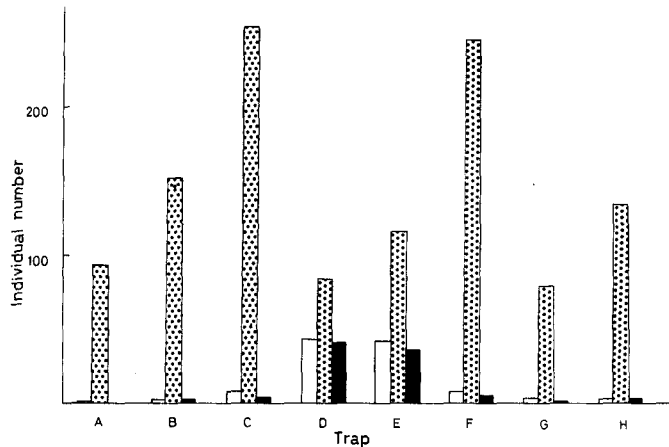


Fig. 2. Distributions of the three species of the *auraria* species complex among eight traps arranged linearly. White: *D. auraria*, dotted: *D. biauraria*, and black: *D. triauraria*.

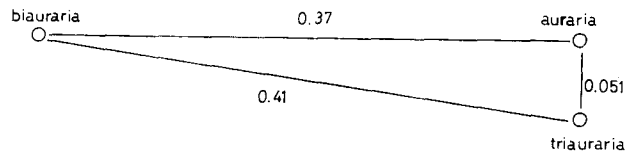


Fig. 3. Geometric distance among the three species of the *auraria* species complex.

but frequently visiting or partially inhabiting grassland. Thus, there are habitat segregations to some extent among the three species, but microenvironmental barriers are not clear.

Daily activity

Fig 4a shows daily activities of *D. auraria* and *D. triauraria* observed at grassland on July 20, and those of *D. biauraria* on the same day are separately given for grassland and forest in Fig. 4b. Changes of light intensity, temperature, and

relative humidity are shown in Table 2 for the open area and forest. At grassland three species showed similar morning activities with a conspicuous peak observed synchronously at 4:00 a.m. On the other hand, in forests the morning activity of

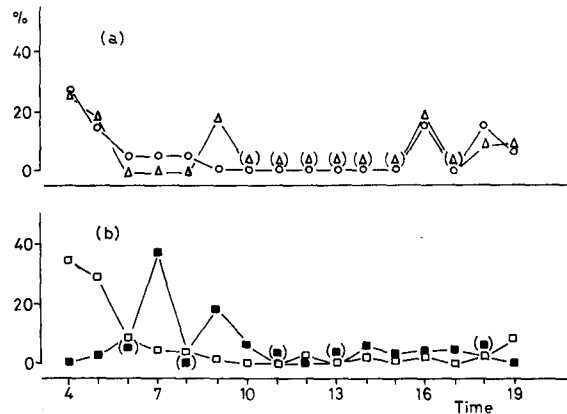


Fig. 4. Daily activities of *Drosophila auraria* (circle), *D. triauraria* (triangle), and *D. biauraria* (square) at grassland (open) and forest (closed) observed on July 20, 1977.

Table 2. Climatic conditions on July 20, 1977.

Time	Secondary forests			Grasslands		
	Temperature (°C)	Humidity (%)	Light intensity (k lux)	Temperature (°C)	Humidity (%)	Light intensity (k lux)
4:00	17.0	97.0	—	18.0	94.5	0.35
5:00	17.5	94.0	0.07	18.5	94.5	2.40
6:00	17.0	94.0	0.13	18.5	97.0	5.00
7:00	17.0	97.0	0.35	18.0	94.5	9.50
8:00	17.0	94.0	0.50	19.0	94.5	11.00
9:00	17.0	94.0	1.00	20.5	94.5	22.50
10:00	17.5	88.5	1.15	19.5	94.5	16.00
11:00	19.5	84.0	2.65	25.0	80.3	25.00
12:00	19.5	79.0	4.20	27.0	69.3	22.00
13:00	19.0	84.0	2.10	22.0	87.0	22.50
14:00	18.5	79.0	1.25	20.5	89.5	17.00
15:00	17.0	88.5	0.60	18.5	91.5	10.50
16:00	17.0	88.5	0.47	18.0	91.5	8.00
17:00	16.5	88.5	0.21	17.5	97.0	4.35
18:00	16.5	88.5	0.08	17.0	94.5	3.18
19:00	16.0	94.0	0.02	16.0	97.0	0.15

D. biauraria was quite different from them, showing a peak 3 hrs. later at 7:00 a.m. . *D. auraria* and *D. triauraria* showed a second peak in evening. The bimodal activity of *D. auraria* has been reported by Kaneko and Shima (1962) and Toda

(1973b). But the evening peak was not clear in *D. biauraria*, though Wakahama *et al.* (1963) and Kaneko (1968) have observed the bimodality also in this species. Similar activity patterns of these species were observed in August, too. But unfortunately, seasonal changes of daily activity patterns were not able to be analyzed due to the small samples in May, June, and September.

Dobzhansky and Epling (1944) and Pavan *et al.* (1950) assumed that light intensity is a direct environmental cue which controls the activity of flies, although the diurnal behavior is an adaptation to humidity and the temperature conditions in the environment. In the present case, the activity of *D. biauraria* must be, if not completely, controlled by light. This species showed different diurnal behavior between grassland and forests in early morning 4:00 to 7:00. During this period, temperature and humidity did not changed radically, but light intensity increased rapidly. Further, the light intensity was surprisingly the same (0.35 k lux) at the time when the morning peak was observed at each vegetation.

Seasonal activity and breeding habits

As shown in Table 3 three species showed unimodal (summer) type activity in the classification by Toda (1973a). Watabe (pers. commun.) observed *D. auraria* produced four, but partially three, generations per year in Sapporo. Their precise bionomics, based on the analysis of female reproductive conditions, will be reported elsewhere.

Table 3. Seasonal activities of *Drosophila auraria*, *D. biauraria* and *D. triauraria*.

	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.
<i>D. auraria</i>	—	1	13	41	50	6	—
<i>D. biauraria</i>	—	1	114	433	503	206	—
<i>D. triauraria</i>	—	—	—	20	71	1	—

From fruits of *Daphne kamtschatica* collected in August 4, 1978 and those of *Rubus phoenicolasius* collected in September 22, 1977, several specimens of *D. biauraria* emerged. These three species are considered as fruit breeders (Kimura *et al.*, 1977). It seems to be considered that these three species breed on fruits of *Morus bombycis*, *Rubus phoenicolasius*, *Prunus donarium*, or *Daphne kamtschatica* in Tomakomai Experiment Forest.

Concluding Remarks

The *auraria* species complex consists of four species. It is considered that *D. quadraria* is the most ancestral form, and each of the other three is independently derived from this species (Lee, 1974). The closeness of the relationships between

the three species, *D. auraria*, *D. bauraria* and *D. triauraria*, was studied by the hybridization test; three species hybridize and produce fertile F_1 and F_2 offspring (Kurokawa, 1960). He examined the sexual isolation among three species at 25°C, and calculated the joint isolation index of 0.845 between *D. auraria* and *D. bauraria*, 0.787 between *D. auraria* and *D. triauraria*, and 0.702 between *D. bauraria* and *D. triauraria*. Lee (1970) also observed 0.845, 0.426, and 0.600 for the above series at 25°C respectively, but he found that these isolation was weakened or broken down at 19°C (0.788, 0.135, and 0.417 respectively.) In consideration with temperature of the natural environment in Hokkaido, the results at 19°C seem to be ecologically meaningful. Kurokawa (1967a) suggested a possibility of their ecological isolation. However, these three species have chances to meet each other in grassland because of the frequent invasion of *D. bauraria* from forest at least in Tomakomai Experiment Forest. Thus the premating isolation mechanisms like sexual isolation and ecological isolation are not fully established among these species. Moreover, as these species produce fertile F_2 hybrid, postmating isolation mechanisms (Mayr, 1963; Dobzhansky, 1970) can not apply in the present case.

Recently it was stressed that the diapause characteristics play a dominant role in isolation between the closely related species (Tauber and Tauber, 1978; Masaki, 1978). In *D. auraria* and *D. bauraria* diapause characteristics are different in qualitative and quantitative aspects (Minami *et al.*, unpubl.). These facts may suggest that the physiological characteristics in relation to hibernation or phenological strategies occupy an important place in the isolation mechanisms of the members of the *auraria* species complex.

Summary

The habitat preferences, daily activities, and seasonal activities of the members of the *auraria* species complex of the genus *Drosophila* were studied in Tomakomai Experiment Forest. *D. auraria* and *D. triauraria* were collected almost in grassland, but *D. bauraria* was more frequent in forest. Daily activities and seasonal activities were not radically different among these three species. The isolation mechanisms between these species were discussed in relation to their crossability and ecology.

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