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POPULATION DYNAMICS OF HOUSEFLIES, *MUSCA DOMESTICA*, ON EXPERIMENTALLY ACCUMULATED REFUSE

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INTRODUCTION

The knowledge on population dynamics of a certain pest species is necessary to establish integrated control measures against the species. The seasonal prevalence of houseflies, *Musca domestica*, has been reported by many investigators. Basing on the results of biweekly surveys with the fly grid method, LABRECQUE et al. (1972) reported that the rates of population growth from generation to generation were less than 6-fold, and WEIDHAAS and LABRECQUE (1970) pointed out the difference between the highest and the lowest densities was only 3 fold. On the other hand, definite peaks of the density were observed with the fly grid (SUENAGA, 1958), the sticky fly ribbon (OGATA, 1960; KURASHIGE, 1968) or the sticky flypaper (SALIBA et al., 1977). These discrepant results and the long intervals of censuses suggest that the rates of population growth estimated by LABRECQUE et al. (1972) are not precise enough to predict the daily changes in the density of field populations.

The mark-release-recapture method is one of the most reliable measures to examine the dispersal and population density of animals. On the houseflies, many studies on dispersal have been carried out by using this method (e.g. OGATA et al., 1960; GREENBERG and BORNSTEIN, 1964; ODA, 1966), but few have been performed on estimation of population number (WADA and ODA, 1963; LURE and ZAKHAROVA, 1974; POSPISIL and BOGAC, 1982). Thus the information obtained so far is not sufficient to draw any definite conclusion on the population dynamics of houseflies.

This paper describes the population changes in houseflies, examined with the flypaper method and the mark-release-recapture technique, on artificial habitats of refuse. The surveys with the flypaper and the release of marked houseflies were performed 11–13 times and 6 times, respectively, for about one month after refuse disposition.

METHODS

Study site

The study was carried out at a corner of the soil-covered area in Hokko Waste Disposal Site which was located in an artificial island in the North Osaka Port, Japan.

This area was 500–700 m far from any operational waste disposal areas, and it received no operational disposition during the experimental periods. To set experimental stations, the refuse collected from Osaka City was filled in areas approximately 10 m × 10 m by about one meter thickness, and no more refuse was added to these stations in the course of experiments.

Experiment I

One station was prepared on 15 May 1979 with a mixture of the garbage and the approximately equal amount of the ash from incinerated refuse. Thus the absolute amount and the relative content of the garbage per unit area of this station was about a half of those in experiments II and III. The density of adult houseflies was examined 12 times for subsequent 35 days by using sticky flypaper (15 cm × 20 cm). In each census, six sheets of flypaper were placed on the surface of the refuse for 30 min, and the relative density was estimated as the average number of flies caught per one flypaper.

Experiment II

Only the garbage without ash was filled on 19 September 1979 into three stations which were 70 m far from each other. The relative density was examined 13 times for subsequent 33 days with the same method as experiment I.

Experiment III

On 5 June 1980, the garbage was disposed into two stations A (135 m^2) and B (80 m^2) which were 70 m far from each other. For subsequent 32 days, the laboratory-reared houseflies marked with paints of different colours were released six times at each station at approximately one week interval, and the recapture was performed 15 times at both stations by using sticky traps. The flies released were 2–3 day old individuals of the first or the second generation of a population collected from the Hokko Site. The paint was attached to the dorsal thorax of each fly one day before releasing. The data obtained were analyzed by the method of Jolly (1965) and Seber (1973). The relative density was also examined 11 times with the same method as experiments I and II.

Results

Figure 1 shows the prevalence of the adult density in experiment I. The density increased slowly towards the 9th day after refuse disposition, and then remained at somewhat stable level till the 29th day. The flies disappeared on the 35th day. The maximum density was 34 individuals per flypaper.

Figure 2 illustrates the results in experiment II. The density reached 104–146 individuals per flypaper on the 13th or 14th day, which was much higher than the maximum density in experiment I. On the days of peak densities, many larvae and pupae were observed in the upper layer of garbage by about 30 cm depth. Then the density

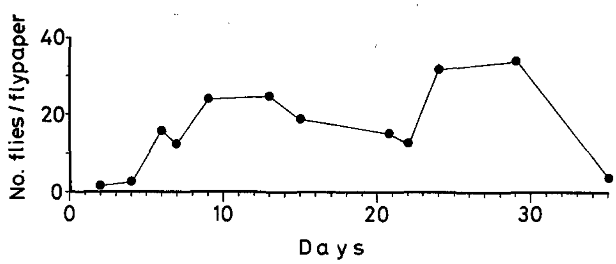

Fig. 1. Prevalence in relative density of houseflies on a mixture of garbage and ash from incinerated refuse.

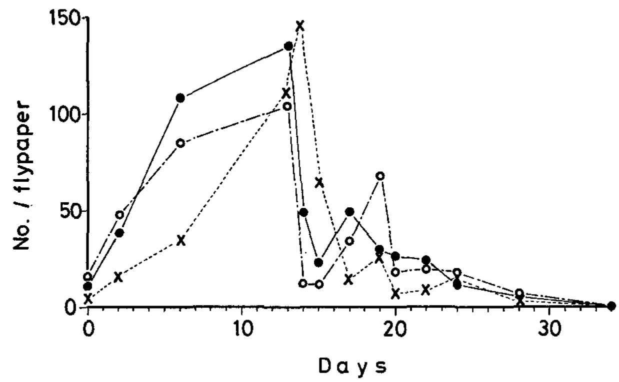

Fig. 2. Prevalence in relative densities of three housefly populations on garbages.

decreased rapidly during subsequent two days. The second peaks of the density were detected on the 17th or 19th day, and thereafter the density decreased slowly to zero on the 34th day.

Table 1 shows the estimates of population parameters calculated by the JOLLY-SEBER's method in experiment III. $\hat{T}_i$ is the total recruitment of flies between i-1 and ith census (INOUE, unpublished). The estimates of total recruitment during the experimental period ($\Sigma\hat{T}_i$) were as follows; females: 48683 (361/m^2) and males: 129887 (962/m^2) in station A; females: 40269 (503/m^2) and males: 78355 (979/m^2) in station B.

Figure 3 shows the prevalence of the relative and the absolute densities on the two stations in experiment III. The relative density fluctuated in a similar manner on both stations, and the changes of the absolute density related to those of the relative density. When compared to the results in experiment II, the initial density was lower and the decrease of the density was somewhat less drastic in this experiment.

Figure 4 indicates that the apparent maximum survival rate was observed between the 6th and 13th day, and that the rate was lower in later periods. This reduction in the rate was more remarkable in males than in females. Figure 5 illustrates the relation between the daily survival rate and the absolute population density. The survival rate of males was 0.600–0.632 when the density was more than 100/m^2, while the rate was

Table 1. Population parameters estimated by mark-release-recapture technique (JOLLY-SEBER's method).

Station	Sex	Date of examination i		Days after disposition of garbage	Population size $N_i \pm \sqrt{V(N_i)}$	Survival rate per day $\Phi_i \pm \sqrt{V(\Phi_i)}$	Number recruited T_i
A	Male	June	6	1	(1200±408)	0.724±0.045	—
			11	6	2786±1264	0.870±0.048	5138
			18	13	39637±20939	0.601±0.082	60385
			25	20	15244±17097	0.600±0.080	51744
		July	2	27	3558±4229	—	12620
			10	35	(37±22)	—	—
	Female	June	6	1	(500±80)	0.727±0.054	—
			11	6	2786±1547	0.810±0.064	5372
			18	13	13338±9038	0.679±0.099	24267
			25	20	4980±6021	0.622±0.089	11915
		July	2	27	2243±2662	—	7129
			10	35	(41±42)	—	—
B	Male	June	6	1	(660±162)	0.631±0.041	—
			11	6	1167±462	0.742±0.046	2814
			18	13	15297±8783	0.617±0.078	36139
			25	20	8142±7782	0.632±0.043	26669
		July	2	27	4131±2283	—	12733
			10	35	(0)	—	—
	Female	June	6	1	(460±212)	0.684±0.065	—
			11	6	1440±887	0.741±0.063	3061
			18	13	8320±6264	0.668±0.094	19476
			25	20	2406±2673	0.640±0.064	5735
		July	2	27	3774±3618	—	11997
			10	35	(0)	—	—

* Numbers in parentheses are estimates by PETERSEN-LINCOLN's method.

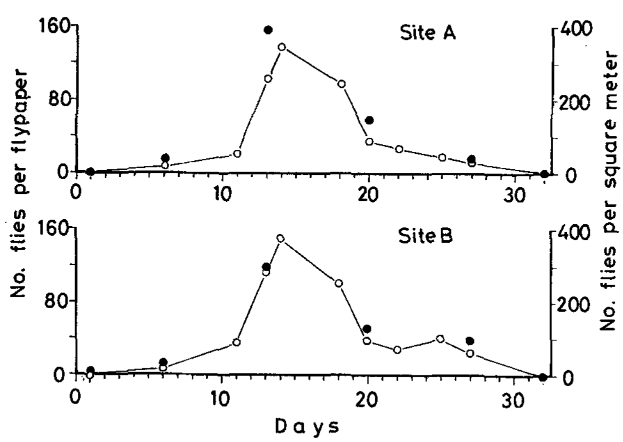

Fig. 3. Prevalence in relative density (-○-) and absolute one (●) on stations A and B.

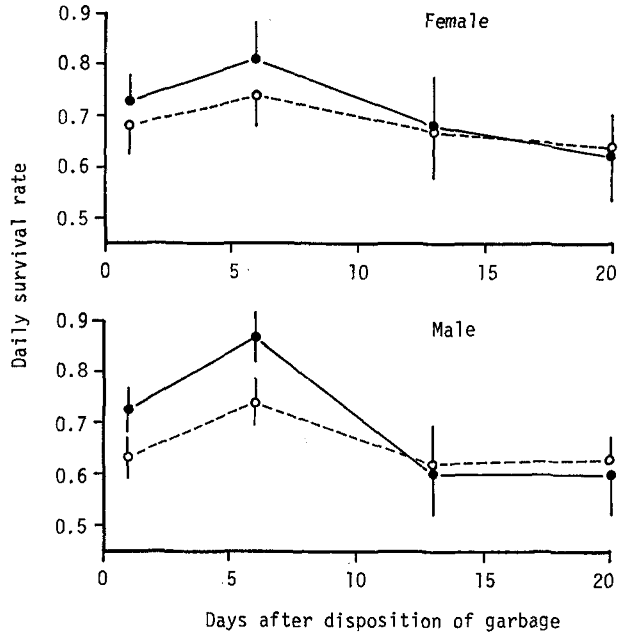

Fig. 4. Relation between days after garbage disposition and apparent survival rates on stations A (-●-) and B (-○-).

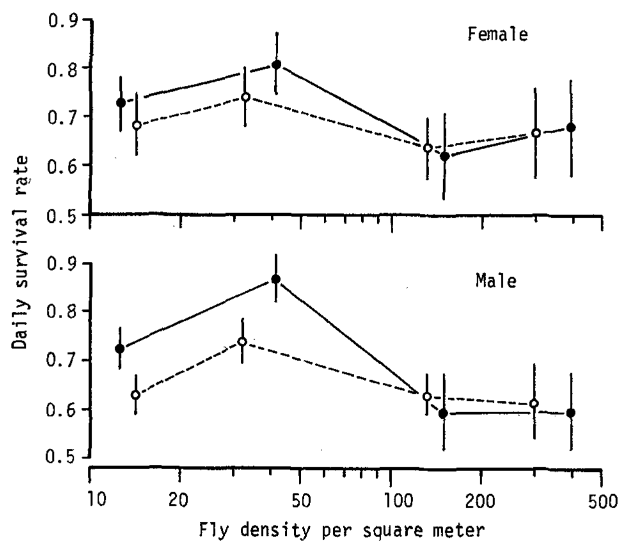

Fig. 5. Relation between fly densities and apparent survival rates on stations A (-●-) and B (-○-).

0.631–0.870 when the density was less than $50/m^2$. Similarly the survival rate of females was a little lower when the density was over $100/m^2$.

The results of the recapture of marked flies are summarized in Table 2. The recapture rate was calculated as $\frac{m_{AA}+m_{AB}+m_{BA}+m_{BB}}{M_A+M_B}$, and the migration rate bet-

Table 2. Recapture of marked houseflies released from stations A and B.

Recapture series		1	2	3	4	5	6
Days afterdisposition		2-6	7-13	14-20	21-27	28-33	34, 35
No. of sampling		3	2	3	2	3	2
Male	M_A	333	630	871	743	676	770
	m_{AA}	41	85	32	31	35	0
	m_{AB}	5	3	8	7	8	0
	M_B	633	666	801	717	754	694
	m_{BB}	135	88	51	27	98	0
	m_{BA}	8	29	14	9	37	0
	$(m_{AA}+m_{AB}+m_{BB}+m_{BA})/(M_A+M_B)$	0.20	0.16	0.06	0.05	0.12	0
	$(m_{AB}+m_{BA})/(m_{AA}+m_{AB}+m_{BB}+m_{BA})$	0.07	0.16	0.21	0.22	0.25	—
Female	M_A	398	721	825	1052	809	790
	m_{AA}	16	64	18	18	17	0
	m_{AB}	2	7	8	5	3	0
	M_B	377	711	830	970	730	719
	m_{BB}	25	51	28	18	36	0
	m_{BA}	3	23	7	5	6	0
	$(m_{AA}+m_{AB}+m_{BB}+m_{BA})/(M_A+M_B)$	0.06	0.10	0.04	0.02	0.04	0
	$(m_{AB}+m_{BA})/(m_{AA}+m_{AB}+m_{BB}+m_{BA})$	0.11	0.21	0.25	0.22	0.15	—

* See text for explanation of each symbol.

Table 3. Population growth in houseflies in earlier periods of three field experiments.

Experiment	Pattern	Rate of increase per day	No. of censuses
I	Exponential	1.47	5
II	Logistic	2.70	4
	Logistic	2.82	4
	Exponential	1.25	5
III	Exponential	1.38	5
	Exponential	1.47	5

ween station A and B was estimated as $\frac{m_{AB}+m_{BA}}{m_{AA}+m_{AB}+m_{BA}+m_{BB}}$, where M_A and M_B were the estimates of total marked flies existing at the beginning of each recapture series at stations A and B, respectively. m_{AA} and m_{AB} were the numbers of marked flies recaptured at station A and B, respectively, after they were released at station A. m_{BB} and m_{BA} were defined in the same manner as m_{AA} and m_{AB}. The recapture rates of males were high from the 2nd to 13th day, and it became lower from the 14th to 27th day. During the 28th–33th day, the rates recovered to somewhat high level. The recapture rates of females showed a similar fluctuation as those of males. The migration rates of males between two stations became higher in the cource of time, but those of females were low during the 2nd–6th day and during the 28th–33th day.

Table 3 summarizes the growth pattern of the housefly populations based on the population trends in the earlier periods of three field experiments. Exponential growth and logistic one were observed in four and two populations, respectively. The daily increase rates were estimated to be 1.25–1.47 in the exponential growth. The rates in the logistic growth were estimated to be 2.70–2.82 by MORISITA (1965)'s method.

DISCUSSION

The fly density was much lower on the mixture of garbage and ash from incinerated refuse, than on garbage alone. This result seemed to be related to the fact that, in experiment I, the absolute amount and the relative content of the garbage in the station were reduced to about a half by mixing the garbage with the ash which contained little substance favorable for fly breeding (IMAI, unpublished). While, the actual habitats of houseflies are restricted to the upper layer of manure because the fermentation heat inhibits the immatures to develop in the inner part (WEST, 1951). A similar phenomenon was also observed in the refuse disposed at the Hokko Site. Therefore the fly breeding capacity of refuse per unit area might be affected by the relative content of the garbage in the upper layer rather than by the absolute amount of the garbage disposed per unit area. Thus it is considered that the fly breeding capacity in waste disposal sites can be deteriorated by mixing garbage with other inorganic wastes, even though the total amount of garbage is not reduced.

Without such deterioration, the accumulated garbage had capacity to produce maximum 1300–1500 houseflies per square meter within one month after being disposed, because most of the recruitment as shown in Table 1 was possibly due to the emergence of new adults.

The rates of apparent population growth were estimated less than 3-fold per day. Theoretically these values were not very precise because each of them was estimated by only four or five data. However the rates are considered to be sufficiently applicable to predict the maximum density in near future at actual landfill sites.

It is generally considered that the conditions of garbage are varied in the time cource by dryness, biodegradation, feeding by inhabiting animals, etc. Unfavorable food conditions will be caused in the time cource after garbage disposition, and such conditions may induce the emigration of adult flies for searching more favorable habitats. In all the three experiments, the fly density decreased to 0 about one month after refuse disposition. Low apparent survival rates and high emigration rates were also observed at that time in experiment III. These results suggest that the emigration occurred in response to the change of habitat conditions from favorable to unfavorable.

In the middle of the experimental periods, between the 13th and 20th day, the fly density decreased rapidly just after it reached more than 100 individuals per flypaper in experiments II and III, and low values of the apparent survival rates and high emigration rates were simultaneously observed. However, such drastic decrease in the density was not detected in experiment I where the density remained less than 34 individuals per flypaper. As the decrease in the apparent survival rates is generally due to mortality and emigration, I examine the contribution of these factors to the above fact.

During the periods of the drastic population decrease, I did not experience any serious changes in weather conditions such as temperature, rainfall, wind, etc. which were probably density-independent mortality factors. Moreover, it seems unlikely that a certain density independent factor acts at almost the same period (the 13th–18th day after garbage disposition) in two different experiments which were carried out in different seasons and different years. Thus I cannot show any positive evidence for the contribution of density independent high mortality. Moreover, I could not detect any drastic increase in the density of natural enemies of adult flies. Furthermore, if natural enemies had reduced the fly density during the two days, the recovery of the density as shown in Fig. 2 had not occurred in subsequent periods when the enemies might maintain their high densities. Thus it is unlikely that the rapid decrease in the fly density was mainly due to high mortality.

There are three kinds of emigration as probable causes; the age-specific emigration, the emigration in response to unfavorable habitat conditions, and density-dependent emigration.

If age-specific emigration occurred, the populations with the same age constitution should show the same manner of emigration. However the mark-release-recapture study revealed that several groups of the marked flies which were released on different days showed different rates of emigration, although their age constitution was almost the same. Thus the age-specific emigration is negligible.

The emigration in response to unfavorable habitats is already pointed out as the most probable cause for the disappearance of flies about one month after refuse disposition. This kind of emigration may somewhat contribute to the phenomenon in the middle of experimental period. However, if the decrease in the density had been mainly due to the response to unfavorable habitats, the recovery of the density had not been attained in subsequent periods because the habitat conditions will become more unfavorable in the time cource. Therefore this kind of emigration is not considered as the main contributing factor.

In contrast to the above four factors, the density-dependent emigration is the most probable cause for the rapid decrease in the fly density. All the results obtained in the period of the rapid decrease can be explained by this type of emigration. The fact that low survival rates were detected in the periods of high densities also suggests the possibility of some density-dependent process. WADA and ODA (1963) pointed out the possibility of the existence of the threshold density for mass migration of the houseflies basing on their observation and the results on *Drosophila melanogaster* by SAKAI et al. (1958). The pattern of the prevalence in the relative density in Fig. 2 suggests that the threshold density for mass migration of the Hokko housefly population was 100–150 individuals per flypaper on the garbage under favorable conditions.

Thus it may be concluded that the houseflies adapt themselves to patchy and unstable habitats consisting of temporarily available substance like garbage, through their high reproductive rate and migration in response to overcrowding and unfavorable changes of food conditions.

Summary

The population dynamics of the housefly, *Musca domestica*, on patchy and unstable habitats consisting of refuse was investigated at a waste disposal site by using sticky flypaper and mark-release-recapture technique (JOLLY-SEBER's method). The newly disposed garbage was favorable for breeding of the flies for about one month after being disposed, while a mixture of garbage and ash from incinerated refuse was less favorable. On the garbage under favorable conditions, the rates of population increase was 1.25–2.82 per day, and approximately 1300–1500 flies were produced per square meter within the available period of one month. The rapid decrease in the fly density was observed just after the appearance of high density peaks. The mark-release-recapture study suggested that this rapid decrease would be mainly due to the density-dependent emigration of adult flies from the patchy habitats. The emigration was also activated when the time after garbage disposition became long.

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実験的に堆積されたごみにおけるイエバエの個体群動態

今　井　長兵衛

実験的に堆積されたごみの上に生息するイエバエ成虫の個体群動態を粘着トラップと標識再捕法を用いて調べた。新鮮な生ごみは堆積後約1カ月間好適な発生源となり，その間に1 m² あたり1300～1500個体の成虫が羽化し，みかけの増殖率は日あたり1.25～2.82と推定された。しかし，このような爆発的な増加は生ごみに等量の焼却灰を混合した場合には観察されなかった。ハエトリガミ30あたり捕集数が100～150に達した直後に密度の急激な減少が観察され，標識再捕の結果から密度依存的移出がおこったものと推測された。