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Host age preference behaviour of *Trichogramma aurosum* Sugonjaev & Sorokina (Hymenoptera: Trichogrammatidae)

R.Y. Samara[1], J.C. Monje[2], T.A Qubbaj[3] and C.P.W. Zebitz[4]

1- Faculty of Applied Science. Palestinian Technical University. Palestinian Authority.
2- State Museum of Natural History, Stuttgart, Germany
3- Palestinian National Agricultural Research Center (NARC). Palestinian Authority
4- Institute of Phytomedicine, University of Hohenheim, 70593 Stuttgart, Germany

***Corresponding Author Email**: rana_samara@yahoo.com

Abstract

Host age selection in several German strains of *Trichogramma aurosum* Sugonjaev & Sorokina was examined in laboratory choice tests under direct observation for 90 min., in order to select candidate strains for attempts at controlling the codling moth, *Cydia pomonella* L. (Lepidoptera: Tortricidae). Experiments were conducted at room temperature by exposing combinations of two host ages (zero vs. four and one vs. five-days old) to a single female wasp. Host age did not appear to affect the wasps parasitization behaviour, although they spent longer time drilling on old eggs (four and five days old) compared with fresh ones (zero and one day old). This not necessarily means that they preferred fresh eggs over old ones, since both type of hosts were parasitized in the choice test. Possibly an increased mechanical resistance of the chorion of older eggs was responsible for the prolonged drilling time. Mean drumming time was independent of host age. Mean duration of drilling and drumming was in general longest in the first and last egg attacked by all *T. aurosum* strains tested and for all host ages. Drilling time made more than 80% of the mean handling time of all strains tested for all host ages, followed by resting and walking.

Keywords: *Trichogramma aurosum*, egg parasitoids, host age, choice test, host selection, parasitization behaviour, *Cydia pomonella*.

Introduction

The use of natural enemies like predators, parasitoids and microorganisms to suppress populations of insect pests is the major aim of biological control. The most widely used beneficial organisms worldwide belong to the genus *Trichogramma* (Hymenoptera: Trichogrammatidae) (Smith, 1996). This genus comprises more than 200 nominal species that are primary egg parasitoids (Pinto, 1999). Cosmopolitan in distribution, *Trichogramma* spp. occupy habitats that range from aquatic to high arboreal. Although these extremely tiny wasps (*ca*. 500 µm) attack mainly eggs of lepidopterous species, they have been collected from well over 200 species belonging to > 70 families and eight orders. Attempts at controlling insect pests using *Trichogramma* spp. started in the beginning of the last century in the USA and in the former Sowjetunion.

Trichogramma aurosum was described in 1975 by Sugonjaev & Sorokina. However, only studies on its distribution have been carried out in the USA and Russia. *Trichogramma aurosum* was found in Germany for the first time in 2000 (Samara 2005, Monje & Zebitz, 2003). According to preliminary host preference experiments it was shown that this species prefers eggs of the codling moth, *Cydia pomonella* L. (Lepidoptera: Tortricidae), over other host eggs. In 2001 - 2002, a wide collection of this species was carried out in the German Federal Republic from eggs of *Nematus tibialis* (Hymenoptera: Tenthredinidae) on *Robinia pseudoacacia*. Pilot experiments revealed that *T. aurosum* may be a potential candidate antagonist for attempts to control *C. pomonella* in apple orchards (Samara et al 2008a, b). Under natural conditions, parasitoids may contact patches of host eggs of different ages, there for investigated this studies weather the parasitoids *T. aurosum* strains has preference to old or fresh eggs, and if they were able to discriminate between parasitized and unprasitized eggs.

Material and Methods

Field trips and collection from the field were done during summer 2002 and 2003 by collecting parasitized (black) eggs of *Nematus tibialis* on leaves of *Robinia* trees in several location in the German Republic and its neighbouring countries. The collected strains of *T. aurosum* are maintained for the laboratory experiments at present. Stock cultures of the apple codling moth, *Cydia pomonella* L., and the Mediterranean flour moth, *Ephestia kuehniella* Zeller, were established under laboratory conditions for the experiments. Stock cultures of the beneficial wasps *T. aurosum* were maintained in the laboratory for the research. About 21 strains of the wasps were reared in large numbers for the different experiments planned.

Host age: Experiments were conducted at room temperature by exposing combinations of two host ages (0 vs. 4 and 1 vs. 5 old day) to a single female wasp in a choice tests. Each test was conducted in a plastic petri-dish (5.3 cm diam.) carrying a piece of graph-paper (2x2 cm). Eight eggs of each age were arranged in an grid square shape alternatively, and 4 mm apart. Then the *Trichogramma* females were released and allowed to parasitize the hosts. Every behavioural event was recorded using the Observer® software for 90 min. after the first contact with one egg: Walking, cleaning, resting (handling time), contact, drumming (touching the host egg with the antennae), acceptance (by starting drilling), or rejection (by leaving the host and walking away), drilling, and oviposition (movement of the abdomen can be clearly seen). Since parasitized hosts were not removed, recurrent visits to parasitized host eggs were also recorded. Each treatment was replicated 20 times. Host age preference was statistically analysed by summing the number of acceptance and that of the rejections of eggs at the first visit for each of the two ages per test and constructing a contingency table for the distribution of contacts. The acceptance / contact ration were then evaluated by chi-square test. Statistical analysis of mean differences in recognition times and number of eggs laid was done ANOVA test using the General Linear Models (PROC GLM) procedure (SAS Institute, 1996). Where the Student-Newman-Keuls (SNK) procedure was used to separate the means.

Results

Time consumed drilling an old egg either four or five day old egg was longer than time consumed on fresh ones (Table 1), where Ta4 (F = 6.34; Pr = 0.0142; DF =1, 68) and Ta13 (F = 6.17; Pr = 0.0145; DF =1, 112) showed a significant longer time drilling in old eggs (in 0 vs. 4 day old eggs test); compared with fresh ones, while Ta10 (F = 2.46; Pr = 0.12; DF =1,96), Ta19 (F = 0.67; Pr = 0.416; DF =1, 93) and Ta20 (F =0.42; Pr = 0.517; DF =1, 118) spend longer time drilling old eggs but of no significant importance. By statistical analysis of the means, drilling time spends on old eggs was about 50-60 % more than fresh eggs (Figure 1 & 2). Drilling time observed longer on five day old eggs compared with one day old day eggs but of no significant importance for the strains tested Ta4 (F = 0.92; DF = 1, 112; Pr = 0.339), Ta10 (F = 5.15; DF = 1, 103; Pr = 0.025), Ta13 (F = 1.72; DF = 1, 106; Pr = 0.19), Ta19 (F = 0.04; DF = 1, 8; Pr = 0.848), and Ta20 (F = 0.42; DF = 1, 88; Pr = 0.52; DF =1). Mean time consumed on drumming either fresh or old eggs did not have any significant differences (Table 2). Although time consumed on drumming fresh eggs seems to last equal or longer than drumming old eggs (Figure 3 & 4).

The five strains of *T. aurosum* studied have no age preference, where the mean number of eggs attacked either old or fresh eggs did not differ significantly. Ta10, Ta13, and Ta20 showed a higher preference to attack fresh eggs at the age of zero day (F =1.15; DF = 1, 36; Pr = 0.29; F =5.8; Pr = 0.021; DF =1, 36; F =1.45; Pr = 0.24; DF =1, 36, respectively) and one day old (F =0.03; Pr = 0.85; DF =1, 36; F =0.64; Pr = 0.43; DF =1, 36; F =0.40; Pr = 0.53; DF =1, 32, respectively) but of no significant difference. Mean while all strains showed a higher preference to parasitized fresh eggs than old one but of no significant importance (figures 5 to 8). Mean number of eggs attacked was noticeably higher than number of parasitized eggs.

Table 3 shows that for most test the acceptance /contact (a/c) ratios were high (>0.7). This indicates that eggs of different ages tested were contacted and examined at similar rates. Chi square test to evaluate the a/c ratios per test revealed a statistical difference at the 5% level between 0 and 4 day old eggs for both Ta13 and Ta19; and between 1 and 5 day old eggs for Ta20 strain. Here the females preferred the younger eggs. In all other tests, no preference was observed for any of the strains to contact and pt accept host eggs above the other.

Host discrimination. Observation of females contacting host eggs previously parasitized by themselves. Evidently showed that each *Trichogramma* strains was able to discriminate between unparasitized and parasitized hosts of different ages. The differences between a/c ratios for parasitized and unparasitized hosts per strain and age were statistically analyzed and the results are shown in table 4. Females of all strains were able to discriminate parasitized eggs of each age of *C. pomonella*, (P $X^2 < 0.05$). Differences between a/c ratios of parasitized and unparasitized hosts were highly significant for all strains, except for Ta20 no significant differences were recorded at five day old eggs (Table 4).

Discussion

The reproductive ability of a female parasitoid is controlled by host factors such as host age, size and physical defenses (Godfray 1994). Host age affects host preference and host suitability of parasitoids (Pak et al 1986). Also, some species of parasitoids can control the sex ratio of their progeny in response to host age (Pak & Oatman 1982), but other don't (Nakamura & Noda 2001). For some parasitoids host age was shown to have a significant effect on offspring size (Husni et al. 2001) and have a greater effect on sex allocation by other parasitoids (Nakamura & Noda 2001). So studying the effects of host age and size on parasitoid reproductive characters will not only allow a better understanding of the ecological strategies of parasitoids, but it will also be useful for developing augmenting parasitoids as biological control agents. Many studies have shown that host stadium at parasitism affects parasitoid host acceptance behavior especially oviposition behavior (Marston & Ertle 1969, Pak et al 1986). After contacting the host, the following three behavioral events were recognized in oviposition behavior of T. aurosum: (1) drumming by antennae, (2) ovipositor penetration and oviposition, and (3) host feeding. Ovipositor penetration and oviposition were not behaviorally distinguishable. After oviposition, parasitoids withdrew their ovipositor and some females started host feeding. Some females repeated ovipositor penetration followed by host feeding two or three times (data not shown). After contacting and drumming the host, some females left the host immediately without trying to oviposit. The acceptance and suitability of various hosts is not direct evidence that the wasps successfully parasitize these species under natural conditions, while preference studies in the laboratory can give an indications for the field conditions (Dijken et al. 1986).

Females of *T. aurosum* spent longer time drilling on old eggs (4 and 5 days old) compared with fresh ones (0 and 1 day old). This not necessarily means that they prefer fresh eggs over old ones, since both type of hosts were parasitized in the choice test. Similar results were obtained by both Brand et. al. (1984) and Godin & Boivin (1994) with T. evanescens and T. pretiosum respectively. Host age generally does not appear to affect contact or acceptance of eggs of different host species, but duration of the oviposition behaviour is sometimes influenced by host age (Pak et. al., 1986). Furthermore, Reznik et al. (1997) found out that host acceptance depends not only on current host age, but also on the age of the previously offered host. Possibly an increased mechanical resistance of the chorion as response of development of the host embryo in the older eggs (Reznik et al. 1997) was responsible for the prolonged drilling time. It was reported that cell masses of the host egg differentiated after 11 hr (Marston & Ertle 1969). Nakamura & Noda, (2001) reported that the duration of ovipositor insertion and oviposition of O. sokolowskii was significantly longer on fourth hosts stadium than on second- and third hosts stadium. Pak (1986) related belonging in handling time due to unsuitability of older host eggs, where by wasps recognized that only after internal examination of the host with the povipositor. Although we recorded that the mean drumming time was independent of host age, where females spent about the same time drumming on fresh and old eggs. Pak & Oatman (1982), reported that the wasps uses drumming to measure the size of the host egg to control number of eggs being oviposited. In general, mean duration of drilling was highest in the first and last attacked egg. It was shorter for the second up to the sixth attacked host. On the contrary, drumming time was always higher for the first host and lower for the subsequent attacked hosts, these results agrees with Nakamura and Noda (2001) findings. Behavioural differences may indicate a difference in chemical and/or visual conditions between young and old hosts and explain how the parasitoid recognizes host size.

Although results showed that a/c ratios were high indicating that eggs of different ages tested were contacted and examined at similar rates. Females observed has no preference for any of the host ages, but some do have showed a preference to younger eggs than old one. T. minutum recorded to deposit more eggs in younger hosts than in older ones of the same size, because old eggs provide fewer resources for the parasitoid larvae than young eggs (Nakamura & Noda 2001). Marston & Ertle (1969), related that parasitoid mortality could be higher in old eggs because the parasitoid eggs collapsed when they were forced into the embryonic tissue.

Table1. Mean duration time consumed by five strains of *T. aurosum* drilling eggs of *C. pomonella* at different host age at room temperature (n=20)

Age day	Ta4	Ta10	Ta13	Ta19	Ta20
0	251.51±130 [b]	414.25±359 [a]	263.87±109 [b]	227. 71±182 [a]	259.44±228 [a]
4	344.64±177 [a]	535.09±404 [a]	322.60±143 [a]	253.72±121 [a]	287.07±237 [a]
1	341.02±237 [a]	366.77±213 [a]	319.00±161 [a]	364.47±316 [a]	378.45±271 [a]
5	386.75±271 [a]	479.45±294 [a]	371.64±249 [a]	353.90±158 [a]	344.98±209 [a]

* Within a column, means followed by the same letter are not significantly different (P > 0.1, Student Newman Keuls (SNK) test)

Table 2. Mean duration time consumed by five strains of *T. aurosum* drumming eggs of C. pomonella at different host age at room temperature (n=20)

Age day	Ta4	Ta10	Ta13	Ta19	Ta20
0	31.59± 11.4 [a]	30.94±15.0 [a]	35.43±27.17 [a]	30.09±20.5 [a]	32.62±17.67 [a]
4	31.43±12.4 [a]	27.26±15.60 [a]	33.88±20.9 [a]	29.55±17.2 [a]	28.27±13.8 [a]
1	37.84±15.3 [a]	30.26±16.6 [a]	30.09±20.5 [a]	31.63±15.4 [a]	31.27±17.0 [a]
5	37.32±16.7 [a]	29.35±12.9 [a]	29.55±17.2 [a]	27.93±9.9 [a]	33.00±19.3 [a]

* Within a column, means followed by the same letter are not significantly different (P > 0.1, Student Newman Keuls (SNK) test)

Table 3. Number of contacts and acceptances for C. pomonella eggs of various ages by five strains of T. aurosum in paired –choice tests and statistical analysis of host preference. (n=20)

Strains	Age (day)	No. Contact	No. Acceptance	a/c ration	Chi square	Df	P 0.05
Ta4	0	64	47	0.73	1.85	1	NS
	4	72	45	0.63			
	1	76	58	0.76	0.03	1	NS
	5	80	62	0.78			
	0	55	45	0.82	0.20	1	NS
Ta10	4	47	40	0.85			
	1	63	52	0.83	2.07	1	NS
	5	60	43	0.72			
	0	90	73	0.81	7.18	1	S
Ta13	4	67	64	0.96			
	1	74	62	0.84	0.38	1	NS
	5	64	56	0.88			
	0	53	44	0.83	6.66	1	S
Ta19	4	56	34	0.61			
	1	56	48	0.86	3.62	1	NS
	5	51	36	0.71			
Ta20	0	71	52	0.73	0.12	1	NS
	4	58	44	0.76			
	1	53	45	0.85	8.11	1	S
	5	47	28	0.60			

Attacking frequency for all strains studied were more than 30% of the offered eggs (Figure 5 and 7) where by the accepted eggs were more than 25% of the offered eggs either old or fresh eggs (Figure 6 and 8). Ta4 attack 40 % of the zero and four days old eggs; and 50% of the one and five day old eggs. Ta10 and Ta19 attack 35 % of the zero and four days old eggs; while it attack 40 and 35%, respectively of the one and five day old eggs. Ta13 attack 55 % of the zero and four days old eggs; and attack 50% of the one and five day old eggs. Ta20 attack 45 % of all the egg ages. Ta4 parasitized 25% of the 0, 4 day old eggs and 35% of the 1, 5 day old egg. Ta10 parasitized 30-35% fresh eggs and 25-30% old eggs. Ta13 parasitized 40-50% fresh eggs, and 35-40% old. Ta19 parasitized 30% fresh eggs and 20% old eggs. Ta20 parasitized 35% fresh eggs and 20-30% old eggs. No significant differences between drilling time consumed by the females wasp for the five strains studied when she drilled the first, second, third and last egg (Figure 9 & 10). But time consumed on drilling decreases from the first egg to the second and the third. By drilling the last egg on obvious pattern was noticed; where it can be decreased or increased from one strain to another.

Salt 1937 reported that T. evanescens can discriminate between parasitized and unparsitized host either by marking their host externally by their antenna and internally by the ovipositor. All the strains studied discriminate between the parasitized and unparasitized host eggs during the drilling phase, it is possibly because they use the ovipositor to detect external stimuli or marks left previously. According to Miura et al. (1994), discrimination between parasitized and unparasitized host may depend on the parasitoid prior ovipositional experience. Pak and Oatman (1982), reported that T. brevicapillum and T. pretiosum females accept host eggs that was parasitized by other species.

Results suggest that learning takes place on the first host encountered, thus reducing handling time on the subsequent hosts. A more detailed analysis of the behaviour events (especially walking and resting) between the host encounters may help to explain the longer duration of drilling time on the last host attacked. The wasps consumed about 75, 80, 85, and 95% of the handling time on drilling the 0,1, 4 and 5 day old eggs, respectively, 5% for drumming and 10% for resting (Figure 11). Future studies should focus on determining host acceptance and preference between different hosts.

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R. Siegel for maintaining the lab culture of *E. kuehniella*

Table 4. Discrimination by five *Trichogramma* strains between parasitized and unparasitizeds host eggs of various ages for C. pomonella (n=20)

strain name	host age	parasitized hosts # cont	# acc.	a / c ratio	unparasitized host a/c ratio	statistical comparison Chi-square	P (0.05)
Ta4	0	37	1	0.03	0.73	47.04	0.001
	4	30	6	0.20	0.63	15.30	0.001
	1	51	5	0.10	0.76	54.01	0.001
	5	58	3	0.05	0.78	70.59	0.001
Ta10	0	24	4	0.17	0.82	30.11	0.001
	4	13	1	0.08	0.85	28.20	0.001
	1	18	1	0.06	0.83	36.68	0.001
	5	10	0	0	0.72	18.58	0.001
Ta13	0	15	1	0.07	0.81	34.25	0.001
	4	14	4	0.29	0.96	38.53	0.001
	1	15	4	0.27	0.84	21.23	0.001
	5	14	2	0.14	0.88	32.30	0.001
Ta19	0	9	3	0.33	0.83	10.36	0.001
	4	23	2	0.09	0.61	17.79	0.001
	1	20	0	0	0.86	46.53	0.001
	5	11	0	0	0.71	18.52	0.001
Ta20	0	12	4	0.33	0.73	7.45	0.006
	4	7	1	0.14	0.76	11.12	0.001
	1	8	3	0.38	0.85	9.32	0.002
	5	5	1	0.20	0.60	2.81	0.09

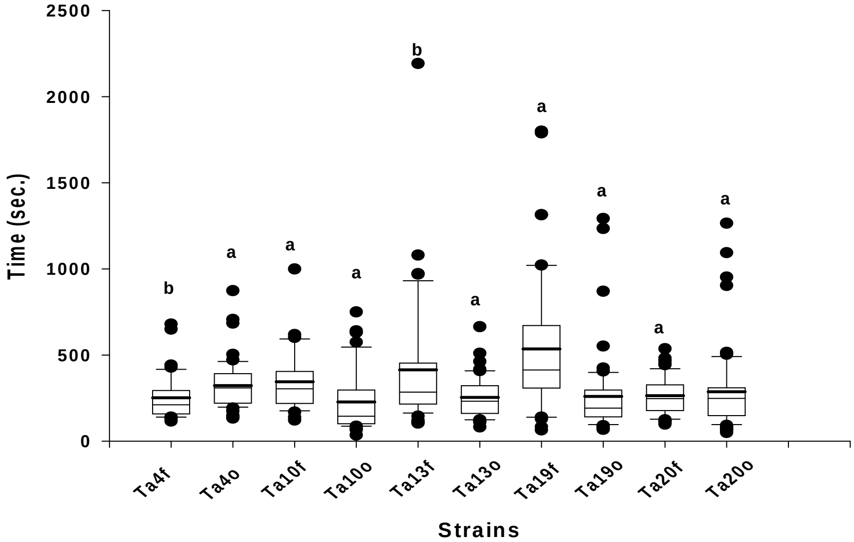

Figure 1. Mean duration of drilling by five *T. aurosum* strains in parasitising 0 vs. 4 day old eggs of *C. pomonella* at room temperature.

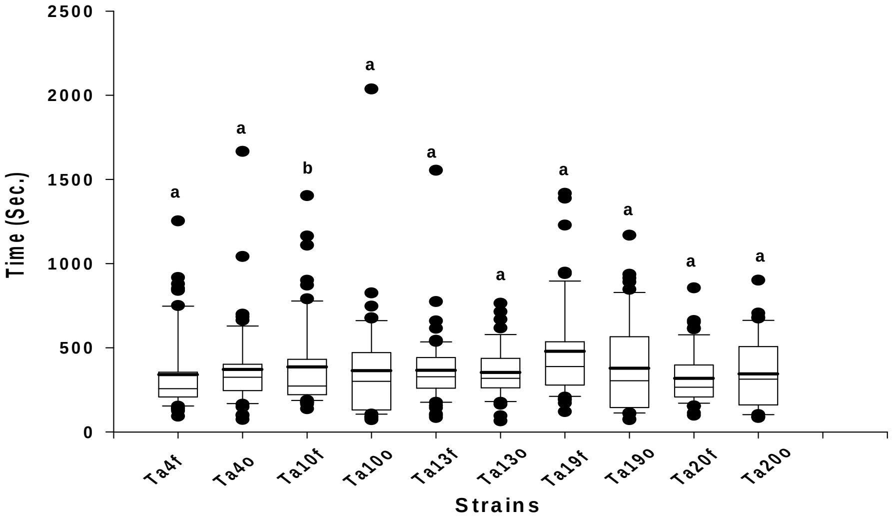

Figure 2. Mean duration of drilling by five *T. aurosum* strains in parasitising 1 vs. 5 day old eggs of *C. pomonella* at room temperature.

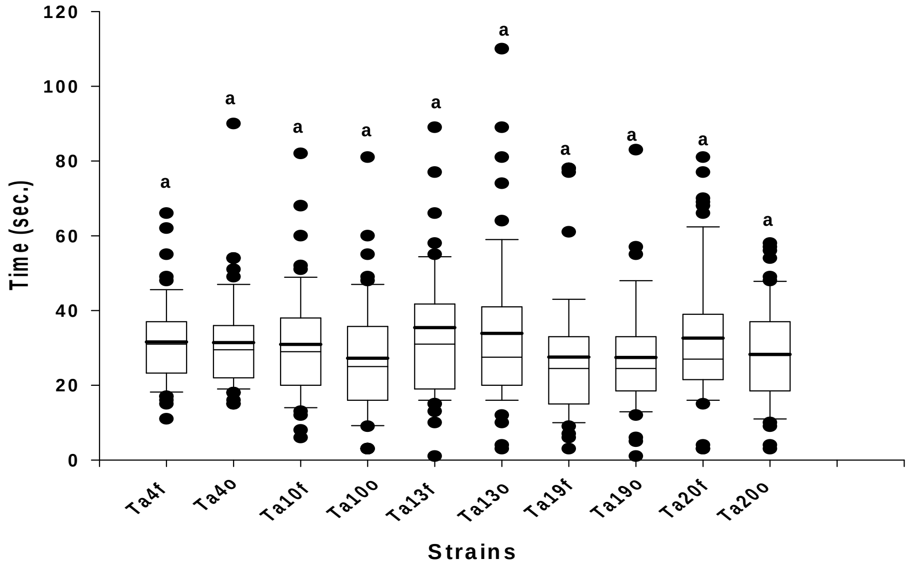

Figure 3. Mean duration of drumming by five *T. aurosum* strains in parasitising 0 vs. 4 day old eggs of *C. pomonella* at room temperature.

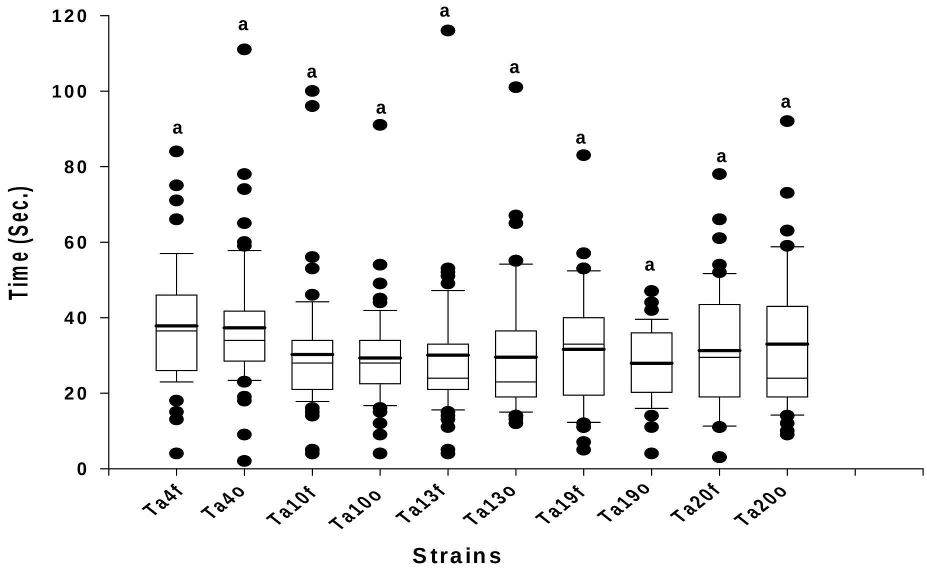

Figure 4. Mean duration of drumming by five *T. aurosum* strains in parasitising 1 vs. 5 day old eggs of *C. pomonella* at room temperature.

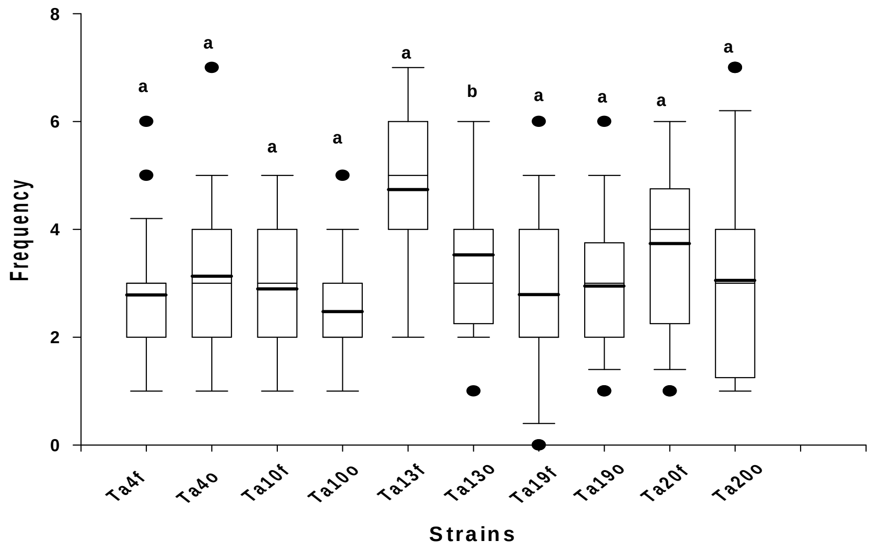

Figure 5. Mean attacking behaviour frequency on 0 and 4 day old eggs of C. pomonella for five strains of *T. aurosum* at room temperature

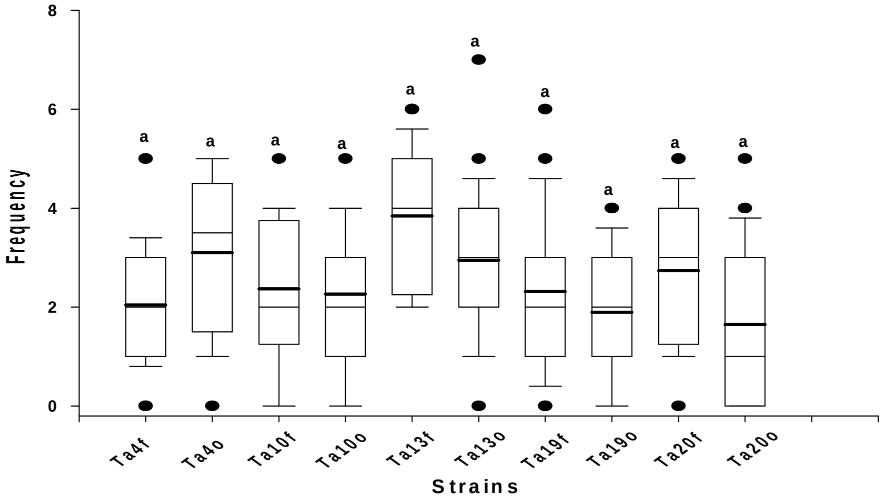

Figure 6. Mean parasitising behaviour frequency on 0 and 4 day old eggs of C. pomonella for five strains of *T. aurosum* at room temperature.

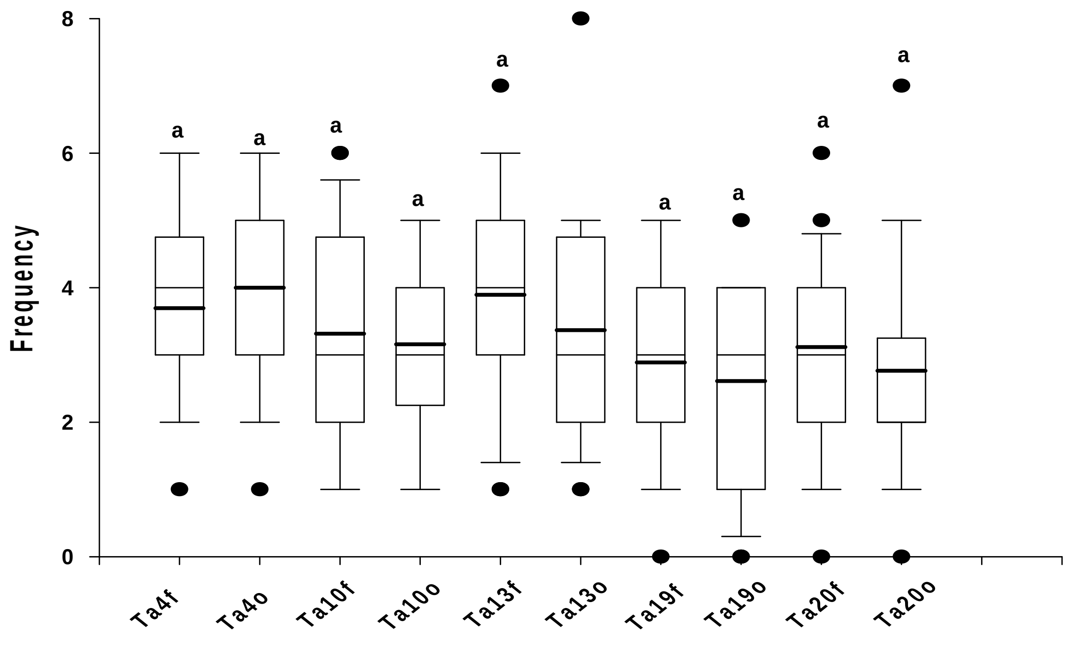

Figure 7. Mean attacking behaviour frequency on 1 and 5 day old eggs of C. pomonella for five strains of T. aurosum at room temperature

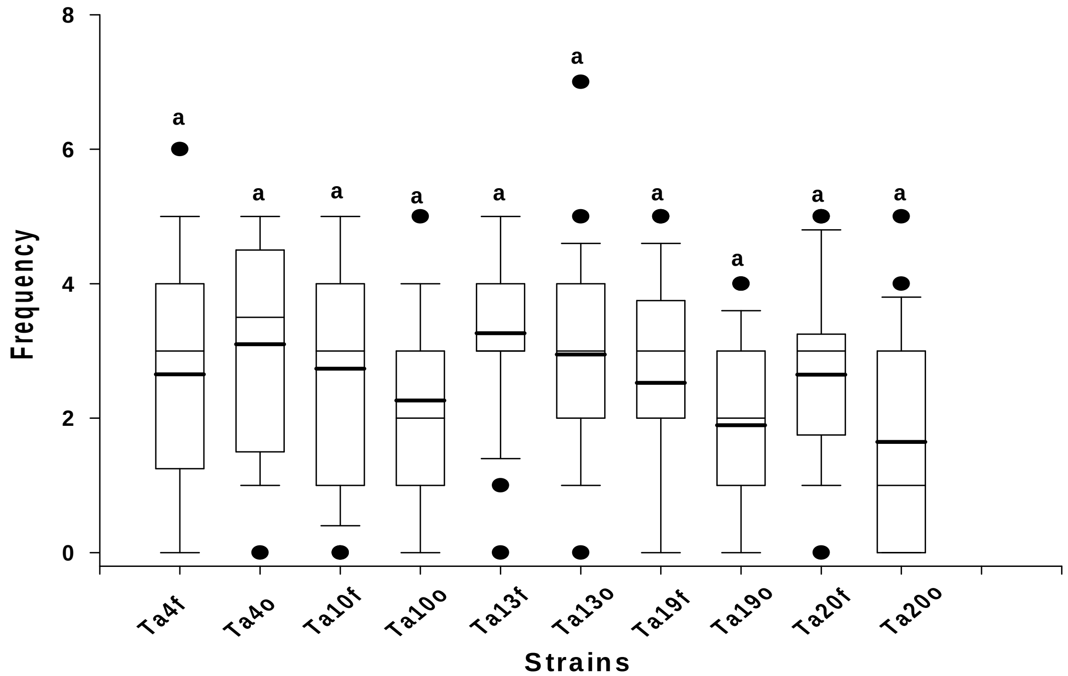

Figure 8. Mean parasitising behaviour frequency on 1 and 5 day old eggs of C. pomonella for five strains of *T. aurosum* at room temperature.

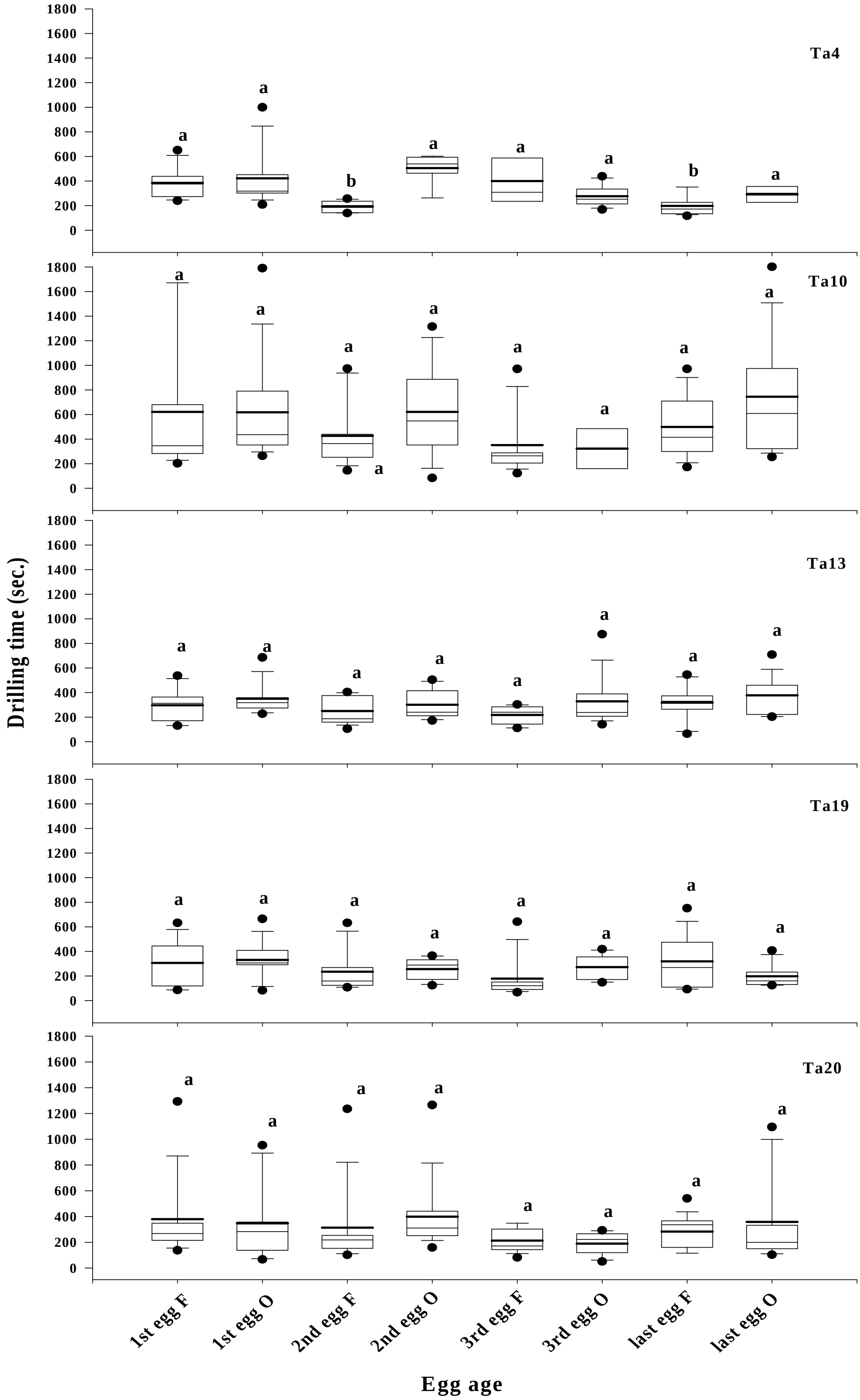

Figure 9. Mean drilling time of the first. second third and last egg by five *T. aurosum* strains in parasitising 0 vs. 4 old day eggs of *C. pomonella* at room temperature.

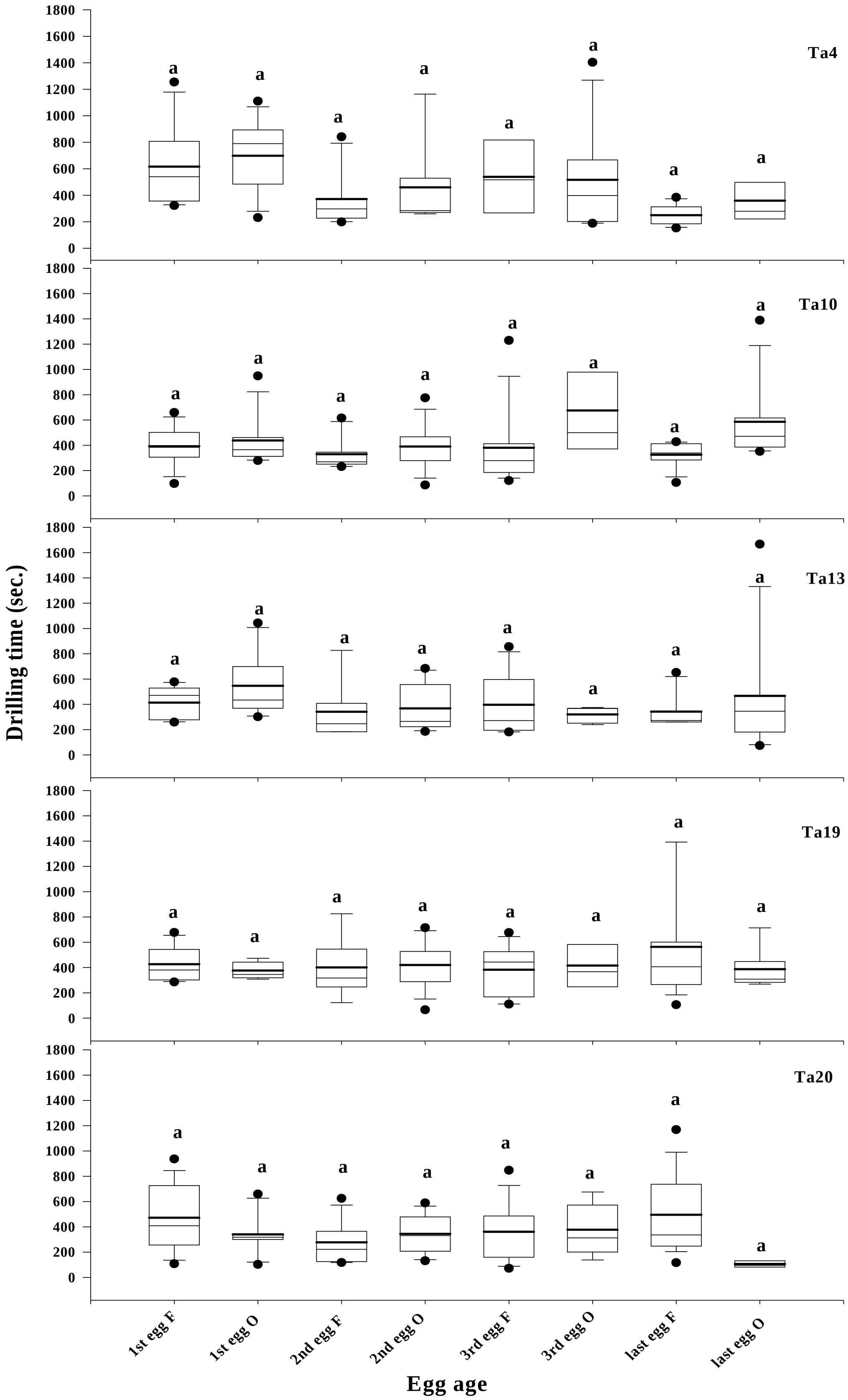

Figure 10. Mean drilling time of the first. second third and last egg by five *T. aurosum* strains in parasitising 1 vs. 5 old day eggs of *C. pomonella* at room temperature.

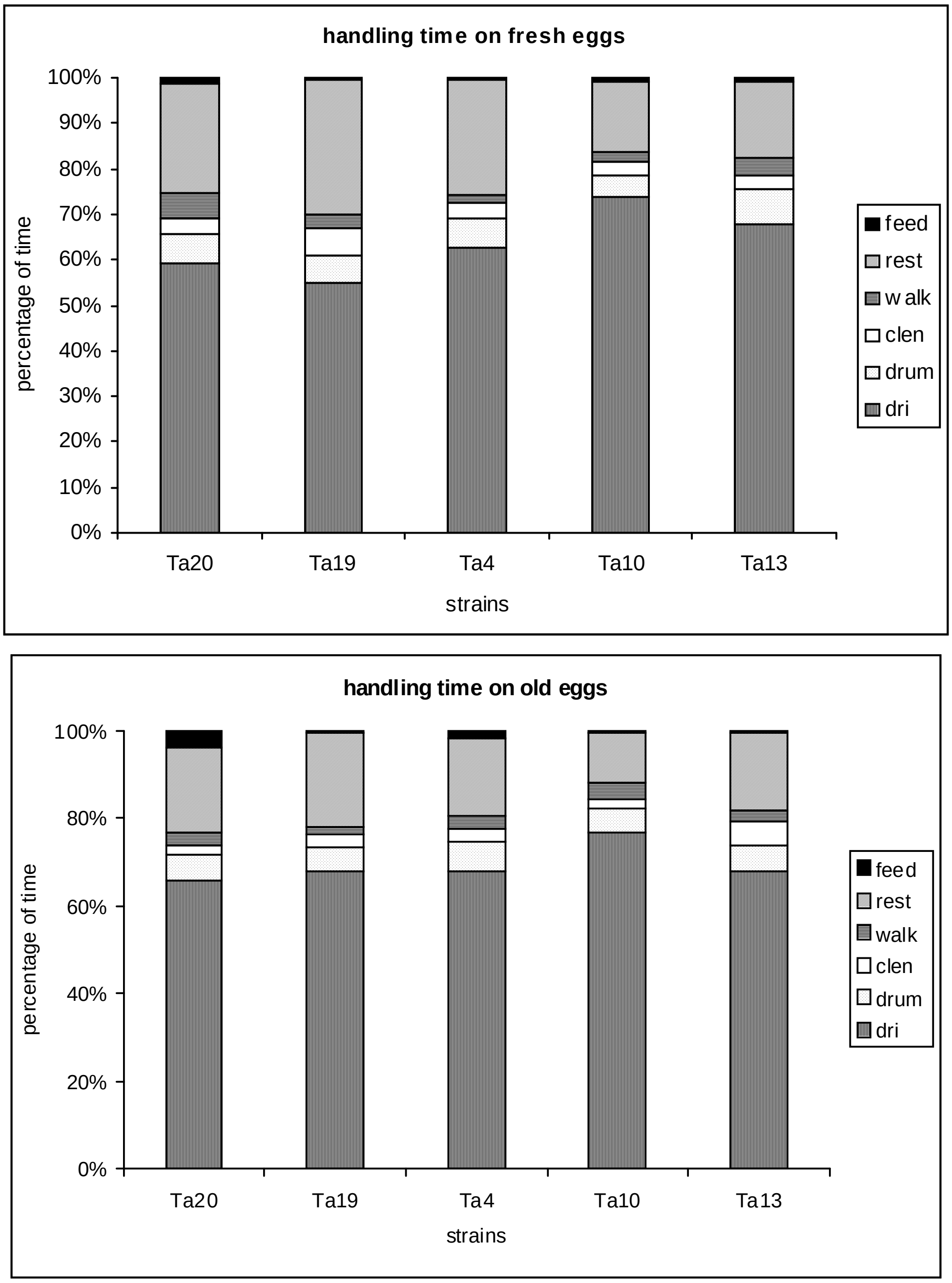

Figure 11. Percentage handling times for five strains of T. aurosum parasitizing fresh or old eggs of C. pomonella at room temperature

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