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ABSTRACT—In order to clarify the fecundity and the number of eggs actually deposited of the yellow swallowtail butterflies, *Papilio xuthus* and *P machaon*, females were captured in the wild and dissected Forewing length was not correlated with age in any of the two species Multiple matings suggested by spermatophore counts were found for *P xuthus* but not for *P machaon* in both spring and summer generations Eggs in the ovaries were classified into three categories according to their degree of maturation The fecundity, which was a total number of eggs, was 500–600 eggs irrespective of generation and species The small body size of individuals belonging to the spring generation seemed to affect not the fecundity but the number and the size of mature eggs in the abdomen Oviposition in the spring generation of *P xuthus* took place mainly at noon but that of the summer generation in the morning Considering the oviposition period of both species, the number of eggs deposited in each generation in each species was about 300 eggs, which was about a half of the fecundity

INTRODUCTION

One of the yellow swallowtail butterflies, *Papilio xuthus*, has been most intensively studied for its population ecology among Japanese swallowtail butterflies [1–2] Its oviposition activity in the summer generation has been studied by Yamanaka *et al* [3] Few studies on the number of eggs deposited by the female during her reproductive life, however, have yet been published This may be due to her longer longevity, and partly due to the difficulty in obtaining eggs under laboratory conditions In addition, no reports have been published on the population ecology in spring generation because of their low abundance compared to summer generation of *P xuthus*

Beside the work on *P xuthus*, few studies on the population ecology of *P machaon hippocrates* have been reported in Japan, though many of such studies have been published elsewhere [4]

The present study deals with the number of eggs in the ovaries of *P xuthus* and *P machaon* counted by dissection and estimates the fecundity and the number of eggs actually deposited by each female during her life span

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MATERIALS AND METHODS

The data in this study were obtained from *P xuthus* and *P machaon*, mainly in Kanagawa, Mie and Kochi Prefectures, warm-temperate zone in Japan Both species have more than four generations per year and overwinter in the pupal stage [5] The imago of each species in spring has characteristic wings different from that in the other seasons Since the adults found in summer are not clearly identified its generation belonged in both species [2], females collected in this study were divided into two, spring (April to early June) and summer (late June to October) generations Their habitats consist of margins of forests and open lands with nectar plants and with host plants of larvae The latter is Rutaceae (mainly *Zanthoxylum ailanthoides*) for *P xuthus* and Umbelliferae for *P machaon* Females were collected on various occasions such as feeding, roosting, coupling and ovipositing, from April to October during

1981 to 1984 When the females were caught, their abdomens were immediately fixed into 50% ethyl alcohol and their wing conditions and sizes were recorded The ages were classified into five degrees from tearing conditions of the wings, as suggested by Nozato *et al* [6]

All females were dissected to determine how many times they had mated, as indicated by the number of spermatophores in their bursa copulatrix, and to determine the number of eggs remaining in the abdomen

Eggs in the ovaries were classified into three categories mature, submature and immature eggs The mature eggs, which were determined by the criterion of Hidaka and Aida [7], were mainly found in the oviducts They were large enough to be ready for oviposition and colored in yellow The submature eggs were mainly found in vitellarium of the ovaries They were small and colored lighter than the mature ones The immature eggs which include oocytes filled the terminal filament, germanium and a part of vitellarium of the ovarioles The eggs in ovarioles decreased in size toward the tip of the terminal filament filled with oocytes Since both immature eggs and oocytes contain no yolk, they look like white

The number of mature and submature eggs were directly counted For the immature eggs, their number was assessed for one ovariole on each side, and the total number was estimated by multiplying by the number of ovaries

RESULTS

In the course of the dissection, we observed a phenomenon which was common to both species As shown in Figure 1, the newly emerged or fresh female (age 0) had the most abundant fat body which filled in the cavity of the abdomen, while the oldest female (age IV) had the smallest one Contrary to this, the volume of the air sac increased in size with ageing of the females

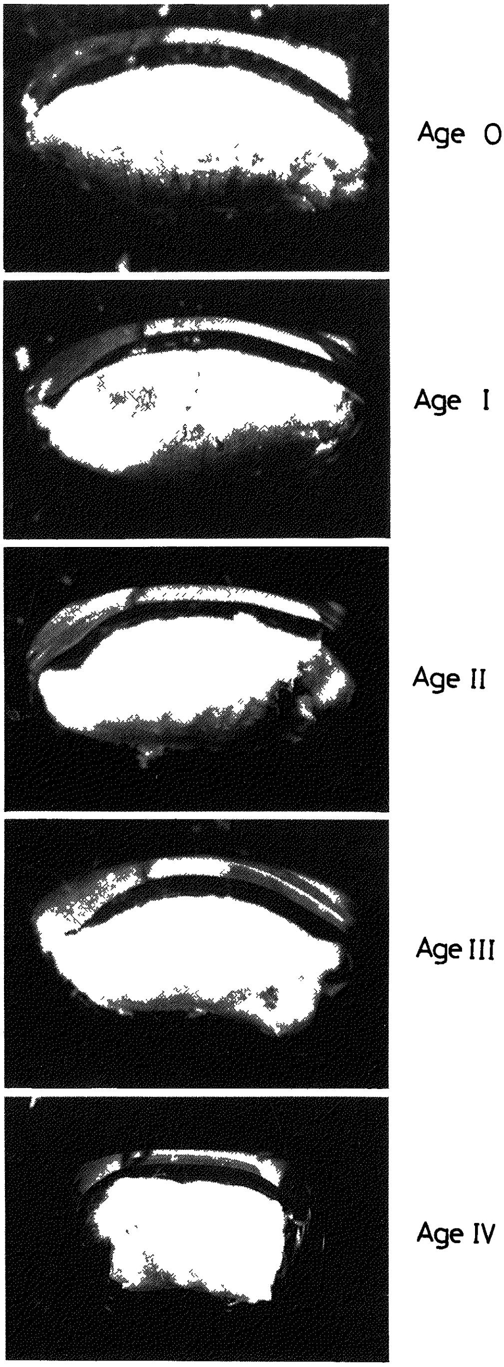

FIG 1 Photographs of the abdomens of *P xuthus*, removing off the cuticle The age class was classified mainly by the wing conditions, i e 0 newly emerged females with no visible damage and lustrous scales, I fine tears with less lustrous scales, II tears with frayed scales, III notched tears with frayed scales, IV broken or extensive tears with frayed scales The abundant fat body without air sac inhibits to observe the eggs in the age 0, while some large mature eggs can be seen in the age IV due to less fat body with a large air sac

It is generally known that the forewing length is a good index of the size of a butterfly The mean lengths derived from different study areas were not significantly different from each other All females from different areas were then pooled 64 and 205 in *P xuthus*, and 22 and 44 in *P machaon*, in spring and summer generations, respectively

The size of butterflies in the spring generation was significantly smaller (P<0 005) than that of summer one (Fig 2) The wing length was not correlated with their longevities in any of the species This suggests that there is no apparent relationship between the body size and the longevity in each generation, as in the case of the black swallowtail butterflies (Watanabe *et al* , unpublished)

Figure 3 shows that many females of *P xuthus* mated more than once Some females of the oldest age (IV) mated maximum five times in both spring and summer generations The females of age 0 have single spermatophore in most but 0 or 2 in a few Therefore, females of *P xuthus* mated soon after emergence and seemed not to mate again during the age 0 The number of times that the females had mated increased significantly with their age (P<0 05) On the other hand, most females of *P machaon* seemed to mate once

The diameter of mature eggs in the oviducts is shown in Figure 4 It remained constant irrespec-

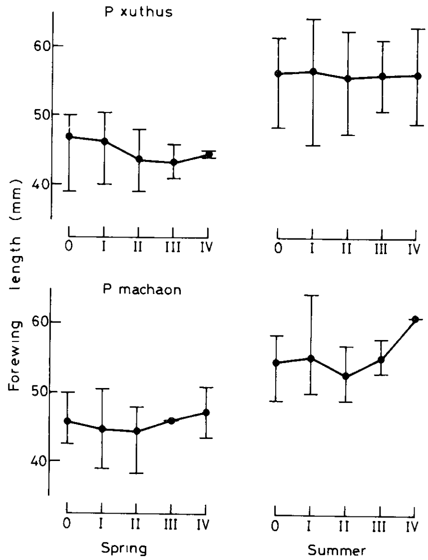

FIG 2 Mean forewing length of females in *P xuthus* and *P machaon* of respective ages in both spring and summer generations with the maximum and minimum length Total number of females examined was 64 and 198 in *P xuthus* and 21 and 42 in *P machaon*, in spring and summer generation, respectively

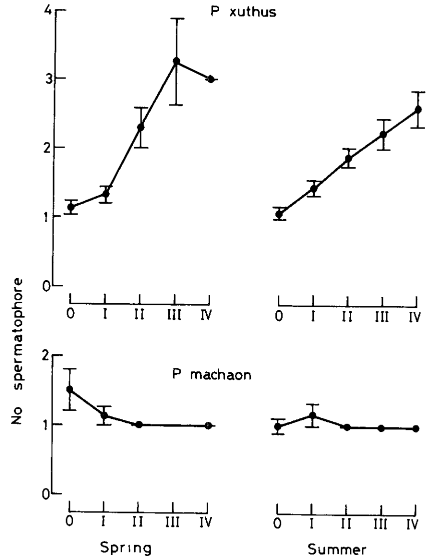

FIG 3 Mean number of spermatophores in *P xuthus* and *P machaon* of respective ages in both spring and summer generations (±S E) Total number of females examined was 46 and 143 in *P xuthus* and 16 and 34 in *P machaon* in spring and summer generation, respectively

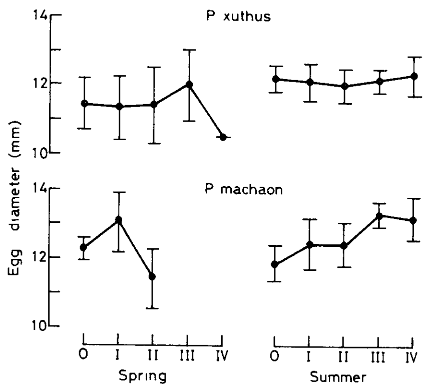

FIG 4 Mean egg diameter in *P xuthus* and *P machaon* of respective ages in both spring and summer generations (±S D) Total number of eggs examined was 44 and 480 in *P xuthus* and 30 and 110 in *P machaon* in spring and summer generation, respectively

tive of age in *P xuthus* but increased with age in the summer generation of *P machaon* (P<0 01) Mean mature egg size in the spring generation of *P xuthus* was slightly smaller than that in the summer generation (P<0 01), while such a difference was not found in *P machaon*

The change in the number of eggs found in the abdomen of both species are shown in Table 1 The numbers of submature, immature and total eggs decreased with the age except the summer generation of *P machaon* However, the number of mature eggs seemed not to decrease with the age in all the generations

In *P xuthus*, the numbers of mature eggs in age 0 to III of the spring generation were smaller than those of summer generation (P<0 01) However, the numbers of submature and immature eggs in age 0 to II were not significantly different between both generation, while those in age III and IV in the spring generation were smaller than those in the summer generation (P<0 05) The fecundities, which were obtained from the total number of eggs, of both spring and summer generations in *P xuthus* were at 570–600, suggesting that the small body of spring generation may affect not the fecundity but the number and the mature egg size in the ovaries

In *P machaon*, the number of mature eggs of spring generation was smaller than that of summer generation in age 0 (0 05<P<0 1) and age I (P<0 005) Although the numbers of submature eggs were significantly different between both generations in ages 0, I and IV, those of immature egg in both were not significantly different each other with probabilities less than 0 05 Thus, the fecundities of *P machaon* in both generations seemed to

TABLE 1 Number of eggs in *P xuthus* and *P machaon* in relation to the age (Mean±S E)

⟨Spring generation⟩

	Age	0	I	II	III	IV
P xuthus	No females examined	17	19	15	8	5
	No mature eggs	17 8± 4 9	25 6± 4 8	23 9± 3 5	17 8± 3 3	16 0± 9 3
	No submature eggs	54 9± 6 2	55 5± 6 8	31 4± 7 6	14 1± 1 8	8 6± 1 9
	No immature eggs	525 6±49 7	443 8±41 2	280 3± 38 2	186 0± 41 6	128 0± 19 4
	No total eggs	602 9±51 0	524 8±40 7	335 6± 44 8	217 9± 41 6	152 6± 19 9
P machaon	No females examined	6	8	5	1	2
	No mature eggs	43 5±11 9	47 4± 6 8	43 2± 6 6	(26)	13 5± 6 5
	No submature eggs	38 0± 5 9	22 4± 6 4	32 6± 6 0	(19)	8 5± 2 5
	No immature eggs	394 7±31 5	407 5±51 0	428 8±110 0	(136)	244 0±148 0
	No total eggs	476 2±19 7	477 3±52 2	504.6±119 2	(181)	266 0±157 0

⟨Summer generation⟩

	Age	0	I	II	III	IV
P xuthus	No females examined	37	64	50	30	24
	No mature eggs	46 8± 4 6	58 3± 4 0	47 4± 3 4	36 9± 3 2	24 7± 3 7
	No submature eggs	48 4± 3 3	48 0± 3 6	38 9± 3 0	28 0± 2 4	17 2± 1 6
	No immature eggs	475 0±21 4	460 2±19 7	367 7± 21 8	359 8± 35 2	274 5± 26 4
	No total eggs	569 7±21 4	567 2±17 2	453 9± 21 8	426 0± 35 9	316 5± 28 9
P machaon	No females examined	15	18	6	3	2
	No mature eggs	75 9± 9 2	88 7± 6 6	40 2± 9 9	66 0± 28 5	72 5± 23 5
	No submature eggs	48 7± 3 8	57 3± 8 5	36 2± 3 9	42 3± 12 3	48 0± 2 0
	No immature eggs	500 8±31 2	480 1±32 5	362 0± 43 3	391 7±130 1	538 0±234 0
	No total eggs	626 2±30 7	626 1±32 6	438 3± 42 2	500 0±140 4	658 5±208 5

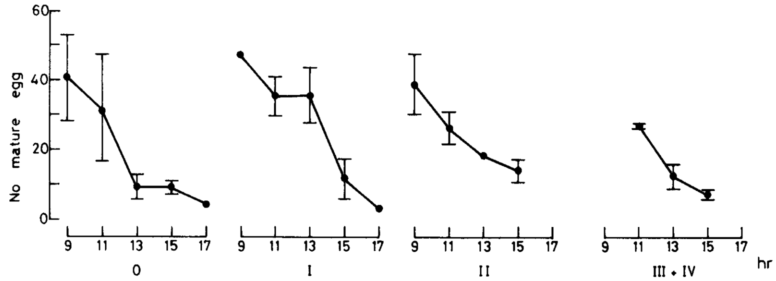

FIG 5 Change in mean number of mature eggs in a day of *P xuthus* of respective ages in spring generation (±S E) The time means a median of 2 hr, e g 9 means from 8 00 to 10 00, 11 does from 10 00 to 12 00 and so on The number of females examined in each age was 17, 19, 15 and 12 in age 0, I, II and III+IV, respectively

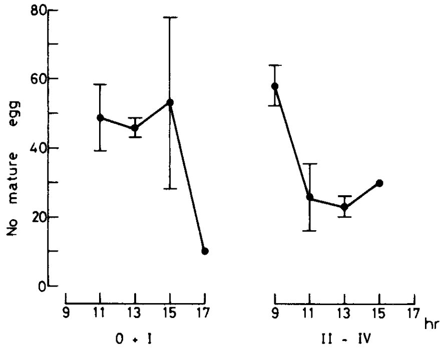

FIG 6 Change in mean number of mature eggs in a day of *P machaon* of respective ages in spring generation (±S E) The number of females examined in each age was 14 and 8 in age 0–I and II–IV, respectively

be similar at 500–600, suggesting that the small body of spring generation may also affect not the fecundity but the number of mature eggs in the ovaries

Females of the oldest age (IV) in both species had a considerable number of eggs, which mainly consisted of submature and immature eggs Since such female was not considered to deposit all of her eggs remained, the female seemed to have more eggs than actually deposited

In order to estimate the number of eggs deposited in a day, we took no account of the number of eggs developed from submature to mature in a daytime When the females were classified in each two-hour intervals according to the time of capture, the time of decrease in mature egg number may be the oviposition time

In *P xuthus* of the spring generation, as shown in Figure 5, the number of mature eggs decreased toward evening in all age classes Steep declination was found in 11–13, 13–15, 9–11 and 11–13 in age 0, I, II and III+IV, respectively Thus, the females seemed to deposit eggs mainly at noon The mean number of eggs deposited in a day was estimated by the difference of the egg number between morning and evening 30, 25, 20 and 20 by a female of age 0, I, II and III+IV, respectively

Because of the relatively small number of the females collected in the spring generation of *P machaon*, Figure 6 shows the change in numbers of mature eggs in two pooled ages in a day The oviposition time in younger females was not detected, while that in the older ones were considered to deposit about 30 eggs in the morning

In the summer generation of *P xuthus*, the younger females had clear tendency that they deposited eggs mainly in the morning (Fig 7) However, the older females had obscure one, and they seemed to deposit fewer eggs than the younger females. It might be estimated that the females of *P xuthus* in summer generation deposited 25, 25, 25, 15 and 20, in age 0, I, II, III and IV, respectively, in a day

In the summer generation of *P machaon*, the obscure oviposition time was also found as in the case of the spring generation (Fig 8) The mean number of eggs deposited in a day was 25 and 30 in younger and older females, respectively

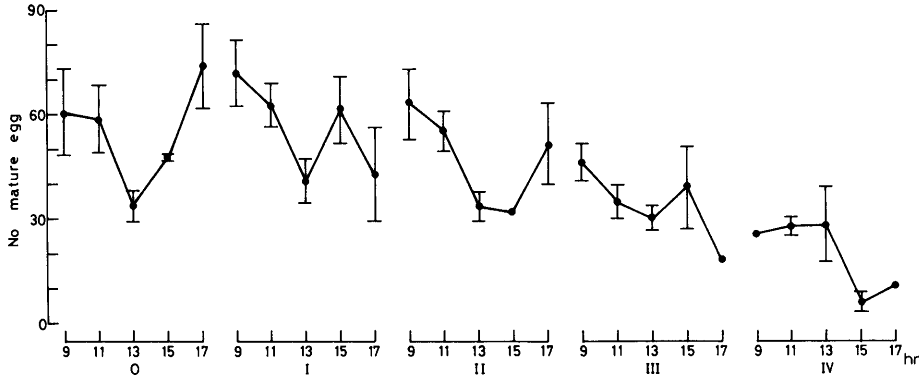

FIG 7 Change in mean number of mature eggs in a day of *P xuthus* of respective ages in summer generation (±S E) The number of females examined in each age was 32, 63, 48, 30 and 24 in age 0, I, II, III and IV, respectively

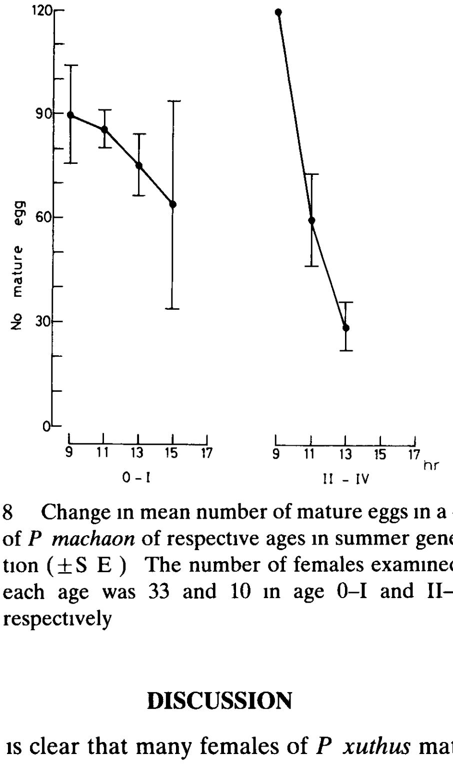

FIG 8 Change in mean number of mature eggs in a day of *P machaon* of respective ages in summer generation (±S E) The number of females examined in each age was 33 and 10 in age 0–I and II–IV, respectively

DISCUSSION

It is clear that many females of *P xuthus* mated more than once with age, while that of *P machaon* did once A number of recent studies show the multiple matings in many butterfly species such as the checkerspot butterfly, *Euphydryas editha* [8] The role of multiple matings in butterfly species has been discussed on sperm competition [9–10] and on energy for females [11] In general, a single insemination may be usually sufficient to fertilize all of eggs Thus, the difference in the number of matings in *P xuthus* and *P machaon* suggests that each has its own characteristic reproductive strategy Further analysis may be necessary for comparison between these two species

As shown in the Result, there is no difference in survival rates with relation to body sizes between two species The female size seemed not also to influence the number of eggs in the ovaries The same has been observed in the black swallowtail butterflies (Watanabe *et al* , unpublished)

Number of deposited eggs decreased with age in *P xuthus* The estimated number of eggs deposited in a day by a female was larger than that observed in a laboratory condition [1] However, Yamanaka *et al* [3] proposed about 40 eggs actually deposited by a female of *P xuthus* in a day, but they did not show any age structure of the females sampled

It has been still unknown when the number of mature eggs recovered after oviposition In *P xuthus* of summer generation, the younger females clearly showed oviposition time in the morning to noon, while the older ones did not show a particular oviposition pattern Figure 7 suggests that the recovery of the mature egg number had began from late-afternoon or evening Although the egg maturation during evening and night was not clarified, the diurnal oviposition activity pattern disappeared with age In the spring generation, on the other hand, the oviposition time shifted to noon instead of morning Lower temperature in the spring than the summer may affect her diurnal oviposition activity This tendency may probably be similar to that in *P machaon*

Few comparative studies between spring and summer generations of the swallowtail butterflies were reported Badawi [12] observed longer and shorter longevities of *P demoleus* in winter and summer generations, respectively In this study, the fecundity in each species of spring generations was similar with that in summer generations, though their eggs were relatively smaller than those of summer generations Wiklund and Persson [13] clarified that smaller eggs were not in any way inferior to larger eggs within a same butterfly species, *Pararge aegeria*

It is still unknown whether the longevities of females are similar with those of the conspecific males According to Abu Yaman [14], adult females of *P demodocus* survived for 7–12 days and males for 5–10 days The males of the Japanese black swallowtail butterflies also survived for 13–18 days [6] Thus, it is likely to assume that the longevities of the adult swallowtail butterflies were about two weeks If the longevity coincides with the duration of oviposition, *P xuthus* would deposit 345 and 330 eggs in spring and summer generations and *P machaon* did 450 and 420 eggs, respectively, by multiplying the estimated egg number deposited a day by the duration of each age (about 3 days in each) However, there must be some bad weather days during their oviposition periods, such as rainy, windy and cool cloudy, all of which inhibit females from oviposition Then, about 300–400 eggs were estimated to be actually deposited by the spring and summer generations of both species This was considered to be a so-called realized fecundity Thus, such value was a half of the fecundity in *P xuthus* and *P machaon*

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