

## LIFE TABLES FOR WORKER HONEYBEES<sup>1, 2, 3</sup>

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### INTRODUCTION

Since the pioneer work by DEEVEY (1947), the importance of life tables for ecological studies has gradually been recognized, either in relation to population studies of particular species (for instance, MORRIS and MILLER, 1954), or for the comparison of various species with different modes of life (ITÔ, 1959, '62). Techniques are being devised and improved for the species the accurate survival data of which are difficult to obtain directly (SOUTHWOOD, 1966). Under such circumstance, it is remarkable that no standard life table for the European honeybee, *Apis mellifera* LINNÉ, has hitherto been published, in spite of the enormous amount of information so far accumulated for this single species, and the availability of quite accurate survival data thanks to its peculiar mode of life. Following the previous paper on brood survival (FUKUDA and SAKAGAMI, 1968), the present paper gives life tables for worker honeybees throughout their all developmental stages.

### MATERIALS AND METHODS

For some technical difficulties in tracing the life history of particular individuals since hatching out to adult stage, survival data for brood and adults, obtained respectively from different sources, were used in combination. The average longevity of adult workers varies seasonally. Under temperate climate it is relatively long in spring, shorter in summer, gradually longer in postsummer and conspicuously prolonged in wintering bees (FREE and SPENCER-BOOTH, 1959; FUKUDA and SEKIGUCHI, 1966). Considering this trend, three life tables representing different seasons were prepared. The sources of data are as follows:

*Immature stages* (FUKUDA and SAKAGAMI, 1968):  $N_1$  (observed June 10~July 12, 1967),  $N_3$  (obs. September 10~October 2, 1967).

*Adults* (SEKIGUCHI and SAKAGAMI, 1966): S6 (obs. June 3~July 18, 1960), S7 (obs. June 17~August 1, 1959), S9-S5a (obs. September 6~October 24 as S9, and

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after wintering, April 13~June 1, 1961 as S 5a)

Detailed descriptions of these cohorts are given in the papers cited above. The combination of brood and adult survival data were made in the following ways:  $N_1+S 6$ ,  $N_1+S 7$ ,  $N_3+S 9-S 5a$ . These composite cohorts are henceforth called respectively *June bees*, *July bees* and *Wintering bees*. The seasonal trend of average longevity obviously varies under different climates. Main climatic conditions in Sapporo, where survival data were obtained, are summarized as follows (from measurements by Hokkaido Regional Meteorological Observatory. Averages of records taken 1899-1950):

Month	Mean air temperature(°C)	Mean rainfall (mm)	Mean depth of snow (cm)	Month	Mean air temperature(°C)	Mean rainfall (mm)	Mean depth of snow (cm)
I	- 6.1	92.2	47.4	VII	19.4	93.3	--
II	- 5.2	71.8	66.9	VIII	21.2	104.6	--
III	- 1.5	63.7	50.9	IX	16.5	134.4	--
IV	5.3	57.5	3.7	X	9.9	113.4	0.0
V	10.6	61.2	0.0	XI	3.3	110.8	2.2
VI	15.1	61.9	--	XII	-3.2	100.5	20.0

From the apicultural point of view, the climate is characterized by, 1) Long winter with severe cold and deep snow cover, being very unfavorable for wintering bee colonies, nearly the half of which succumb annually and 2) Relatively short but quite favorable postspring and summer, with mild thermal conditions and continuous supply of flowers without summer dearth. The peak of the blooming of White Clover, the most important food source, is June to early July, corresponding to the observation period of *June bees*.

In preparing life tables, immature stages were divided into three stages: eggs (3 days), unsealed brood (=feeding larvae, 5 days following the previous result by FUKUDA and SAKAGAMI, 1968, instead of 6 days as usually adopted), sealed brood (=postfeeding larvae and pupae, 12 days). The figures for these stages are given in column  $l_x$  in tables. Age interval of five days were adopted for adults and  $l_x$  of each interval was obtained from linear interpolation of original measurements, except for wintering period, which was not subdivided.

## RESULTS

Tables 1-3 present life tables for *June*, *July* and *Wintering bees* for their entire life span, with the columns as follows: 1)  $x$ , Age interval; 2)  $x'$ , Age interval given by percentage deviation from average longevity; 3)  $l_x$ , Number alive at beginning of respective age interval out of 1,000 born; 4)  $d_x$ , Number dying during respective age interval out of 1,000 born; 5)  $q_x$ , Number dying per 1,000 alive at beginning of respective age interval.

Tables 4-6 are life tables for the same cohorts given in Tables 1-3, but dealing

Table 1. Life table for *June bees* (average longevity 40.175 days).  
 Explanations for tables 1-7 in text.

Stage	$x$ (days)	$x'$	$l_x$	$d_x$	$q_x$
Egg	0~3	-100	1,000	42	42
Unsealed brood	3~8	-92	958	137	143
Sealed brood	8~20	-80	821	10	12
Adult	20~25	-50	811	15	18
	25~30	-38	796	16	20
	30~35	-26	780	14	18
	35~40	-14	766	27	35
	40~45	+ 1	739	149	202
	45~50	+11	590	221	374
	50~55	+24	369	256	694
	55~60	+36	113	76	672
	60~65	+49	37	32	865
	65~70	+61	5	5	1,000
	70~75	+71	0		

Table 2. Life table for *July bees* (average longevity 43.359 days).

Stage	$x$ (days)	$x'$	$l_x$	$d_x$	$q_x$	
Egg	0~3	-100	1,000	42	42	
Unsealed brood	3~8	-93	958	137	143	
Sealed brood	8~20	-81	821	10	12	
Adult	20~25	-54	811	33	41	
	25~30	-43	778	30	38	
	30~35	-31	748	8	11	
	35~40	-19	740	46	62	
	40~45	- 8	694	49	71	
	45~50	+ 4	645	53	82	
	50~55	+16	592	142	240	
	55~60	+27	450	317	704	
	60~65	+39	133	97	729	
	65~70	+51	36	20	556	
	70~75	+62	16	16	1,000	
		75~80	+74	0		

with adults alone. Column  $q_x$  was omitted because it did not essentially differ from that given in Tables 1-3, except for minor deviations produced in the course of calculation. Instead, three additional columns were prepared: 1)  $e_x$ , Mean life remaining to those attaining respective age interval. MORRIS and MILLER suspected the significance of this column for insect population studies. However, as far as honeybees are concerned, this column seems to be useful for further analysis. 2)  $f_x$ ,

Table 3. Life table for *wintering bees* (average longevity 136.763 days).  
 PR : rewintering; W : Wintering; Ps : Postwintering.

Stage	$x$ (days)	$x'$	$l_x$	$d_x$	$q_x$
Egg	0~3	-100	1,000	109	109
Unsealed brood	3~8	-98	891	99	111
Sealed brood	8~20	-92	792	20	25
Adult, PR	20~25	-85	772	41	53
	25~30	-81	731	41	56
	30~35	-78	690	8	12
	35~40	-74	682	21	31
	40~45	-71	661	5	8
	45~50	-67	656	10	15
	50~55	-64	646	8	12
	55~60	-60	638	80	125
	60~65	-56	558	16	29
65~70	-53	542	21	38	
Adult, W	70~240	-49	521	126	242
Adult, PS	240~245	+70	395	3	8
	245~250	+78	392	46	117
	250~255	+82	346	90	260
	255~260	+86	256	41	160
	260~265	+90	215	23	107
	265~270	+94	192	64	333
	270~275	+97	128	56	438
	275~280	+101	72	34	472
	280~285	+104	38	28	737
285~290	+108	10	10	1,000	
290~295	+112	0			

Number of potential foragers<sup>1</sup> during respective age interval out of 1,000 born. 3)  $g_x$ , Number of potential foragers per 1,000 alive at beginning of respective age interval. The last two columns are particular to honeybees. Their utility for apicultural researches is obvious. Probably a similar column could be prepared for insects with age-conditioned differentiation of activities during adult stage.

Finally Table 7 deals with postwintering adults (=S5a), prepared as in Table 4-6 (Age interval 220-225 days in Table 6 corresponds to 0-5 days in Table 7), with omission of  $e_x$ , which is given in Table 6. This table could be directly applied to postwintering bees in general. Wintering colonies contain groups born at various periods in autumn. But caused by special physiological conditions during winter, all postwintering workers are seemingly physiologically same-aged, as shown by the convergence of their survivorship curves (NICKEL und ARMBRUSTER, 1937; FUKUDA

<sup>1</sup> Bees which have already participated in foraging activities at least once, irrespective of they made foraging further on each day or not (c. f. SEKIGUCHI and SAKAGAMI, 1966).

Table 4. Life table for *June adult bees* (average longevity 28.345 days).

$x$ (days)	$l_x$	$d_x$	$e_x$	$f_x$	$g_x$
0~5	1,000	17	28.3		
5~10	983	23	23.8	0	0
10~15	960	17	19.3	122	127
15~20	943	33	14.6	154	269
20~25	910	183	10.0	614	674
25~30	727	272	6.9	647	890
30~35	455	316	4.6	422	927
35~40	139	93	4.4	139	1,000
40~45	46	40	3.6	43	935
45~50	6	6	2.5	6	1,000
50~55	0				

Table 5. Life table for *July adult bees* (average longevity 32.424 days).

$x$ (days)	$l_x$	$d_x$	$e_x$	$f_x$	$g_x$
0~5	1,000	38	32.3		
5~10	962	40	28.4	0	0
10~15	922	10	24.6	7	7
15~20	912	67	19.8	69	76
20~25	855	60	15.9	139	162
25~30	795	70	12.0	337	424
30~35	725	174	7.9	439	606
35~40	551	387	4.6	446	811
40~45	164	120	4.5	164	1,000
45~50	44	24	4.8	44	1,000
50~55	20	20	2.5	20	1,000
55~60	0				

and SEKIGUCHI, 1966).

Fig. 1, A, B, C, present survivorship curves,  $l_x$ , for *June*, *July* and *Wintering bees*, together with fluctuations of  $d_x$ ,  $q_x$  and, recalculated from Tables 1-3  $f_x$ . Survivorship curves for *June* and *July bees* are closely similar for each other, with two periods of high mortality, the first at egg and feeding larval stages, and the second at the late adult stage, when most bees became potential foragers. In general both curves are characterized by a distinctly convex shape, which is exceptional in insects. There are two minor differences between *June* and *July bees*: 1) Mortality at early adult stage is slightly *July* > *June*. 2) Mortality at late adult stage is appreciably *June* > *July*. The first difference is, for the time being, difficult to interpret, while the second one corresponds to the higher number of potential foragers at the period of main honey flow. Certainly intense foraging activities evoke a higher mortality, either by accelerated consumptions or by frequent outdoor hazards.

As seen in Fig. 1, C, *Wintering bees* are characterized by a remarkable prolongation

Table 6. Life table for *wintering adult bees* (average longevity 154.095 days).

	$x$ (days)	$l_x$	$d_x$	$e_x$	$f_x$	$g_x$
PR	0~5	1,000	53	154.2		
	5~10	947	53	157.7	0	0
	10~15	894	10	160.8	23	26
	15~20	884	27	158.6	109	129
	20~25	857	7	158.6	162	189
	25~30	850	16	154.8	214	252
	30~35	834	10	152.8	214	257
	35~40	824	103	149.6	214	260
	40~45	721	23	165.6	214	297
	45~50	698	26	166.0	204	292
W	50~220	672	162	167.3	211	314
PS	220~225	510	4	23.3	53	104
	225~230	506	60	18.5	96	196
	230~235	446	116	15.7	132	296
	235~240	330	53	15.3	139	421
	240~245	277	30	12.8	125	451
	245~250	247	82	9.0	119	482
	250~255	165	73	7.2	119	721
	255~260	92	43	5.9	63	684
	260~265	49	36	3.9	49	1,000
	265~270	13	13	3.0	13	1,000
	270~275	0				

Table 7. Life table for *Postwintering adult bees* (average longevity 23.431 days).

	$x$ (days)	$l_x$	$d_x$	$f_x$
	0~5	1,000	6	105
	5~10	994	117	188
	10~15	877	227	260
	15~20	650	104	273
	20~25	546	58	247
	25~30	488	163	234
	30~35	325	143	234
	35~40	182	84	124
	40~45	98	72	98
	45~50	26	26	26
	50~55	0		

of life span. A closer inspection of the curve shows a few more peculiarities: 1) Slight increase of egg mortality, probably due to autumn contraction of bee cluster (c. f. FUKUDA and SAKAGAMI, 1968). 2) Mild and linear decrease before wintering, approximately with the same rate. A rapid drop on 55th day was probably caused by autumn feeding. 3) Relatively mild decrease during wintering (naturally in

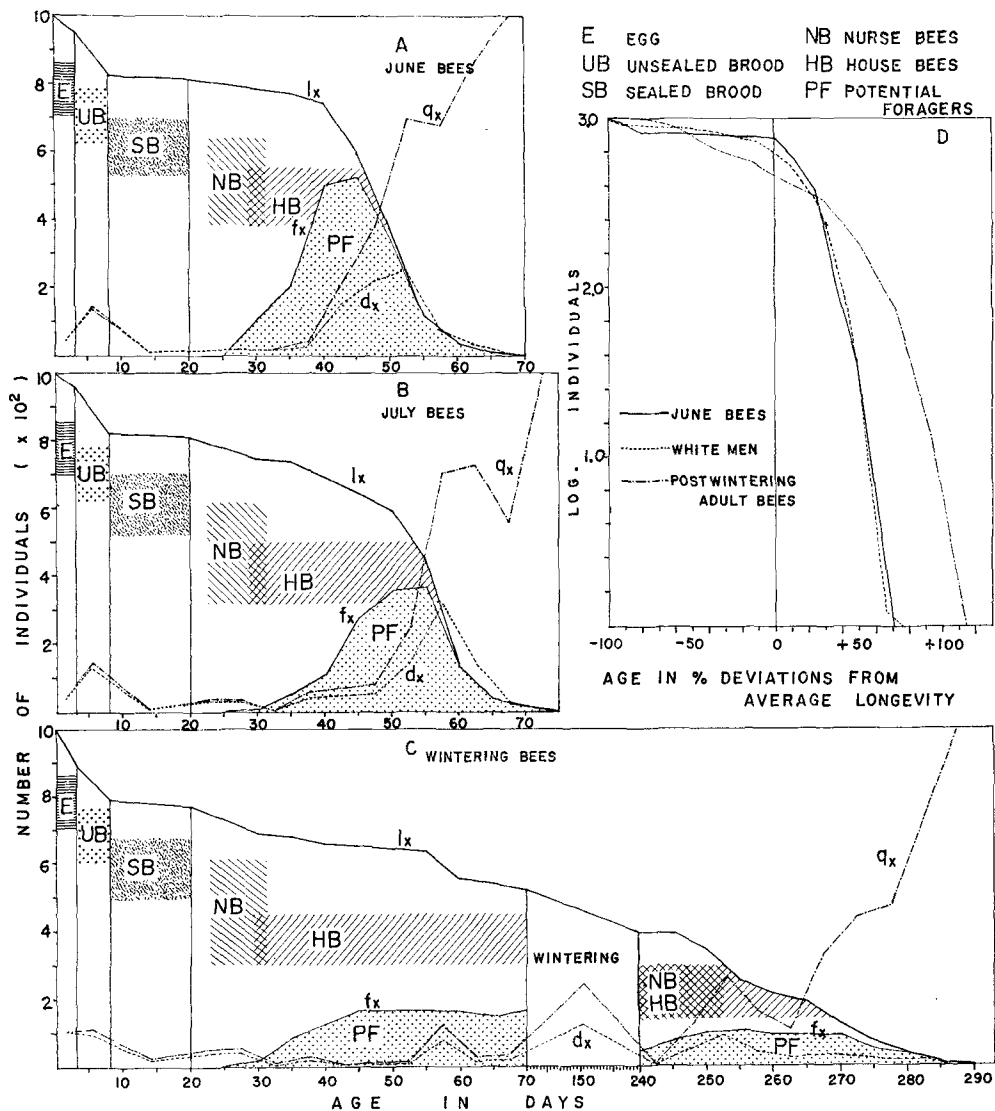


Fig.1. A-C. Survivorship curves ( $l_x$ ) for *June*, *July* and *Wintering* bees, together with curves of  $d_x$ ,  $q_x$  and  $f_x$ . Successive stages are shown by different hatchings. D. Survivorship curves for *June* bees, white men, and postwintering adult bees. Age shown in % deviations from average longevity.

successfully wintered colonies such as in the case cited). 4) Mild and linear decrease after wintering.

In all *June*, *July* and *Wintering* bees, the maximum longevity is about two times as long as the mean longevity.

The comparison of survivorship curves for *June* bees (Table 1), postwintering adults (Table 7) and white men (HILL, 1936, after PEARL, 1940, calculated from Table 22 in ALLEE *et al.*, 1949, p.296), is presented in Fig.1, D, in which age

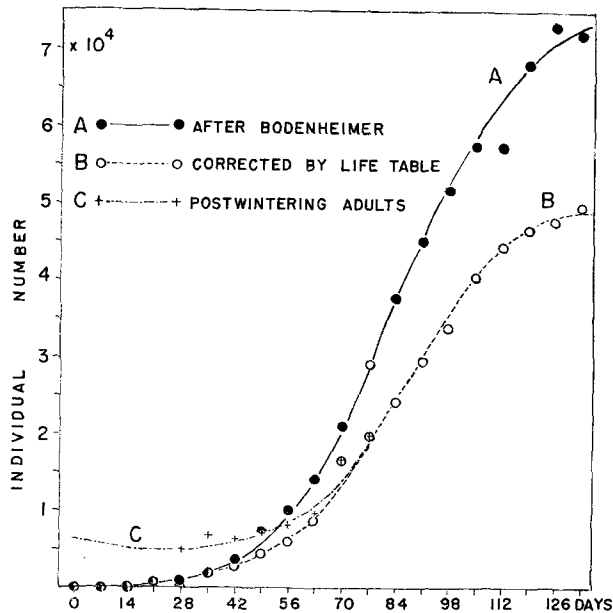


Fig.2. Population growth of a Cyprian bee colony measured by NOLAN (1928).  
 A. Curve prepared by using BODENHEIMER'S method. B. Curve corrected by Life table for *July bees*. C. Curve showing gradual decrease of postwintering adult bees.

expressed by deviations from average longevity is plotted against logarithm of individual number. At a glance in the figure, the similarity between men and honeybees is conspicuous. In *June bees* the drop at initial growing period (eggs and feeding larvae) is relatively large and the drop at later adult stage is contrasting to the very low mortality until earlier one third of adult stage. But as far as the two curves are compared, the resemblance indubitably exceeds the difference.

The curve for postwintering adults, added to because of its deviation from *June* and *July bees*, shows drops relatively more conspicuously at the earlier half while less at the later half. These characteristics are probably explained respectively by: 1) Presence of a relatively large number of potential foragers since liberation from winter quarters and 2) Lower foraging activities in early spring.

In order to show the importance of life table data for population studies of honeybee colonies, the population growth curve for a Cyprian bee colony, prepared by BODENHEIMER (1937) based upon the data by NOLAN (1928), was corrected by using our life table data and original and corrected curves presented in Fig.2. Several remarks concerning the preparation of these curves were commented on.

1) BODENHEIMER'S procedure of estimating total size of population from that of sealed brood contains several defects. But the errors caused by these defects become greater after the population reaches the peak of its increase. Therefore, his method was followed without modification.

2) BODENHEIMER recognized the following life schedule in worker honeybees:



Egg 3 days, unsealed brood 6 days, sealed brood 12 days, nurse bees 10 days, house bees 10 days, field bees 22 days. He assumed the absence of deaths until the end of field bee stage, that is, in his premise, all bees die synchronously on the 63rd days after hatching out. In our procedure, the life table for *July bees* (Table 2) was chosen for correction, because it was closest to the survivorship curve for spring bees (SEKIGUCHI and SAKAGAMI, 1966), that is, the bees born in the season chosen by BODENHEIMER in preparing his curve.

3) Our uncorrected curve was prepared from Table 6 in BODENHEIMER, but data for drones were discarded, because we have still no life table for drone bees. Therefore, our curve runs lower than the original figure by BODENHEIMER (Fig. 4A, cited in ALLEE *et al.*, 1949, ODUM, 1959). For instance, the total population on June 26 is, after BODENHEIMER, 75,492, consisted of 71,939 workers and 3,553 drones. The drones are excluded in our corrected curve.

4) BODENHEIMER's curve is likely to give a false impression of the population growth starting from a small number of individuals, as in experimental populations of stored food pests started by a few pairs of adults. Virtually, at the appearance of the first batch of eggs, there must remain a considerable number of postwintering adult workers. Based upon the description by NOLAN, the presence of 5,000 adult workers on March 13, one month before the first oviposition, was assumed, and the gradual decrease of these adults was calculated by using Table 7. The result is added to in Fig. 2 as curve C. Obviously postwintering bees are consisted of various age groups. But as already mentioned, postwintering bees are regarded physiologically same-aged so that the curve C may approximately reflect the population trend soon after wintering.

Fig. 2 illustrates how the life table data are important for estimation of population size. Parallel to the increase of individuals, the difference between uncorrected and corrected curves gradually becomes greater, on June 20, reaching 25,000 or about one third of the size attained by the uncorrected curve on that day. Although BODENHEIMER's curve is cited in some standard books of ecology (ALLEE *et al.*, Fig. 102; ODUM, Fig 41), most beekeepers regarding his curve may suspect such rapid increase under the conditions described by NOLAN. On the other hand, the size attained by our corrected curve more or less accords to the experience obtained in managing weak to medium sized colonies.

#### DISCUSSION

The life table for honeybees developed in the present paper are certainly one of the most precise ones so far published for animals, not because of the excellence of our procedure, but chiefly due to the particular mode of life in honeybees. DEEVEY (1947) pointed out three kinds of ecological information sources which could be used for preparation of life tables: 1) Age at death directly observed, 2) Survivorship directly observed and 3) Age structure directly observed. Among

these sources, the second one was regarded by him as the most reliable data, because it was independent of the change of age structure of cohorts concerned. In most free living animals, these items of information can not directly be obtained (MORRIS and MILLER, 1954). Various recent studies on life tables mainly concern how to estimate these necessary items of information based upon the data indirectly useful (SOUTHWOOD, 1966).

In honeybees, however, it is not difficult to have a reasonable number of individuals born on the same day, to distinguish them by individual marking, and, thanks to their homing habit, to trace their individual life history nearly as precise as in stored food pests reared in closed containers. DEEVEY mentioned the observation by HATTON (1938) on *Balanus balanoides* as the best example of life tables hitherto published, because this table was prepared based upon the second source of information cited above, "cases where the survival ( $l_x$ ) of a large cohort (born more or less simultaneously) is followed at fairly close intervals throughout its existence". Our data sufficiently fulfil this condition and, by the inclusion of immature stages, better than the result by HATTON, who started his life table by establishment of *Cypris* larvae, not by hatching out. But, for the particular mode of life in honeybees, our result may not much help the life table work in other animals, although certainly useful for population studies of honeybee colonies. On the other hand, our life tables, prepared for one of the best studied insects, must help comparative studies in various animals.

From the comparison of life tables for various insects, ITÔ (1959) found two characteristics in insects: 1) In many insects, there are three periods of high mortality, eggs-first-larvae, last-larvae-pupae, and senescent adults, whereas many other animals have only two high mortality periods, juvenile and senescent stages, although this two periods type is found in some insects, too. 2) Increased parental care decreases total mortality in general and 3) Juvenile mortality in particular. Further he added two other important comments (1961): 4) Deaths at early life stages are mainly caused by density independent factors such as climate, polyphagous predators, etc., and 5) Deaths at later stages principally by density dependent factors such as specialized predators, parasites, diseases, etc.

With respect to the item 2) given above, our result may offer a super-appropriate example. The resemblance of survivorship curve for honeybees to that for men was already stressed by ITÔ, based upon the curve for honeybees prepared by him from the data by BODENHEIMER (1937) and SAKAGAMI (1953). Our result vividly confirms this resemblance. Both in men and honeybees, the parental care reaches a stage not realized in other animals. The complicated social organization achieved by honeybees enables a high survival at the early life history of each individual, or more adequately, *individuoid* (SAKAGAMI, 1968).

As to the other four items, however, honeybees escape from generalizations by ITÔ as follows:

1) The mortality at later larval-pupal stage is remarkably low, because of an advanced protection, resulting in the possession of two high mortality periods.

3) Contrary to the opinion by ITÔ, the mortality at early juvenile stage is "relatively" high. However, this fact requires an explanation. The early juvenile mortality of honeybees is itself incomparably lower than in other insects. It is relatively high only in relation to the mortality in late juvenile mortality, which is extraordinary low.

4) For deaths at juvenile period, density independent factors are most unlikely responsible. Here density dependent factors play the leading role. But the latter is quite different from those commonly operate on other insects. In normal colonies the conditions necessary for brood survival are kept within the optimal range by adult workers, resulting in a very low mortality. The deaths are attributed to some physiological defects and a remarkable event "population control by workers themselves" (c.f. FUKUDA and SAKAGAMI, 1968), which depends on the equilibrium between oviposition rate by the queen and brood rearing capacity by workers.

5) Mortality factors operating at senescent adults are also quite complicated. FUKUDA and SEKIGUCHI (1966) divided mortality factors at foraging period into three components, ecological hazards ( $E$ , including weather, non-specialized predators, etc.), physiological consumption due to intense foraging ( $P_2$ ) and that due to intense brood rearing during earlier adult stages ( $P_1$ ). Separation of these components is for the time being impossible. Certainly some density dependent factors are included in  $E$ . But the influence of density independent factors is also obvious. Moreover, either density dependent or independent, the nature of the action of these factors are quite different from the cases in other insects.

Consequently, the discrepancy between generalizations by ITÔ and our results in honeybees does not invalidate his theory but simply indicates the extreme differentiation of the mode of life in honeybees which is so modified that escapes from the rules governing life histories of most insects.

The considerations given above expose the defects in our results. MORRIS and MILLER (1954) proposed the necessity of an additional column  $d_x F$  in life tables for insects, which specifies principal mortality factors operating at each stage, together with their relative importance. In spite of our "precise" life tables, we cannot prepare this column for honeybees, again caused by their overdifferentiated mode of life. Main mortality factors affecting other insects, such as climate, predators, parasites, etc. often operate on honeybees in an all-or-none way, or, not at individual (=individuoid) level, but at colony (=individual) level. While these factors affect negligibly normal colonies, they give catastrophic results under unfavorable circumstances. Apparently caused by this mode of action, there are few accurate reports which give the influence of mortality factors in terms of the number of individuals killed by them. Besides the application of life tables for population dynamics in honeybee colonies, the closer analysis of these mortality factors,

however their mode of action deviates from the cases in other insects, would be required for the future population studies of honeybees.

#### SUMMARY

Life tables for worker honeybees covering all life span, and those for adults, were prepared for three seasonal cohorts, *June bees*, *July bees* and *wintering bees*. Survivorship curves for *June* and *July bees* show a convex type being exceptional for insects, with relatively high mortality at egg and feeding larval stages and at later adult stage after most bees became potential foragers. Adult longevity greatly lengthens in *Wintering bees* and survivorship curve drops approximately with the same rate. A remarkable similarity of survivorship curves for men and honeybees was demonstrated, apparently due to highly developed social care in both. Some comments were given on mortality factors. The importance of life tables for population researches was shown by applying our result to the population growth curve made by BODENHEIMER, based upon the data by NOLAN. At the asymptote of the uncorrected curve, the ratio of total population estimated by uncorrected curve to that by corrected curve reaches about 3 : 2.

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### ミツバチのハタラキバチの生命表

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ヨーロッパミツバチの全生存期間および成虫期間の生命表を6月、7月および越冬ハタラキバチについてつくった。6、7月の生存曲線は昆虫類に稀な凸形をしめし、卵一摂食幼虫期および老令成虫期に高い死亡率をしめす。越冬バチの寿命はいちじるしくのび、生存曲線はほぼ同一の率で低下する。ミツバチとヒトの生存曲線のいちじるしい類似、他の昆虫との比較、および死亡要因についての考察がくわえられた。生命表の応用として、NOLANの資料にもとづきBODENHEIMERのつくった群の生長曲線をわれわれの生命表で修正してみた。修正曲線ともとの曲線との差は、生長のピークにおいて、後者のとる数値の $\frac{1}{2}$ に達する。