

Acarologia

A quarterly journal of acarology, since 1959
Publishing on all aspects of the Acari

All information:

<http://www1.montpellier.inra.fr/CBGP/acarologia/>
acarologia-contact@supagro.fr



**Acarologia is proudly non-profit,
with no page charges and free open access**

Please help us maintain this system by
encouraging your institutes to subscribe to the print version of the journal
and by sending us your high quality research on the Acari.

Subscriptions: Year 2021 (Volume 61): 450 €

<http://www1.montpellier.inra.fr/CBGP/acarologia/subscribe.php>

Previous volumes (2010-2020): 250 € / year (4 issues)

Acarologia, CBGP, CS 30016, 34988 MONTFERRIER-sur-LEZ Cedex, France

ISSN 0044-586X (print), ISSN 2107-7207 (electronic)

The digitalization of Acarologia papers prior to 2000 was supported by Agropolis Fondation under the reference ID 1500-024 through the « Investissements d'avenir » programme (Labex Agro: ANR-10-LABX-0001-01)



Supporting agricultural research
for sustainable development

Acarologia is under **free license** and distributed under the terms of the
Creative Commons-BY.

Bisexual and oedipal reproduction of *Macrocheles muscaedomesticae* (Acari, Macrochelidae) feeding on *Musca domestica* (Diptera, Muscidae) eggs

Sara Farahi^a, Parviz Shishehbor^a, Alireza Nemat^b

^a Department of Plant Protection, College of Agriculture, Shahid Chamran University of Ahvaz, Ahvaz, Iran.

^b Department of Plant Protection, College of Agriculture, Shahrekord University, Shahrekord, Iran.

ABSTRACT

Macrocheles muscaedomesticae (Scopoli) is a predatory mesostigmatic mite that inhabits different manure microhabitats and preys mostly on housefly (*Musca domestica* L.) eggs. When a virgin female colonizes a new manure substrate, it produces male offspring through parthenogenesis (arrhenotoky); when her sons reach maturity, oedipal mating takes place and the female begins to produce bisexual offspring. In order to examine the consequence of oedipal reproduction on population development, we designed two separate experiments to compare life history traits and life table parameters of oedipal versus bisexual cohorts of *M. muscaedomesticae*, using the age-stage, two sex life table method. Experiments were conducted at 28 ± 1 °C, using a photoperiod of 14:10 (L: D) h, and $65 \pm 5\%$ relative humidity, with housefly eggs used to feed mites. Mean adult female longevity was 38.63 days, and fecundity 128.51 offspring under bisexual reproduction, and 37.48 days and 68.23 offspring under oedipal reproduction. In the bisexual cohort, the intrinsic rate of increase (r_m), the finite rate of increase (λ), the net reproduction rate (R_0), the gross reproductive rate (GRR) and the mean generation time (T) of *M. muscaedomesticae* were 0.2938 d^{-1} , 1.3415 d^{-1} , 54.216 offspring/individual, 77.7 offspring/individual and 13.5885 days, respectively. Because only male eggs were produced during the first 5.62 days (on average) of the oviposition period in the oedipal cohort, it was theoretically incorrect to compute the population parameters using the survival and fecundity values for this group, even though bisexual reproduction did occur after this period. Our findings determined that the effect of oedipal reproduction could be correctly defined and analyzed by using the age-stage, two-sex life table method. Our results demonstrated that virgin females are able to produce and copulate with their sons (oedipal mating), which then allows those females to produce both sexes. This reproductive system can enable this valuable natural enemy to considerably extend its distribution potential.

Received 29 May 2017
Accepted 23 November 2017
Published 15 March 2018

Corresponding author
Sara Farahi: sara.farahi@gmail.com

Academic editor
Lise Roy

DOI
10.24349/acarologia/20184251

© Copyright
Farahi S. et al.

Distributed under
Creative Commons CC-BY 4.0

Keywords Life table, *Macrocheles muscaedomesticae*, *Musca domestica*

Introduction

House flies, *Musca domestica* L., face flies, *Musca autumnalis* De Geer, and stable flies, *Stomoxys calcitrans* L. are the primary dipterous pest species occurring in sheep, cattle, buffalo and poultry farms in Iran (Khoobdel and Davari, 2011). All use animal manure as the substrate for their eggs. The eggs hatch in the manure with the larvae developing and pupating within or under the manure. Current control of these pests still relies mainly on insecticides, although these species have developed resistance to most available insecticides due to their overuse (Keiding, 1999; Sharififard and Safdari, 2013). Increasing awareness in the public and among

farmers has encouraged researchers to look for alternative methods of managing these pest flies. The predatory mite, *Macrocheles muscaedomesticae* (Scopoli) (Acari: Macrochelidae), which is the best known and most abundant species found in cattle and poultry manure in Iran (Fathipour, 1994; Kazemi and Rajaei, 2013), preys on, and is disseminated by many filth flies. *M. muscaedomesticae* lives in the outermost layers of manure heaps, the region in which flies usually oviposit. This predator feeds mainly on fly eggs (which it prefers) and on first instar larvae (Gerson *et al.*, 2003). The possibility of mass production of *M. muscaedomesticae* as a candidate biological control agent was evaluated by Filipponi (1964) who verified that Macrochelidae held promise as biological control agents of pest flies. He pointed out that mass production of macrochelids needed elucidation of optimum ecological conditions for each potential mite species, and that the selection of particularly prolific strains that would increase production levels needed to be determined (Filipponi, 1964). Currently, the soil-dwelling predatory mite, *Macrocheles robustulus* (Berlese) has been commercially available since 2010 for control of thrips and soil inhabiting fly larvae such as Sciaridae (Koppert, 2010).

Although the life history traits and life table parameters of *M. muscaedomesticae* have been previously studied (e.g. Pereira & de Castro, 1945; Axtell, 1961, 1963; Wade & Rodriguez, 1961; Filipponi, 1964; Cicolani, 1979; Abo-Taka *et al.*, 2014), it has since been shown that different strains (also termed races or ecotypes) of acarine species used as biocontrol agents that originate from different regions, differ in biological attributes that can potentially effect their success rate. For instance, an Israeli strain of *Phytoseiulus persimilis* Athias-Henriot (Acarina: Phytoseiidae) was more tolerant to low humidity than a California strain (Perring and Lackey, 1989), a trait that affects field survival. Galazzi and Nicoli (1996) compared the life histories of populations of *P. persimilis* that originated from different regions of Italy, and noted that some lived significantly longer and had higher fecundity than others. Use of pesticide resistant strains of phytoseiids has usually resulted in improved pest control (Gerson *et al.*, 2003). In addition, under natural conditions, especially earlier in the year, virgin female mites may become isolated and reproduce parthenogenetically. Unmated females produce only male offspring; later on, the same mothers can mate with their sons to produce females (Oedipal reproduction) (Ho, 1985; Adamson and Ludwig, 1993). To help understand the complex reproductive biology of *M. muscaedomesticae* (Iranian strains), we conducted two separate life table experiments in the present study to quantitatively analyze bisexual and oedipal reproduction strategies in *M. muscaedomesticae*, using the age-stage, two-sex life table which, unlike traditional life tables, includes male individuals and the stage differentiation (Chi and Liu, 1985; Chi, 1988).

Materials and methods

Fly and mite colonies

The biology and demographic parameters of *M. muscaedomesticae* were investigated in a growth chamber set at 28 ± 1 °C, a photoperiod of 14:10 (L: D) h and $65 \pm 5\%$ relative humidity (RH). Because most of the previous studies related to the life history of *M. muscadomesticae* were conducted at 28°C (e.g. Cicolani, 1979; Abo-Taka *et al.*, 2014), this temperature was selected in order to maintain similarity in experimental conditions. Specimens of *Mu. domestica* adults were originally field collected on the campus of Shahid Chamran University of Ahvaz ($31^{\circ}17'59''\text{N}$, $48^{\circ}39'39''\text{E}$) and kept in rearing cages (30×30×40 cm). Adult flies were provided with water, powdered milk and sugar. Larvae were reared on a mixture of alfalfa, date extract, wheat bran and water (Sharififard *et al.*, 2011). Housefly eggs were collected daily from larval medium in rearing cages using a fine brush and used as food for mites.

M. muscadomesticae adults were collected from cow manure from the dairy farm on the campus of Shahid Chamran University of Ahvaz and then extracted by Berlese funnel to establish a colony. Stock colonies of mites were maintained in covered, clear, polystyrene storage containers (6 cm dia. × 3.5 cm h.), with ca. 15 cc of sterilized cow manure added.

The life table study of *M. muscaedomesticae* was conducted in plastic containers of 1×1×1 cm rearing cells filled with sterilized cow manure.

Life table study

Before introducing the mites, water was added to the manure and the surface of the substrate tamped down to facilitate observation of the different mite stages within the rearing cells. In order to maintain the humidity in the rearing cells, water drops were added daily as necessary. Pairs of *M. muscaedomesticae* were randomly selected from the mite colony and placed in containers. Monitorings were conducted hourly until egg laying occurred, after which adults were removed, and each egg was placed into an individually numbered cell. “Tanglefoot” was applied to the rim to prevent escape by the mites.

Life table of bisexual *M. muscaedomesticae*

In total, 64 eggs were used at the start of the life table experiment. The development time of immature stages was recorded hourly. When the adults eclosed, virgin male and female mites were paired and kept together in rearing containers. Adult survival, longevity, and fecundity data were recorded daily until the death of all individuals. If one member of a pair died, another adult of the same sex and same age was recruited from the mass-rearing colony and paired with the surviving individual. Data relevant to the recruited individual were not included in the data analysis. The eggs laid by each female mite at different ages were kept separately under the aforementioned conditions until reaching adulthood to determine the sex of the offspring.

Life table of oedipal *M. muscaedomesticae*

Eggs used for the study were collected as in the bisexual life table study above. Virgin females were isolated in individual rearing cells after reached the adult stage. Data relevant to development time, survival, and fecundity were analyzed for the 64 females used in the study. New eggs laid by virgin females were moved to separate cells for daily monitoring until mites reached adulthood. The first male offspring developing to the adult stage was retransferred to its mother’s rearing cell to mate with her. Daily survival and fecundity were registered until the death of the mother. Dead male mites were replaced with another adult male from the progeny of the same female. Each egg laid by females after oedipal mating was reared separately until adulthood to record the sex of the progeny.

Data analysis

The life history data of *M. muscaedomesticae* were analyzed using the age-stage, two-sex life table theory (Chi and Liu, 1985; Chi, 1988) and the computer program TWOSEX-MSChart (Chi, 2017). The survival rate (S_{xj}) (x = age, j = stage), was calculated as the probability that a newly laid egg would survive to age x and stage j . To take both sexes into consideration, the age-specific survival rate (l_x) was then calculated as:

$$l_x = \sum_{j=1}^m S_{xj}$$

where m is the number of stages. The age-specific fecundity (m_x) was calculated as:

$$m_x = \frac{\sum_{j=1}^m S_{xj} f_{xj}}{\sum_{j=1}^m S_{xj}}$$

the population parameters, the intrinsic rate of increase (r_m), the finite rate of increase (λ), the net reproductive rate (R_0), and the mean generation time (T), were estimated in sequence. The net reproductive rate (R_0) was calculated as follows:

$$R_0 = \sum_{x=0}^{\infty} l_x m_x$$

The intrinsic rate of increase was estimated by using the iterative bisection method from the Euler-Lotka formula:

$$\sum_{x=0}^{\infty} e^{-r(x+1)} l_x m_x = 1$$

with age indexed from 0 (Goodman, 1982). The mean generation time, which is defined as the period of time needed by a population to increase to R_0 -fold of its size at the stable age-stage distribution, i.e., $e^{rT} = R_0$ or $\lambda^T = R_0$, was calculated as $T = (\ln R_0)/r_m$.

The reproductive value (v_{xj}) is considered as the expectation of future offspring of individuals of age x and stage j (Fisher, 1930). Both the age-stage-specific reproduction value (v_{xj}) and age-stage life expectancy (e_{xj}) were calculated using the program TWSEX-MSChart (Chi, 2017). The standard errors were estimated by using the bootstrap method (Efron and Tibshirani, 1993; Huang and Chi, 2012; Akköprü *et al.*, 2015), with 100,000 bootstraps to obtain stable estimates of standard errors (Akca *et al.*, 2015). The paired bootstrap test was used to compare differences (Efron and Tibshirani, 1993).

Results

The mean developmental times of different stages are presented in Table 1. Developmental times of all preadult stages, except the egg stage, were significantly different between males and females in bisexual reproduction (Table 1).

The total preadult duration was significantly longer in females than in males in the bisexual cohort ($P < 0.0001$). There was no significant difference between total preadult duration of bisexual and oedipal females ($P = 0.292$).

The mortality of juvenile mites ranged from 1% in oedipal reproduction to 9% in bisexual reproduction (Table 2). Most of the mortality occurred during the protonymph stage of *M. muscaedomesticae*. There were no significant differences between total preadult mortality in bisexual and oedipal reproducing cohorts ($P = 0.80$). The sex ratio in bisexual reproduction was 42% (female / total offspring).

Both the adult preoviposition period (APOP) (i.e., the period from adult eclosion to first egg laid) and total preoviposition period (TPOP) (i.e., the period from egg to first egg laid) required for producing female and male offspring were significantly longer in oedipal reproduction than in bisexual reproduction ($P < 0.0001$) (Table 3). It was calculated for males and females by only including male or female offspring separately in the analysis. Neither the APOP ($P = 0.33301$) nor the TPOP ($P = 0.33239$) was significantly different for producing female over male offspring in the bisexual cohort. As would be expected, both the APOP and TPOP were significantly much longer for producing female than male offspring in the oedipal treatment ($P < 0.0001$).

The oviposition periods for producing male offspring were significantly longer than those for producing females in both the oedipal ($P < 0.0001$) and bisexual cohort ($P = 0.01683$). The oviposition periods for producing male and female offspring in the oedipal cohort were significantly shorter than those in the bisexual group ($P < 0.0001$) (Table 3). Oedipal female *M. muscaedomesticae*, on the average, reproduced parthenogenetically during the first 5.62 days of their oviposition period; but produced bisexually during the remainder of their oviposition time following oedipal mating.

The age-stage-specific survival rate (S_{xj}) represents the probability that an egg can survive to age x and stage j (Figure 1). Significant overlaps were observed between stages in both of the reproductive cohorts of *M. muscaedomesticae* due to variable developmental rates occurring

among individuals. The ability to observe the beginning and ending of subsequent stages (*i.e.*, protonymph to deutonymph stages) in the survival curve for each stage is an advantage of using the age-stage, two-sex life table.

Table 1 Development time (days; mean \pm SE) of *Macrocheles muscaedomesticae* feeding on *Musca domestica* eggs.

Reproductive status	<i>n</i>	Bisexual reproduction		Oedipal reproduction	
		Male	<i>n</i>	Female	<i>n</i>
Egg	28	0.64 \pm 0.02 ^{a*}	27	0.61 \pm 0.02 ^{aA**}	54
Larva	28	0.24 \pm 0.02 ^a	27	0.18 \pm 0.01 ^{bA}	54
Protonymph	28	0.84 \pm 0.02 ^b	27	0.96 \pm 0.02 ^{aA}	54
Deutonymph	28	0.91 \pm 0.02 ^b	27	1.09 \pm 0.02 ^{aA}	54
Total preadult	28	2.62 \pm 0.04 ^b	27	2.84 \pm 0.03 ^{aA}	54

* Values in rows followed by the same lower case letter are not significantly different between males and females of bisexual cohorts, using the paired bootstrap test at 5% significance level.

** Values in rows followed by the same capital letter are not significantly different between females of bisexual and oedipal cohorts, using the paired bootstrap test at 5% significance level.

Table 2 Mortality (mean \pm SE) within immature stage of *Macrocheles muscaedomesticae* feeding on *Musca domestica* eggs.

	Bisexual reproduction	Oedipal reproduction
Egg mortality	0 ^{a**} (0)	0 ^a (0)
Larva mortality	0.02 \pm 0.01 ^a (1)	0.05 \pm 0.03 ^a (3)
Protonymph mortality	0.09 \pm 0.04 ^a (6)	0.09 \pm 0.04 ^a (6)
Deutonymph mortality	0.03 \pm 0.02 ^a (2)	0.01 \pm 0.01 ^a (1)
Total preadult mortality	0.14 \pm 0.04 ^a (9)	0.16 \pm 0.04 ^a (10)

* Sample size (*n*) in parenthesis is number dying in each stage. Initial number entering the egg stage was 64.

** Values in rows followed by the same lower case letter are not significantly different, using the paired bootstrap test at 5% significance level.

The age-specific survival rate (l_x), fecundity rate (m_x) and age-specific maternity ($l_x m_x$) were calculated and are displayed in Figure 2. The age-specific survival rate demonstrates a simplified overview of the survival history when all stages are pooled (Figure 2). Females started to produce male and female offspring at age three days in bisexual reproduction, with the daily fecundity of producing male offspring being slightly higher than that of producing female offspring in the majority of cases (Figure 2). In oedipal reproduction, virgin females started

Table 3 Mean ± SE of adult preoviposition period (APOP), total preoviposition period (TPOP), oviposition period and total fecundity of two reproductive types of *Macrocheles muscaedomesticae* feeding on *Musca domestica* eggs.

Statistic	Reproductive status							
	Bisexual				Oedipal			
	Female		Male		Female		Male	
	n	Production of female offspring	n	Production of male offspring	n	Production of female offspring	n	Production of male offspring
APOP	27	2.37 ± 0.14 ^{aB}	27	2.59 ± 0.18 ^{aB}	28	9.43 ± 0.21 ^{aA}	28	4.00 ± 0.16 ^{bA}
TPOP	27	5.21 ± 0.14 ^{aB}	27	5.43 ± 0.18 ^{aB}	28	12.30 ± 1.27 ^{aA}	28	6.87 ± 0.16 ^{bA}
Oviposition period	27	26.11 ± 0.59 ^{bA}	27	28.33 ± 0.70 ^{aA}	28	19.03 ± 0.53 ^{bB}	28	22.64 ± 0.61 ^{aB}
Total fecundity	27	57.96 ± 0.76 ^{bA}	27	71.07 ± 0.81 ^{aA}	54	22.89 ± 3.02 ^{bB}	54	44.35 ± 5.84 ^{aB}

Means in the same row followed by the same capital letter indicates no significant difference between the same sex of bisexual and oedipal cohorts, while means followed by the same lower case letter indicates no significant difference between male and female in the same treatments based on the paired bootstrap test

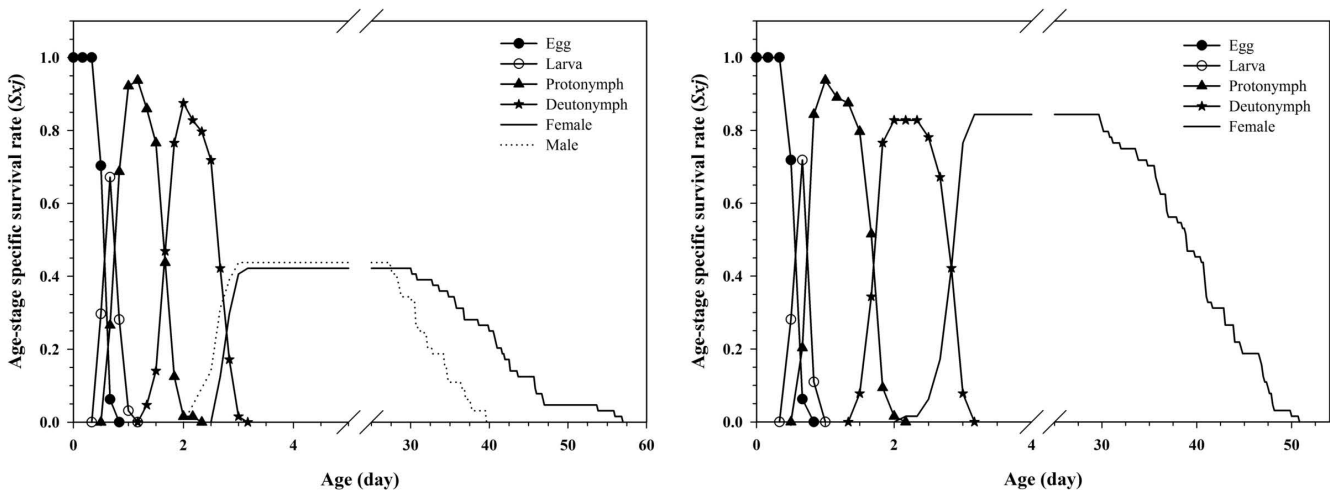


Figure 1 Age-stage-specific survival rate (S_{xy}) of *Macrocheles muscaedomesticae* feeding on *Musca domestica* eggs: bisexual (left) and oedipal (right) cohorts.

to produce male-only offspring from age five days, while female offspring were not produced until age 10 d; which was five days after mating with their parthenogenetically produced male offspring (Figure 2).

Mean adult female longevity were 38.63 ± 0.68 and 37.48 ± 0.75 days in bisexual and oedipal reproduction, respectively. There was no significant difference between the longevity of females in either reproduction system ($P > 0.05$). Mean adult male longevity was 30.25 ± 1.32 days in bisexual reproduction.

Mean daily fecundity were 4.04 and 2.56 offspring in bisexual and oedipal reproduction systems, respectively. In bisexual reproduction, females produced a mean total of 128.51 ± 1.4 offspring (57.96 female and 71.07 male offspring) during their lifetime, while oedipal females produced a mean total of 68.23 ± 8.9 offspring (22.89 female and 44.35 male offspring) (Table 3). There was significant difference between the total fecundity of females in the two reproductive systems (Table 3). The daily mean fecundity of females decreased after insemination in the oedipal group, while male eggs were still being produced in large numbers (Figure 2).

Population parameters for both reproductive types of *M. muscaedomesticae* are presented

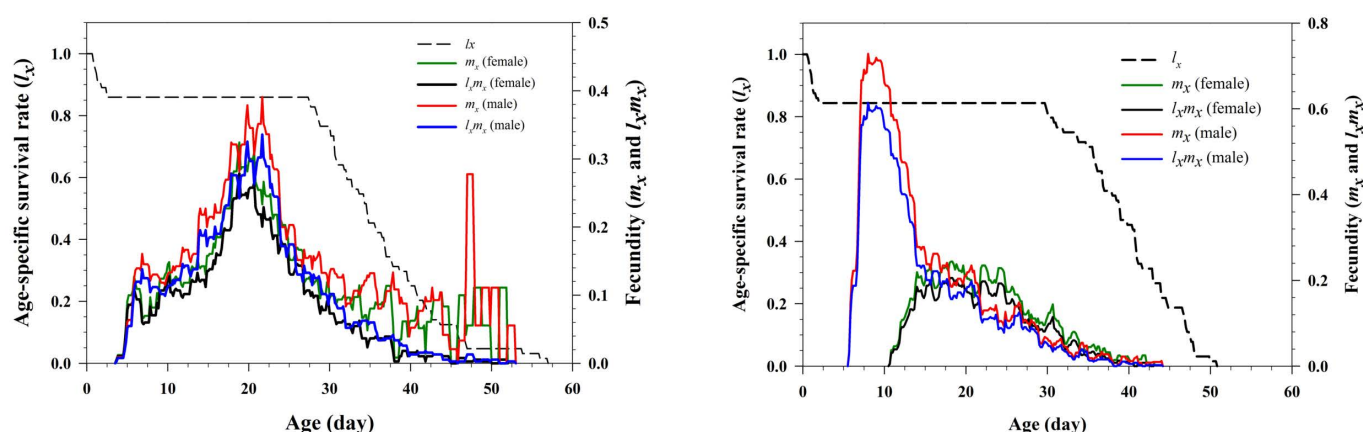


Figure 2 Age-specific survival rate (l_x), fecundity (m_x) and maternity ($l_x m_x$) of *Macrocheles muscaedomesticae* feeding on *Musca domestica* eggs: bisexual (left) and oedipal (right) cohorts.

in Table 4. In bisexual reproduction the life table parameters were calculated as: the intrinsic rate of increase (r_m) = 0.2938 females/female/day, the finite rate of increase (λ) = 1.3415 population multiplication/day, the net reproduction rate (R_0) = 54.216 offspring/individual, the gross reproductive rate (GRR) = 77.7 offspring/individual and the mean generation time (T) = 13.5885 days (Table 4). In the oedipal cohort, by including all eggs in the analysis, values of r_m (0.3420 d⁻¹) and λ (1.4073 d⁻¹) were significantly higher than those obtained in the bisexual cohort ($P < 0.05$), while the mean generation time had a smaller value than that in bisexual reproduction ($P < 0.05$). The GRR and R_0 values did not differ significantly between the two reproductive cohorts ($P > 0.05$) (Table 4). By including only female eggs in the calculation of population parameters (not shown in Table 4), values of r_m , λ and R_0 were 0.1510 ± 0.0083 d⁻¹, 1.1629 ± 0.0098 d⁻¹ and 19.3107 ± 2.7509 offspring, respectively. These parameters were significantly lower than corresponding ones in the bisexual group ($P < 0.05$). The mean generation time (19.60 ± 0.2844 d) was significantly longer than in the bisexually reproducing group, as well as in the oedipal one by including all eggs in the analysis ($P < 0.05$). However, because the oedipal cohort changed its reproductive strategy to bisexual after oedipal mating, it would be invalid to calculate population parameters for this cohort. This will be explained later in the discussion.

The age-stage life expectancy curves (e_{xj}) of *M. muscaedomesticae* for bisexual and oedipal cohorts are plotted in Figure 3. The life expectancy of an egg was 32.1 d in the bisexual cohort, compared to 34.2 d in the oedipal cohort. After reaching adulthood, a female's life expectancy increased to 38.8 d in the bisexual cohort and 38.2 d in the oedipal cohort.

The peak reproductive value (v_{xj}) of the bisexual cohort occurred at age 17 d (Figure 4). The v_{xj} curve for the oedipal cohort was not plotted because computing the reproductive value for this cohort is not applicable.

Discussion

Life history parameters

A summary of life history parameters of *M. muscaedomesticae* based on the present study and published literature is presented in Table 5. Accordingly, the mean egg incubation period

Table 4 Mean \pm SE of population parameters of bisexual and oedipal cohorts of *Macrocheles muscaedomesticae* feeding on *Musca domestica* eggs.

Parameter	Reproductive status	
	Bisexual	Oedipal
Intrinsic rate of increase (r_m) (d^{-1})	0.2938 ± 0.0164^b	0.3420 ± 0.0164^a
Finite rate of increase (λ) (d^{-1})	1.3415 ± 0.0230^b	1.4073 ± 0.0231^a
Net reproductive rate (R_0) (offspring)	54.2160 ± 7.9606^a	57.5670 ± 8.1400^a
GRR	77.7000 ± 8.8110^a	69.6600 ± 9.3560^a
Mean generation time (T) (d)	13.5885 ± 0.3520^a	11.8501 ± 0.2211^b

Values in rows followed by the same lower case letter are not significantly different using the paired bootstrap test at 5% significance level.

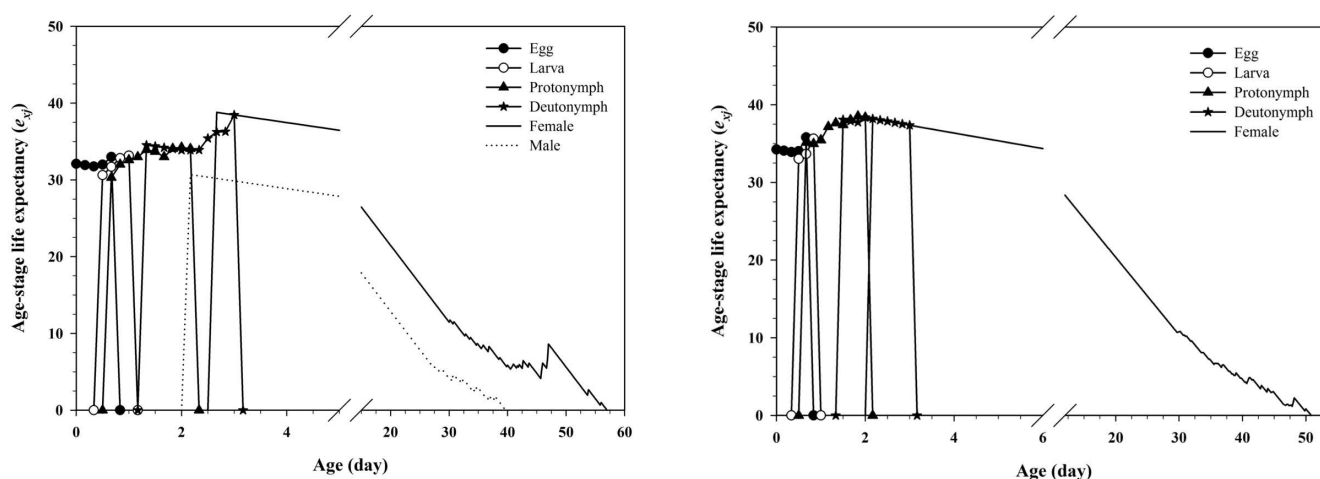


Figure 3 Age-stage-specific life expectancy (e_{xj}) of *Macrocheles muscaedomesticae* feeding on *Musca domestica* eggs: bisexual (left) and oedipal (right) cohorts.

determined in our study is similar to the findings of Abo-Taka *et al.* (2014), but longer than values reported by Wade and Rodriguez (1961). In our study, the highest percentage of developmental time among the juvenile stages was spent in the deutonymph stage, whereas the larval stage was the shortest period. Similarly, Wade and Rodriguez (1961) reported the deutonymph as the longest period, but the egg was the shortest stage in a bisexual population. Wade and Rodriguez (1961) and Filipponi *et al.*, (1971) found no significant differences between the mean total preadult duration in males and females of bisexual colonies of the mite. In our study, the mean total preadult duration was slightly longer in females (68.16 h) compared to 62.88 h for males. The longest mean total preadult duration value was reported by Abo-Taka *et al.* (2014). The differences may be explained by disparities in experimental conditions or differences between strains of *M. muscaedomesticae*.

No mortality was observed in the egg stage of either studied cohort. However, *M. muscaedomesticae* tend to secrete their eggs in the substrate and it is possible that an occasional unnoticed egg could die in an obscure area of the experimental container and be overlooked. This possibility would likely result in the egg mortality being, at best, speculative, - a point noted by Cicolani (1979) as well.

In our study, the calculated sex ratio (females / total offspring) in the bisexual cohort (42%)

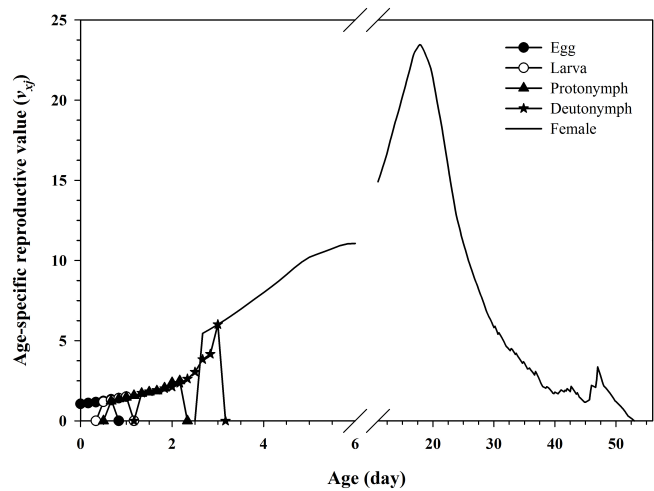


Figure 4 Age-stage-specific life expectancy (v_{xj}) of *Macrocheles muscaedomesticae* feeding on *Musca domestica* eggs: bisexual cohort.

Table 5 Summary of life history parameters of *Macrocheles muscaedomesticae* based on the present study and available literature.

	Wade & Rodriguez, 1961		Filipponi <i>et al.</i> , 1971	Cicolani, 1979	Abo-Taka <i>et al.</i> , 2014	This study	
Origin	USA		Italy	Italy	Egypt	Iran	
Reproduction type	Bisexual	Virgin females	Bisexual	Virgin females except for sex ratio	Bisexual	Bisexual	Oedipal
Prey	housefly eggs	housefly eggs	housefly eggs and nematodes	housefly eggs and nematodes	housefly eggs	housefly eggs	housefly eggs
Temperature	26.7 °C	26.7 °C	28 °C	28 – 30 °C	28 °C	28 °C	28 °C
Mean egg incubation period	7.3 h ♂ 6.9 h ♀	8.8 h ♀	-	-	16.8 h	15.4 h ♂ 14.6 h ♀	15.1 h ♀
Mean developmental time	54.51 h ♂ 56.35 h ♀	58.34 h ♀	59.0 h ♂ 59.8 h ♀	42.3 h ♀ 30 °C	96 h ♀	62.9 h ♂ 68.1 h ♀	69.1 h ♀
Sex ratio (females / total offspring)	43.3%	-	44%	44% 28 °C	-	42%	-
Mean adult female longevity	23.9 d	24.3 d	-	11.3 d 28 °C	25.2 d	38.6 d	37.5 d
Mean total fecundity	61.4	91.7	159.6	159.6 28 °C	-	128.5	68.2

was near to the findings of Wade and Rodriguez (1961), Filipponi *et al.* (1971) and Cicolani (1979). However, the sex ratio (females / total adults) was reported to be 75.8% in a population of *M. muscaedomesticae* studied by Filipponi *et al.* (1971) (Table 5).

The adult preoviposition period was not significantly different between mated and virgin females in the study by Wade and Rodriguez (1961), which was similar to the value observed in the bisexual cohort of our study. Based on our findings, the oviposition period of females in the bisexual cohort lasted, on average, 16% longer than females of the oedipal cohort.

According to our results, females in the bisexual group had a mean fecundity nearly two times greater than data reported by Wade and Rodriguez (1961). On the other hand, mean egg production observed by Filipponi *et al.* (1971) and Cicolani (1979) was higher than our figure. Mean adult female longevity was the longest in our study, and the shortest in Cicolani (1979) (Table 5).

The intrinsic rate of increase (r_m) for *M. muscaedomesticae* feeding on *Mu. domestica* eggs in this study (0.293) was lower than the only other reported value for this species (0.905) (Cicolani, 1979). Differences in several experimental variables such as prey species, strain of predatory mite, temperature, as well as calculation method may explain the lower r_m value found for *M. muscaedomesticae* reared on *Mu. domestica* in our study compared to Cicolani's results. Cicolani (1979) studied the biology and life table parameters of *M. muscaedomesticae* fed on a combination of *Mu. domestica* eggs and live rhabditid nematodes at 30°C. In addition, he stressed that due to atypical features of macrochelid biology, e.g., facultative larviparity and arrhenotoky, non-standard analyses were necessary to estimate the r_m rather than the usual methods used in demographic analysis. By taking these points, particularly the last one, into consideration we believe that Cicolani overestimated the true value of r_m in *M. muscaedomesticae*.

The r_m value is a key demographic parameter for forecasting the potential success of a pest species. It can also be useful as a means of assessing promising biocontrol candidates on the basis of their reproductive potential (Roy *et al.*, 2003). According to Sabelis (1992) and Sabelis *et al.* (2002), theoretically, a predator that has a potential growth rate equal to or greater than its prey should actively control the prey population. Nurita *et al.* (2012) studied the life table parameters of *Mu. domestica* reared on three different diets and reported r_m values as 0.237, 0.245 and 0.268 (d^{-1}) on solid waste, poultry manure and standard laboratory diet, respectively. The intrinsic rate of increase (r_m) of *M. muscaedomesticae* feeding on *Mu. domestica* eggs in the current study (0.293) is higher than the r_m values reported for *Mu. domestica* by Nurita *et al.* (2012). The Iranian strain of *M. muscaedomesticae*, therefore, has the potential to be used as an agent for biological control of *Mu. domestica* in manure microhabitats.

Oedipal reproduction

Based on our findings, mated females produced an average of 128 offspring, which is about twice the average number produced by females in the oedipal cohort (68 offspring). The reduction of female fecundity in oedipal mating may be attributed to an inherent penalty experienced by the female in this type of mating. When males are absent, females are forced to wait to inbreed with a parthenogenetically produced son. This delay in sexual reproduction is a cost or devaluation to her fecundity (Adamson and Ludwig, 1993).

Many mites are haplodiploid and several groups have life histories that could potentially adapt mother-son mating (Adamson and Ludwig, 1993). In our study, we found that a single virgin female was capable of initiating a population through oedipal reproduction. This finding is consistent with those of Oliver (1962), Bergh (2001), McCulloch and Owen (2012) and Tuan *et al.* (2015) who reported oedipal reproduction in *Histiostoma murchiei* Hughes and Jackson (Acari: Histiostomatidae), *Phyllocoptruta oleivora* (Ashmead) (Acari: Eriophyidae), *Ornithonyssus sylviarum* (Canestrini and Franzago) (Acari: Macronyssidae) and *Tetranychus urticae* Koch (Acari: Tetranychidae), respectively.

Dispersal of *M. muscaedomesticae* can be accomplished by phoretic association with dipterans when the dung desiccates and deteriorates. Our laboratory tests showed that

a combination of bisexual and oedipal reproduction can result in the founding of a new population by a single inseminated or virgin female *M. muscaedomesticae*. Because most female macrochelids are likely inseminated prior to dispersal, sib-mating among F1 progeny would be most relevant to the initiation of a new population. A dispersing female mite might also arrive in the midst of an established population on a new manure substrate. Alternatively, when populations are low early in the season or following a pesticide application there may be few or no conspecific males to mate with in her environment. Under such conditions, oedipal reproduction provides a means for female *M. muscaedomesticae* to establish a new population without being constrained by opportunities to mate.

Anderson stated in 1983 that, at that time, *M. muscaedomesticae* offered the greatest potential as an effective predator against all major dipteran species associated with confined poultry and livestock worldwide. He also claimed that the species exhibited the four fundamental traits of an effective natural enemy listed by Douthett and DeBach (1964), *i.e.*, (1) high searching ability; (2) high degree of host (prey) specificity; (3) high rate of increase in relation to the pest population; and (4) ability of occupying all of the host (prey) colonized microhabitats (Anderson, 1983). In addition to having these desirable traits, our results have demonstrated that unmated female *M. muscaedomesticae* are also able to produce and later copulate with their sons (oedipal mating), allowing virgin females to eventually produce both sexes. In the context of predator ecology, this reproductive system is advantageous because it allows females to disperse to new manure substrates and begin colonizing in the absence of males and without prior mating. This interesting reproductive behavior considerably extends the dissemination potential of this predator, and, to some extent, helps to explain why it is as cosmopolitan and predominant a natural enemy as it is.

Acknowledgments

We are thankful to Prof. Hsin Chi (Ömer Halisdemir University, Turkey) for his help in data analysis. We also thank two anonymous reviewers for their helpful comments on an earlier draft of this manuscript. The study was financially supported by the Shahid Chamran University of Ahvaz.

References

- Abo-Taka S.M., Heikal H.M., Abd El-Raheem A.M. 2014. Macrochelid mite, *Macrocheles muscaedomesticae* (Acarina: Macrochelidae) as a biological control agent against house fly, *Musca domestica* (Diptera: Muscidae) in Egypt. *Int. J. Zool. Res.*, 10: 30-36. doi:10.3923/ijzr.2014.30.36
- Adamson M., Ludwig D. 1993. Oedipal mating as a factor in sex allocation in haplodiploids. *Philos. Trans. R. Soc. Lond., B, Biol. Sci.*, 341: 195-202. doi:10.1098/rstb.1993.0103
- Akköprü E.P., Atlihan R., Okut H., Chi H. 2015. Demographic assessment of plant cultivar resistance to insect pests: a case study of the dusky-veined walnut aphid (Hemiptera: Callaphididae) on five walnut cultivars. *J. Econ. Entomol.*, 108: 378-387. doi:10.1093/jee/tov011
- Anderson J.R. 1983. Mites as biological control agents of dung-breeding pests: Practical consideration and selection for pesticide resistance. In: Hoy M.A., Cunningham G.L., Knutson L. (Eds) *Biological control of pests by mites*: University of California Press. p. 99-102.
- Akca I., Ayvaz T., Yazıcı E., Smith C.L., Chi H. 2015. Demography and population projection of *Aphis fabae* (Hemiptera: Aphididae): With additional comments on life table research criteria. *J. Econ. Entomol.*, 108: 1466-1478. doi:10.1093/jee/tov187
- Axtell R.C. 1961. New records of north American Macrochelidae (Acarina: Mesostigmata), and their predation rates on the house fly. *Ann. Entomol. Soc. Am.*, 54: 748-748. doi:10.1093/aesa/54.5.748
- Axtell R.C. 1963. Acarina occurring in domestic animal manure. *Ann. Entomol. Soc. Am.*, 56: 628-633. doi:10.1093/aesa/56.5.628
- Bergh G.C. 2001. Ecology and aerobiology of dispersing citrus rust mite (Acari: Eriophyidae) in central Florida. *Environ. Entomol.*, 30(2): 318-326. doi:10.1603/0046-225X-30.2.318
- Chi H. 1988. Life-table analysis incorporating both sexes and variable development rates among individuals. *Environ. Entomol.*, 17: 26-34. doi:10.1093/ee/17.1.26
- Chi H. 2017. TWOSEX-MSChart: a computer program for the age-stage, two-sex life table analysis [Internet]. Available from: <http://140.120.197.173/Ecology/>
- Chi H., Liu H. 1985. Two new methods for the study of insect population ecology. *Bull. Inst. Zool. Acad. Sinica*, 24: 225-240.

- Cicolani B. 1979. The intrinsic rate of natural increase in dung macrochlid mites, predators of *Musca domestica* eggs. *Boll. Zool.*, 46(3): 171-178. doi:10.1080/11250007909440296
- Doutt R.L., Debach P. 1964. Some biological control concepts and questions. In: Debach, P. (Ed). *Biological control of insect pests and weeds*. London, Chapman & Hall. p. 118-142.
- Efron B., Tibshirani R.J. 1993. *An introduction to the bootstrap*. New York, Chapman & Hall, pp. 456. doi:10.1007/978-1-4899-4541-9
- Fathipour Y. 1994. Soil mites fauna in orchards of Tabriz and population fluctuation and abundance of important species [MSc thesis]. Tarbiat Modarres University of Tehran. pp. 213.
- Filipponi A. 1964. The feasibility of mass producing macrochelid mites for field trials against house flies. *Bull. World Health Organ.*, 31: 499-501.
- Filipponi A., Mosna B., Petrelli G. 1971. The optimum temperature of *Macrocheles muscaedomesticae* as a population attribute. *Riv. Parassitol.*, 32: 193-218.
- Fisher R.A. 1930. *The genetical theory of natural selection*. Oxford, Clarendon Press. pp. 318.
- Galazzi D., Nicoli G. 1996. Comparative study of strains of *Phytoseiulus pesimilis* Athias-Henriot (Acarina: Phytoseiidae). I. Development and adult life. *Boll. Ist. Entomol. "G. Grandi" Univ. Bologna*, 50: 215-231.
- Gerson U., Smiley R.L., Ochoa R. 2003. *Mite (Acari) for pest control*. Oxford, Blackwell Science Ltd. pp. 539. doi:10.1002/9780470750995
- Goodman D. 1982. Optimal life histories, optimal notation, and the value of reproductive value. *Am. Nat.*, 119: 803-823. doi:10.1086/283956
- Ho C.-C. 1985. Mass production of the predaceous mite, *Macrocheles muscaedomesticae* (Scopoli) (Acarina: Macrochelidae), and its potential use as a biological control agent of house fly, *Musca domestica* L. (Diptera: Muscidae) [PhD thesis]. University of Florida. pp. 196.
- Huang Y.B., Chi H. 2012. Age-stage, two-sex life tables of *Bactrocera cucurbitae* (Coquillett) (Diptera: Tephritidae) with a discussion on the problem of applying female age-specific life tables to insect populations. *Insect Sci.*, 19: 263-273. doi:10.1111/j.1744-7917.2011.01424.x
- Kazemi S., Rajaei A. 2013. An annotated checklist of Iranian Mesostigmata (Acari), excluding the family Phytoseiidae. *Persian J. Acarol.*, 2 (1): 63-157.
- Keiding J. 1999. Review of the global status and recent development of insecticide resistance in field populations of the housefly *Musca domestica* (Diptera: Muscidae). *Bull. Entomol. Res.*, 89 (Suppl. 1): S9-S67.
- Khoobdel M., Davari B. 2011. Fauna and abundance of medically important flies of Muscidae and Fanniidae (Diptera) in Tehran, Iran. *Asian Pac. J. Trop. Dis.*, 4(3): 220-223. doi:10.1016/S1995-7645(11)60073-4
- Koppert 2010. New soil-dwelling predatory mite very effective against thrips infestations [Internet]. Available from: <https://www.koppert.com/news-biological-systems/new-soil-dwelling-predatory-mite-very-effective-against-thrips-infestations/>
- McCulloch J.B., Owen J.P. 2012. Arrhenotoky and oedipal mating in the northern fowl mite (*Ornithonyssus sylvarum*) (Acari: Gamasida: Macronyssidae). *Parasit. Vectors*, 5: 281-285. doi:10.1186/1756-3305-5-281
- Nurita A.T., Abu Hassan A., Aiman Hanis J. 2012. Life tables and development of *Musca domestica* (Diptera: Muscidae) on three different diets. 24th International Congress of Entomology, 19-25 August, Daegu, South Korea.
- Oliver J.H. 1962. A mite parasitic in the cocoons of earthworms. *J. Parasitol.*, 48: 120-123. doi:10.2307/3275424
- Pereira C., de Castro M.P. 1945. Contribution to the knowledge of the type species of *Macrocheles* Latr. (Acarina): *M. muscaedomesticae* (Scopoli, 1772). *Emend. Arq. Inst. Biol.*, 16: 153-186.
- Perring T.M., Lackey L.J. 1989. Temperature and humidity effect on mortality and preadult development of two *Phytoseiulus persimilis* strains (Acari: Phytoseiidae). *Int. J. Acarol.*, 15: 47-52. doi:10.1080/01647958908683821
- Roy M., Brodeur J., Cloutier C. 2003. Effect of temperature on intrinsic rates of natural increase (r_m) of a coccinellid and its spider mite prey. *Biocontrol*, 48: 57-72. doi:10.1023/A:1021289832664
- Sabelis M.W. 1992. Predatory arthropods. In: Crawley M.J. (Ed) *Natural enemies: The population biology of predators, parasites and disease*. Oxford, Blackwell Scientific Publications, p. 225-264. doi:10.1002/9781444314076.ch10
- Sabelis M.W., van Baalen M., Pels B., Egas M., Janssen A. 2002. Evolution of exploitation and defense in plant-herbivore-predator interactions. In: Dieckmann U., Metz J.A.J., Sabelis M.W., Sigmund K. (Eds) *The adaptive dynamics of infectious diseases: In Pursuit of virulence management*. Cambridge, UK, Cambridge University Press, p. 279-321. doi:10.1017/CB09780511525728.028
- Sharififard M., Mossadegh M.S., Vazirianzadeh B., Zarei-Mahmoudabadi A. 2011. Interactions between Entomopathogenic fungus, *Metarhizium anisopliae* and sublethal doses of spinosad for control of house fly, *Musca domestica*. *J. Arthropod. Borne Dis.*, 5(1): 28-36.
- Sharififard M., Safdari F. 2013. Evaluation of resistance or susceptibility of the house fly, *Musca domestica* L., of semi-industrial livestock farms to some pyrethroid insecticides in Ahvaz, southwestern Iran. *Jundishapur J. Health. Sci.*, 5(3): 201-206.
- Tuan S.-J., Lin Y.-H., Yang C.-M., Atlihan R., Saska P., Chi H. 2016. Survival and reproductive strategies in two-spotted spider mites: demographic analysis of arrhenotokous parthenogenesis of *Tetranychus urticae* (Acari: Tetranychidae). *J. Econ. Entomol.*, 109(2), 502-509. doi:10.1093/jee/tov386
- Wade C.F., Rodriguez J.G. 1961. Life history of *Macrocheles muscaedomesticae* (Acarina: Macrochelidae) a predator of the house fly. *Ann. Entomol. Soc. Am.*, 54: 776-788. doi:10.1093/aesa/54.6.776