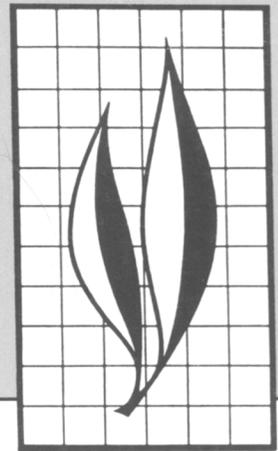


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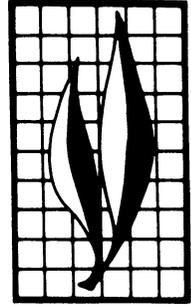
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## Hybridization in Principal Parasitoids of Synanthropic Diptera: The Genus *Muscidifurax* (Hymenoptera: Pteromalidae)

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## ABSTRACT

Parasitoid vigor measured by female longevity, progeny production, and host destruction, is compared among cohorts from different populations of four *Muscidifurax* species: *M. raptor* Girault and Sanders, *M. zaraptor* Kogan and Legner, *M. raptorellus* Kogan and Legner and *M. uniraptor* Kogan and Legner, parasitoids of synanthropic flies. Different populations of the species are ranked according to their parasitization rates. Hybridization between populations usually produced an immediate post-mating parasitization depression in the female, with partial or full recovery occurring in randomly mated F<sub>1</sub> or F<sub>2</sub> progeny. Parasitization intensity approached an asymptote when females were 6 to 7 days old. Single matings were sufficient to guarantee female-biased sex ratios in progeny through 10 oviposition days, after which senescing females fertilized fewer eggs. Virgin females either approximated or exceeded mated females in parasitization activity. Preintroduction assessments of different parasitoid populations may be desirable for biological control to avoid postmating depression and the creation of inferior hybrids. Such assessments may also reveal cases where intercompatibility results in superior hybrids.

*Key Words* = Diptera, Parasitoids, *Muscidifurax*, Hymenoptera.

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# Hybridization in Principal Parasitoids of Synanthropic Diptera: The Genus *Muscidifurax* (Hymenoptera: Pteromalidae)<sup>1</sup>

## INTRODUCTION

SYNANTHROPIC FILTH-BREEDING DIPTERA (Povolny 1971) are a major problem for poultry and dairy producers and feedlot operators in many areas of the United States. The problem is particularly acute in California, where rapid suburban expansion has often encroached on agricultural areas. Because of problems associated with unilateral chemical fly control, integrated management programs for synanthropic flies have been under development in several regions (Axtell 1970; Legner and Dietrick 1974; Legner, Sjogren, and Hall 1974; Petersen and Meyer 1983). Natural enemies are important control components, particularly in the more stable manure communities found in many caged-layer, dairy, and feedlot operations.

Among the natural enemies, parasitic wasps have received the most research emphasis. Research has dealt with observations on seasonal occurrence (Ables and Shepard 1976*a,b*; Legner and Brydon 1966; Legner and Olton 1971; Legner and Greathead 1969; Mullens, Meyer, and Mandeville 1986; Petersen and Meyer 1983; Rutz and Axtell 1980), experimental parasitoid releases (Legner and Brydon 1966; Legner and Dietrick 1974; Morgan et al. 1975; Olton and Legner 1974, 1975; Rutz and Axtell 1979), and introduction of new species and strains (Legner 1978).

Parasitic insects contribute significantly to the natural biological reduction of endophilous synanthropic flies, where population density is largely dependent on human activity (Legner 1971; Legner and Olton 1971; Legner, Sjogren, and Hall 1974; Mullens, Meyer, and Mandeville 1986). Control of this group, including the common house and stable flies and several species of *Fannia*, has been increased by inundation with parasitic insects, most effectively species of *Muscidifurax* and *Spalangia* (Legner 1971, 1981; Legner and Brydon 1966; Legner and Dietrick 1972; Legner, Dietrick, and Blehm 1982; Morgan 1981; Morgan et al. 1975, 1979; Olton and Legner 1975; Rutz and Axtell 1979). An expanding world market for these parasitoids exists (Dietrick 1981; Morgan 1981).

Although parasitoid inundation when combined with proper waste management (Legner and Bowen 1973; Legner et al. 1973) may reduce fly abundance to below the annoyance threshold, the degree of control varies in different climates and seasons (Legner 1977; Morgan et al. 1975; Petersen and Meyer 1983; Legner and Dietrick, unpublished data 1977). The parasitic insects available for inundation have usually been restricted to cohorts from a single population of a few species, usually those acquired at subtropical latitudes where initial experiments were conducted to show their effectiveness.

Investigations have shown that distinctive populations of a single species of fly parasitoid may exist in different geographical and climatic areas each differing in its activity (Kogan and Legner 1970; Legner 1969, 1972, 1976, 1977, 1983, 1986*a,b*; 1987*a,b*, 1988*a*; Legner and Greathead 1969; Legner and Olton 1968; Legner, Bay, and White 1967; Legner, Moore, and Olton 1976; Legner, Dietrick, and Blehm 1982), a finding that is becoming increasingly apparent in other host-parasitoid

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relationships. The utilization of different species and populations that are capable of greater parasitization rates in a wider variety of climates offers possibilities for substantial gains in the biological control of synanthropic flies.

For example, cohorts from a drought-resistant population of the pupal parasitoid *Spalangia endius* Walker from New Zealand (Legner and Olton 1968; Legner, Dietrick, and Blehm 1982) have considerable potential in the semiarid American West. This New Zealand relative also demonstrates greater activity at lower temperatures (22°C) than the resident form, and hybridizes with other populations of the same species where it is liberated. Commercial mass production may be greatly facilitated because of hybrid vigor, lower rearing temperature, and humidity requirements (Legner, Dietrick, and Blehm 1982).

A population of *Muscidifurax zaraptor* Kogan and Legner in the central part of the western Great Plains of Colorado and New Mexico (Legner 1977; Legner, Dietrick, and Blehm 1982) shows enhanced qualities of fecundity, cold-hardiness, heat tolerance and habitat-foraging capability. Populations of this parasitoid in California and the central United States, however, are much more restricted in their ability to penetrate the breeding habitat in search of fly puparia, and in their fecundities and tolerances to high temperatures and winter cold (Legner 1977; Legner, unpublished data 1980).

Discoveries that hybrids of interbred synanthropic fly parasitoid populations may demonstrate heterotic behavior (Legner 1972, 1987*b*, 1988*b*; Legner and Warkentin 1985), or acquire a fully parthenogenic reproductive mode (Legner 1987*a,c*), widens possibilities for biological control through inoculative releases. The direct effects of host mortality wrought by the individuals released may be compounded if heterotic offspring show enhanced killing power, greater longevity, and superior reproductive capacity.

*Production of Superior Hybrids.* Research has been performed at Riverside to direct heterosis to favor certain desirable parasitoid traits. The process entails locating two compatible populations of a species, each with characteristics that would be advantageous to form a single superior hybrid. An example was found in *M. raptorellus* Kogan and Legner from South America. One population from central Chile is gregarious, but possesses poor host-searching capacity (Legner 1967, 1987*b*, 1988*a*). Although its oviposition rate is higher than another population from coastal Peru, the Chilean form distributes its eggs among fewer hosts. Adults of the Chilean population are also comparatively smaller, thigmotactic, and lethargic (Kogan and Legner 1970; Legner 1969, 1983; Legner unpublished data 1979). The Peruvian form demonstrates higher mobility and aggressiveness, but is largely solitary in its ovipositional behavior.

Cross-matings and backcrosses of cohorts from the two *M. raptorellus* populations produce offspring that show degrees of gregarious oviposition in proportion to the quantity of polygenic heritage (Legner 1987*b,d,e*; 1988*a*). These hybrids are heterotic in their greater output of total progeny and superior host kill, depending on which female initiated the original cross (Legner 1987*b*, 1988*a*, and unpublished data). The heterosis has been observed to persist through 15 generations (Legner, unpublished data 1987). The use of such heterotic strains to control synanthropic flies in the field might result in improved biological control.

*Population Intercompatibility.* A detailed analysis of hybridization in *Muscidifurax* has not been performed, although previously mentioned positive heterotic effects have been measured in a few cases. Postmating behavior and hybrid parasitization capabilities

have not been adequately compared. This study examines cohorts from several populations of four species, and compares hybrids to their parents. Certain guidelines are evident for the transfer of parasitoid populations to new localities.

## MATERIALS AND METHODS

Parasitization and reproductive rates were measured among cohorts from several populations of four *Muscidifurax* species and hybrids, utilizing fifteen 1-day-old females, isolated in screened polystyrene vials (46 cm<sup>3</sup>) with a basal area of 7 cm<sup>2</sup>. These females were mated within 24-hour to  $\leq$ 1-day-old males. Randomness in virgin partners from the respective populations was attained by manual selection of parasitoids emerging in gelatin capsules (10 × 25mm). Each female was supplied daily with twenty 24-hour- to 30-hour-old puparia of *Musca domestica* L. ( $6.4 \pm 0.5$  mm ×  $2.8 \pm 0.2$  mm), distributed randomly over the vial base. Flies were reared to pupation using commercial CSMA medium. Parasitization efficiency at this host density and in this environment at 25.5°C was near maximum (Legner 1967, 1979a,b, 1987a,b).

The parasitoids were studied in their third or fourth generation from field collection and included, respectively, cohorts of four populations of *M. zaraptor* Kogan and Legner from Riverside, California, Denver, Colorado, Las Cruces, New Mexico, and Lincoln, Nebraska; four populations of *M. raptor* Girault and Sanders from Rehovot, Israel, Raleigh, North Carolina, Huntsville, Utah, and Riverside, California; two populations of *M. raptorellus* Kogan and Legner from Quillota, Chile and La Molina, Peru; and two populations of *M. uniraptor* Kogan and Legner collected in Cayey, Puerto Rico in 1965 and 1981. Only one species, *M. raptoroides* Kogan and Legner from Central America, was not represented. Collections in each locality were made from a minimum of six field sites, with cultures established from a mixture of these sites.

Host puparia were exposed to parasitoids for 24 hours at  $25.5^\circ \pm 1^\circ\text{C}$ , 55 percent RH, and 13L:11D photoperiod of about 269 lux irradiance at table level. Light was supplied by fluorescent lamps. Puparia were then incubated separately in gelatin capsules for the emergence of F<sub>1</sub> parasitoid and host progeny. An aliquot of five replicates was dissected to assess the total number of eggs laid, and unemerged puparia in the remaining ten replicates were also dissected to detect abortive parasitism (unhatched eggs and dead larvae).

Parasitoid longevity, total progeny, and sex ratio were recorded for 10 females for 14 days, beginning when females were 3 days old, which is a compromise in experimental time representing about half the life expectancy of 90 percent of females in a population (Coats 1976; Legner 1987a,b; Legner and Gerling 1967; Markwick 1974). The importance of extended experimental time for recording behavior is apparent also in other groups of parasitoids (Hey and Gargiulo 1985). Dissections revealed < 5 percent abortive parasitism, which gave credibility to adult emergence data.

The net reproductive rate ( $R_0 = \sum l_x m_x$ ) and intrinsic rate of natural increase ( $r_m$ ) were derived according to Birch (1948) from an initial cohort of 10 ovipositing females. A close approximation of  $r_m$  described by Birch (1948) was made using the formula

$$\sum e^{-rx} l_x m_x = 1.$$

Additionally, a net total progeny rate (males + females) ( $R_t$ ) was calculated as  $R_t = \sum_x l_x t_x$  and the intrinsic total progeny rate ( $r_t$ ) was derived using Birch's (1948) formula, modified as follows:

$$\sum e^{-r_t x} l_x t_x = 1$$

where  $t_x$  = mean number of total male and female progeny per parent at age  $x$ . These computations are useful for appraising a female's total oviposition activity (Legner 1988*b*).

Finally, a net host destruction rate (number of hosts killed as determined by Abbott's Formula 1925) was calculated as  $R_d = \sum_x l_x d_x$  and the intrinsic total destruction rate ( $r_d$ ) was derived using Birch's (1948) formula, modified as follows:

$$\sum e^{-r_d x} l_x d_x = 1$$

where  $d_x$  = mean number of hosts destroyed per female parasitoid at age  $x$  as determined by Abbott's formula. These computations enable a precise measurement of host destruction (Legner 1979*c*, 1988*b*).

The pivotal age (Birch 1948) was estimated as the mean length of development of females at  $25.5^\circ \pm 1^\circ\text{C}$ , 55 percent RH plus 3 days. Because females were 3 days old (posteclosion) when first caged, their mean pivotal age was 23.5 days. An estimated 90 percent survival rate of immature females from oviposition was used to calculate  $l_x$ . Although the value  $m_x$  measures only the "effective" number of female offspring per female in the age interval  $x$ , based on emerged offspring, dissections showing <5 percent abortive parasitism indicate  $m_x$  being very close to the actual number of female eggs deposited.

Experiments were conducted with replicates arranged in a completely random design in space. Backcrosses were simultaneously compared with parental fecundities by staggering the generations. Analyses of variance were performed on the data transformed to the  $\log_{10}(X+0.5)$  for total progeny (Steel and Torrie 1980). Significant differences were tested at  $P \leq 0.05$  on transformed data by multiple mean separation using Duncan's (1955) new multiple range test.

## RESULTS AND DISCUSSION

*Distinctions Among Species and Populations.* Total progeny and their sex ratio are recorded for separate populations of each species (table 1), while additional fecundity and host destruction data are shown graphically for arrhenotokus-mated and virgin, and thelytokous females (figs. 1*a-3b*, pp. 12-32), respectively. Significant differences among cohorts were especially evident in total progeny (tables 1-4). For example, ranking the populations of *M. zaraptor* according to total progeny production, the Colorado isolate was highest, followed by Nebraska, New Mexico, and California. In *M. raptor*, the Utah population produced the most progeny, followed by California, Israel, and North Carolina. The gregarious Chilean population of *M. raptorellus* produced significantly more total progeny than its Peruvian counterpart (table 4), but there were no differences among the two chronological isolates of *M. uniraptor* from Puerto Rico, which continued to maintain their characteristics through 25 generations in culture (table 1, figs. 3*a* and 3*b*). These data reflect total eggs laid as dissections showed <5 percent unhatched eggs and dead larvae.

TABLE 1. TOTAL PROGENY OF PARENTAL COHORTS OF MUSCIDIFURAX RAPTOR, M. ZARAPTOR, M. RAPTORELLUS AND M. UNIRAPTOR, WHERE 10 FEMALES OVIPOSIT CONTINUOUSLY AT 25.5° ± 1°C, 55% RH ON 20 MUSCA DOMESTICA PUPARIA DAILY FOR 14 DAYS

♀	Average Total Progeny/S.E./% ♀♀												
	<i>M. zaraptor</i>						<i>M. raptor</i>						<i>M. raptorellus</i>
	Virgin	Calif.	Colorado	Nebraska	Mexico	New	Israel	North Carolina	Utah	Calif.	Chile	Peru	
<i>M. zaraptor</i>	Calif.	83.7	71.5	58.9	35.7	96.0	*	*	*	*	*	*	
		(2.3)	(13.8)	(3.4)	(2.2)	(3.3)							
		0%	69.2%	68.7%	76.6%	79.2%							
Colorado		174.3	147.2	169.6	97.5	97.7	*	*	*	*	*	*	
		(9.7)	(4.0)	(12.2)	(19.1)	(1.9)							
		0%	77.6%	90.4%	87.2%	89.3%							
Nebraska		89.0	41.5	47.5	97.6	63.3	*	*	*	*	*	*	
		(19.7)	(7.1)	(11.5)	(11.1)	(4.2)							
		0%	77.1%	85.3%	84.6%	80.0%							
New Mexico		109.3	69.7	88.3	31.0	75.4	*	*	*	*	*	*	
		(11.8)	(2.7)	(7.3)	(1.3)	(7.1)							
		0%	75.6%	81.2%	72.6%	75.8%							
<i>M. raptor</i>	Israel	119.3	*	*	*	*	124.0	63.0	97.7	—†	*	*	
		(25.5)					(19.1)	(13.0)	(4.0)				
		0%					67.9%	81.7%	80.0%				
North Carolina		43.3	*	*	*	*	48.3	46.4	—	*	*		
		(2.7)					(3.6)	(9.0)					
		0%				65.6%	63.8%						

(Continued on next page.)

TABLE 1. (Continued)

♀	Average Total Progeny/S.E./% ♀♀												
	<i>M. zaraftor</i>						<i>M. raptor</i>					<i>M. raptorellus</i>	
	Virgin	Calif.	Colorado	Nebraska	New Mexico	Israel	North Carolina	Utah	Calif.	Chile	Peru		
<i>M. raptor</i> (continued)													
Utah	173.0 (5.5) 0%	*	*	*	*	80.3 (6.3) 85.8%	84.7 (12.3) 83.0%	204.5 (9.8) 82.9%	—	*	*		
Calif.	121.2 (9.8) 0%	*	*	*	*	—	—	—	126.8 (10.6) 70.4%	*	*		
<i>M. raptorellus</i>													
Chile	135.3 (30.0) 0%	*	*	*	*	*	*	*	*	165.4 (34.1) 61.6%	132.4 (17.3) 61.1%		
Peru	84.7 (2.7) 0%	*	*	*	*	*	*	*	*	86.3 (6.9) 76.6%	85.0 (3.6) 79.6%		
<i>M. uniraptor</i>													
1965	101.1 (6.1) 98.5%	*	*	*	*	*	*	*	*	*	*		
1981	119.6 (6.1) 21.7%	*	*	*	*	*	*	*	*	*	*		

\* Incompatible.

† — = Cross not performed.

Population reproduction statistics ( $R_o/r_m$ ) showed parallel trends with total progeny in all cohorts except the 1981 isolate of *M. uniraptor*, where male progeny predominated after the fourth oviposition day (table 1, figs. 1a-3b).

Host population destruction statistics also showed similar trends with total progeny production except in *M. raptorellus*. In this case, although the gregarious Chilean population produced almost twice as many progeny, the solitary Peruvian cohort demonstrated a much higher host-destruction capacity (tables 1 and 4, figs. 1i and 1j), suggesting that gregarious behavior may compensate for poor host-searching and destruction.

*Hybridized Cultures.* The total progeny among various hybridized cultures compared to parental cohorts are shown in tables 2, 3, and 4, with separate lines discussed as follows:

*Riverside, California line of M. zaraptor.* Slight but nonsignificant differences in total progeny were found among virgin and mated California *M. zaraptor* (table 2, figs. 1a and 2a). Mating with New Mexico males significantly increased total progeny, whereas mating with Nebraska males significantly decreased them. Hybrids mated to random males, which actually represents a backcross to the maternal line, did not attain the equivalent progeny production of their parents. These results indicate the presence of considerable hybrid dysgenesis among *M. zaraptor* hybrids. Mixing different populations in this species might not be expected to increase host impact, and could produce adverse effects on population balance, especially if the hybrids are capable of persisting in the environment.

*Denver, Colorado line of M. zaraptor.* The Colorado population of this species demonstrated the greatest parasitization activity of all cohorts tested (table 1, figs. 1b and 2b). Hybridization with other populations did not improve performance, but significantly reduced it when matings were with cohorts from Nebraska, New Mexico, and California (table 2). However, backcrosses to California, Colorado, and New Mexico populations tended to significantly restore the high productivity.

*Las Cruces, New Mexico line of M. zaraptor.* New Mexico females were significantly affected by matings only with Nebraska males, where marked and significant reductions in both longevity and progeny production were observed (table 2). However, a significant recovery was observed in randomly mated  $F_1$  cultures.  $F_1$  hybrids mated with California and Colorado males showed some nonsignificant tendencies toward positive heterosis.

*Lincoln, Nebraska line of M. zaraptor.* Progeny production in Nebraska females was significantly reduced by matings with both California and Colorado males (table 2). However,  $F_1$  hybrids mated to random males restored the vigor of the cultures.

*Rehovot, Israel line of M. raptor.* Parasitization by Israel females was significantly reduced only by matings with North Carolina males; but as noted in the previous *M. zaraptor* example, hybrids mated to random males showed a restoration in vigor (table 3).

*Raleigh, North Carolina line of M. raptor.* The North Carolina population demonstrated the lowest fecundity and progeny production of all tested (tables 1 and 3, figs. 1f and 2f). However, hybridization with Israel males gave a significant positive heterotic response in the  $F_1$  hybrid (table 3).

*Huntsville, Utah line of M. zaraptor.* Utah females were significantly and adversely affected by mating with Israel and North Carolina males (table 3). But in each case, a significant trend toward restoration of vigor was observed in the  $F_1$  hybrids.

TABLE 2. TOTAL PROGENY AND SURVIVAL OF *MUSCIDIFURAX ZARAPTOR* PARENTAL COHORTS AND BACKCROSSES TO PARENTAL MALES, WHERE 10 FEMALES OVIPOSIT CONTINUOUSLY AT  $25.5^{\circ} \pm 1^{\circ}\text{C}$ , 55% RH ON 20 *MUSCA DOMESTICA* PUPARIA DAILY FOR 14 DAYS

Parents and backcross	Females surviving to 16 days	Average* total progeny	S.E.	♀♀ (%)
	(%)			(%)
Calif. ♀ — virgin	70	83.7bcd	2.3	0
Calif. ♀ × Calif. ♂	30	71.5cd	13.8	69.2
Calif. ♀ × Colorado ♂	0	58.9c	3.4	68.7
Calif. ♀ × New Mexico ♂	70	96.0bd	3.3	79.2
Calif. ♀ × Nebraska	40	35.7e	2.2	76.6
Colorado ♀ — virgin	100	174.3a	9.7	0
Colorado ♀ × Colorado ♂	80	169.6a	12.2	90.4
Colorado ♀ × Calif. ♂	30	147.2a	4.0	77.6
Colorado ♀ × Nebraska ♂	30	97.5bd	19.1	87.2
Colorado ♀ × New Mexico ♂	100	93.7bd	1.9	89.3
Nebraska ♀ — virgin	100	89.0cd	19.8	0
Nebraska ♀ × Nebraska ♂	100	97.6bd	11.1	84.6
Nebraska ♀ × Colorado ♂	50	47.5e	11.5	85.3
Nebraska ♀ × New Mexico ♂	100	63.3c	4.2	80.0
Nebraska ♀ × Calif. ♂	50	41.5e	7.1	77.1
New Mexico ♀ — virgin	70	109.3abd	11.9	0
New Mexico ♀ × New Mexico ♂	40	75.4cd	7.1	75.8
New Mexico ♀ × Calif. ♂	100	69.7cd	2.7	75.6
New Mexico ♀ × Colorado ♂	40	88.3bd	7.3	81.2
New Mexico ♀ × Nebraska ♂	20	31.0e	1.3	72.6
(Calif. ♀ × New Mexico ♂) ♀ × random ♂ ‡	100	63.5c	2.8	76.4
(Calif. ♀ × Nebraska ♂) ♀ × random ♂ ‡	100	26.5e	0.2	50.9
(Colorado ♀ × Calif. ♂) ♀ × Calif. ♂	50	162.7a	25.8	88.3
(Colorado ♀ × Calif. ♂) ♀ × Colorado ♂	100	146.2ab	19.6	89.1
(Colorado ♀ × Nebraska ♂) ♀ × Colorado ♂	100	164.0a	11.8	87.6
(Colorado ♀ × New Mexico ♂) ♀ × random ♂ ‡	100	140.3a	4.1	86.7
[(Colorado ♀ × Calif. ♂) ♀ × Calif. ♂] ♀ × random ♂	100	190.0a	5.0	87.5
[(Colorado ♀ × Calif. ♂) ♀ × Colorado ♂] ♀ × random ♂	80	184.0a	17.6	91.6
[(Colorado ♀ × Nebraska ♂) ♀ × Colorado ♂] ♀ × random ♂	80	121.5abd	14.3	82.7
(New Mexico ♀ × Calif. ♂) ♀ × random ♂ ‡	70	123.0ab	7.8	79.9
(New Mexico ♀ × Colorado ♂) ♀ × random ♂ ‡	70	117.0ab	6.9	74.9
(New Mexico ♀ × Nebraska ♂) ♀ × random ♂ ‡	40	71.0cd	11.0	78.4
(Nebraska ♀ × Colorado ♂) ♀ × random ♂ ‡	100	82.3cd	10.9	85.4
(Nebraska ♀ × New Mexico ♂) ♀ × random ♂ ‡	100	105.3abd	6.1	58.9
Mean squared error (306 df) †		0.028		

\*Values within a column followed by same letter are not significantly different ( $P \leq 0.05$ ; Duncan's new multiple range test, Steel and Torrie 1980); analyses performed on transformed expressions of single females.

†On transformed scale (see Materials and Methods).

‡Male genotype assumed to be of parental female line.

*Riverside, California line of M. raptor.* There were no significant differences between virgin and mated California *M. raptor* (table 3); and no lines were established with other populations.

*Quillota, Chile line of M. raptorellus.* Significant increases in total progeny occurred in Chile females mated to their own males, but no such increases were noted in matings to Peruvian males (table 4, figs. 1*i* and 2*b*). The oviposition behavior of hybrids was significantly affected by matings to both Peru and Chile males (table 4). In this species, heritable traits for fecundity and other reproductive behavior are expressed immediately after mating at an intensity dictated by the male's genome (Legner 1987*b*, 1988*a*). Such traits are subsequently fixed into the genome of resulting offspring. Variable degrees of expression of a trait in backcrosses are consistent with a polygenic mode of inheritance. In the first phase of inheritance, at mating about ½ the intensity of a particular quantitative trait is expressed in the mated female, while full expression occurs in the F<sub>1</sub> diploid virgin hybrid female. In matings of female hybrids produced from subsequent backcrosses, the magnitude of expression depends on the genome of the female being mated (Legner 1987*b*, 1988*a*).

Genes of this sort that are somehow partially expressed in mated females before being inherited by progeny might be termed "wary genes" because they, or their precursors, test the environment in an attenuated manner before nuclear fixation. Whether such genes possess chemical precursors or are inherited extranuclearly after mating is unknown (Legner 1988*a*). Indeed, a whole new type of molecule could be involved. Nevertheless, signals are sent to a female within hours of mating, either via the sperm or seminal fluid, which bear the code of the genes themselves and are later fixed into the genome of the progeny (Legner 1987*e*). Because inheritance of wary genes occurs in a stepwise manner, the entire process may be termed "accretive inheritance" (Legner 1986*b*, 1988*b*).

*La Molina, Peru line of M. raptorellus.* The same response was shown when the line was begun with Peruvian stock of this species (table 4) and can be explained by the same polygenic inheritance scheme referred to in the previous case.

*Patterns of Progeny Emergence.* Typically, progeny production approached an asymptote when parasitoid females were 6 and 7 days old, followed by a gradual decline in oviposition rates thereafter (figs. 1*a-3b*). Some notable exceptions to this may be found in the Colorado population of *M. zaraptor* (figs. 1*b* and 2*b*), where declines were not observed for several days once the asymptotic level was assumed; and in the 1981 isolate of *M. uniraptor* from Puerto Rico (fig. 3*b*), which turned out high numbers of progeny through the sixteenth day, albeit only of the male sex.

Figures 1*a* through 3*b* also clearly illustrate the close relationship between total numbers of male and female progeny and host destruction, with the latter being principally a function of reproduction. Host destruction was always greater than total progeny in solitary species, with that portion above progeny emergence resulting from probing, host feeding and abortive parasitism.

*Adequacy of a Single Mating.* Under the experimental conditions provided, a single mating was adequate to guarantee a preponderance of female progeny through the tenth oviposition day for most arrhenotokous parasitoids (figs. 1*a-1i*). A gradual shift toward male progeny was often observed after this time, which may have been due to sperm depletion. However, as host destruction and total progeny rates frequently declined in 10-day-old females, such sex ratio shifts may also have been a product of senescence.

TABLE 3. TOTAL PROGENY AND SURVIVAL OF *MUSCIDIFURAX RAPTOR* PARENTAL COHORTS AND BACKCROSSES TO PARENTAL MALES, WHERE 10 FEMALES OVIPOSIT CONTINUOUSLY AT  $25.5^{\circ} \pm 1^{\circ}\text{C}$ , 55% RH ON 20 *MUSCA DOMESTICA* PUPARIA DAILY FOR 14 DAYS

Parents and backcross	Females surviving to 16 days	Average* total progeny	S.E.	♀♀
	(%)			(%)
Calif. ♀ — virgin	70	121.2b	9.9	0
Calif. ♀ × Calif. ♂	60	126.8b	10.6	70.4
Israel ♀ — virgin	70	119.3b	25.4	0
Israel ♀ × Israel ♂	80	124.0b	19.1	67.9
Israel ♀ × Utah ♂	100	97.7bc	4.0	80.0
Israel ♀ × North Carolina ♂	50	63.0d	13.0	81.7
Utah ♀ — virgin	100	173.0ab	5.5	0
Utah ♀ × Utah ♂	100	204.2a	9.9	82.9
Utah ♀ × Israel ♂	50	80.3bc	6.4	85.8
Utah ♀ × North Carolina ♂	70	84.7bc	12.3	83.0
North Carolina ♀ — virgin	100	43.3d	2.7	0
North Carolina ♀ × North Carolina ♂	40	46.4d	9.0	63.8
North Carolina ♀ × Israel ♂	70	48.3d	3.6	65.6
(Israel ♀ × Utah ♂) ♀ × random ♂ <sup>†</sup>	100	133.0ab	2.4	76.2
(Israel ♀ × Utah ♂) ♀ × Utah ♂	100	133.2ab	17.5	82.9
(Israel ♀ × Utah ♂) ♀ × Israel ♂	70	196.2a	6.0	72.1
(Israel ♀ × North Carolina ♂) ♀ × random ♂ <sup>†</sup>	100	127.6ab	5.2	77.6
(North Carolina ♀ × Israel ♂) ♀ × random ♂ <sup>†</sup>	100	115.7bc	3.6	73.2
(Utah ♀ × Israel ♂) ♀ × Israel ♂	100	155.5ab	0.5	81.4
(Utah ♀ × North Carolina ♂) ♀ × random ♂ <sup>†</sup>	100	125.0b	4.8	57.1
mean squared error (180 df) <sup>‡</sup>		0.039		

\*Values within a column followed by same letter are not significantly different ( $P \leq 0.05$ ; Duncan's new multiple range test, Steel and Torrie 1980); analyses performed on transformed expressions of single females.

<sup>†</sup>Male genotype assumed to be of parental female line.

<sup>‡</sup>On transformed scale (see Materials and Methods).

*Virgin Versus Mated Females* Virgin females either approximated or exceeded mated females in host destruction, as shown in tables 1, 2, 3, and 4 and figs. 1a through 2i. The cases exceeding may reflect a tendency to more readily probe in a host, thereby killing it, when there was no selection stimulus for female progeny oviposition sites. In both the solitary and gregarious populations, dissections showed that this destruction did not result from superparasitism.

*Biological Control Considerations.* The present data provide some interesting indications for biological control strategy. Among the several species and populations studied, it was possible to rank such attributes as host kill and reproductive rates. Thus, within the *M. zaraptor* group, the Colorado population clearly showed the highest parasitization activity (table 1, figs. 1b and 2b). Based on these experimental results in a constant environment, the introduction to the Denver, Colorado area of other populations of *M. zaraptor* from California, New Mexico, and Nebraska would not be

TABLE 4. TOTAL PROGENY AND SURVIVAL OF *MUSCIDIFURAX RAPTORELLUS* PARENTAL COHORTS AND BACKCROSSES TO PARENTAL MALES, WHERE 10 FEMALES OVIPOSIT CONTINUOUSLY AT 25.5° ± 1°C, 55% RH ON 20 *MUSCA DOMESTICA* PUPARIA DAILY FOR 14 DAYS

Parents and backcross	Females surviving to 16 days	Average* total progeny	S.E.	♀♀
	(%)			(%)
Chile ♀ — virgin	40	135.3b	30.1	0
Chile ♀ × Chile ♂	80	165.4a	34.1	61.6
Chile ♀ × Peru ♂	60	132.4b	17.3	61.1
Peru ♀ — virgin	50	84.7c	2.7	0
Peru ♀ × Peru ♂	80	85.0c	3.6	79.6
Peru ♀ × Chile ♂	20	86.3c	7.0	76.6
(Chile ♀ × Peru ♂) ♀ × Chile ♂	70	165.4a	13.3	75.4
(Chile ♀ × Peru ♂) ♀ × Peru ♂	80	123.3b	4.1	72.8
(Peru ♀ × Chile ♂) ♀ × Peru ♂	100	118.8b	6.6	68.8
(Peru ♀ × Chile ♂) ♀ × Chile ♂	80	155.8a	11.2	83.3
mean squared error (90 df)†		0.036		

\*Values within a column followed by same letter are not significantly different ( $P \leq 0.05$ ; Duncan's new multiple range test, Steel and Torrie 1980); analyses performed on transformed expressions of single females.

†On transformed scale (see Materials and Methods).

advisable. Most likely there would be a depression of activity immediately following mating, which in turn would be followed by only a partial recovery in the  $F_1$  generation. By the  $F_2$  generation, parasitization activity would probably be restored, so that long term depression could be avoided. However, it might be better to begin by making liberations of the Colorado form in its own area.

Because the Colorado population showed such a relatively high parasitization rate, it would therefore seem suitable for introduction into areas where other, lesser active populations are native. But clearly, the present data show that there would be no apparent advantage because parasitization activity tended to be similarly depressed, followed by a recovery only in later hybrids (tables 2, 3, and 4).

Among the *M. raptor* group, the Utah population demonstrated the highest parasitization activity (table 1, figs. 1g and 2g). However, crossing the lesser active Israel population with both Utah and North Carolina populations significantly decreased progeny production (table 3), with only a trend to restoration in the  $F_1$ . But attempts to attain increased parasitization by mating Utah males to the relatively weaker Israel population were unsuccessful (table 3).

A notable exception to these trends was found by crossing the Israel population with the much inferior one from North Carolina (table 3). The hybrid mated to random males showed considerable positive heterosis with a threefold increase in progeny production (table 3).

Crosses between the Peru and Chile populations of *M. raptorellus* demonstrated some positive heterosis among the  $F_1$  progeny (table 4, Legner 1988b). For biological control, it might be advisable to introduce either strain into either respective area since resultant hybrids could provide a greater host destructive impact through enhanced activity and longevity (table 4).

Muscidifurax zaraptor CALIFORNIA-(P-I)

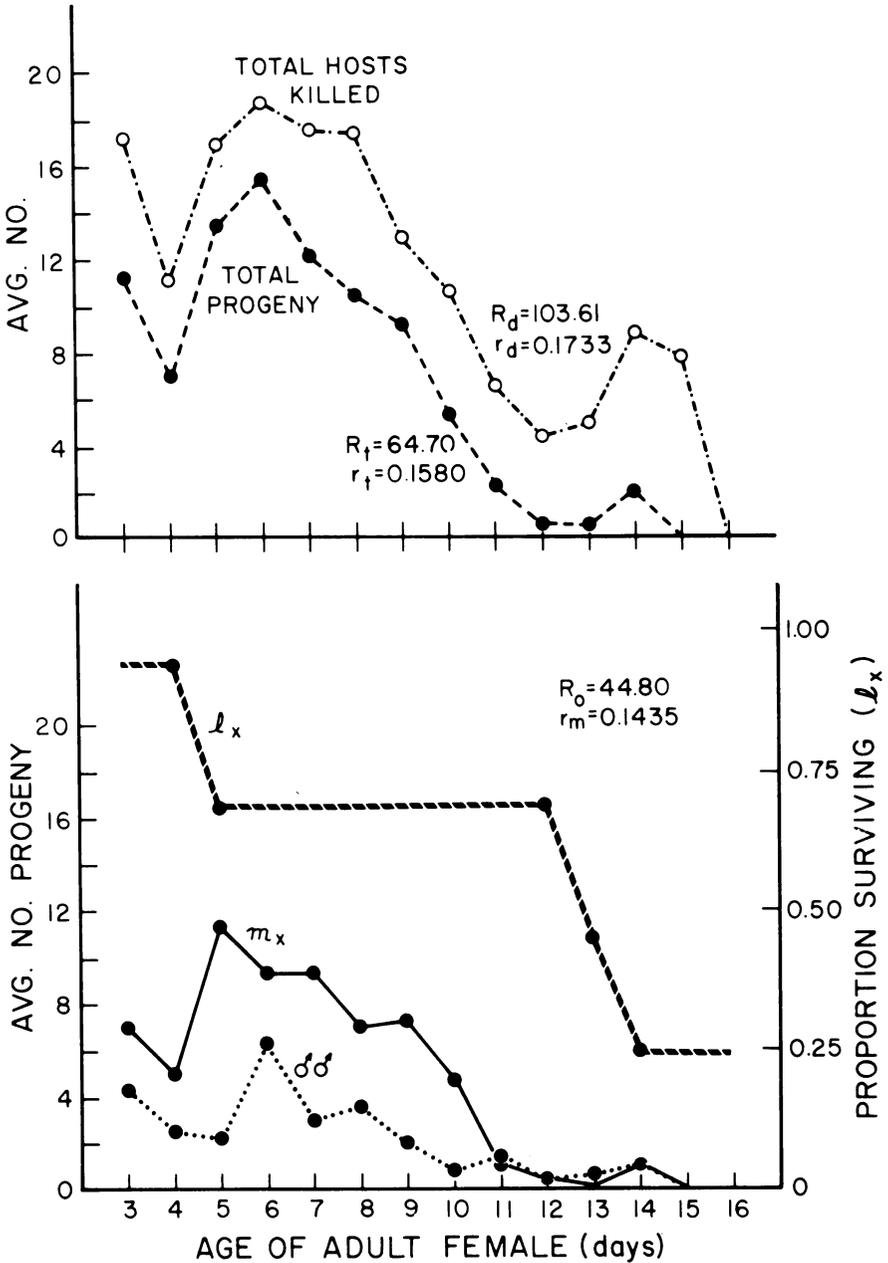


Fig. 1. Survival rate ( $l_x$ ), daily fecundity ( $m_x$ ), total progeny production ( $t_x$ ) and host destruction ( $d_x$ ) for 10 mated arrhenotokous females ovipositing continuously at  $25.5^\circ \pm 1^\circ\text{C}$ . and 55% RH; this is also fig. 1a. Riverside, California population of *Muscidifurax zaraptor*.

Muscidifurax zaraptor COLORADO - (P-I)

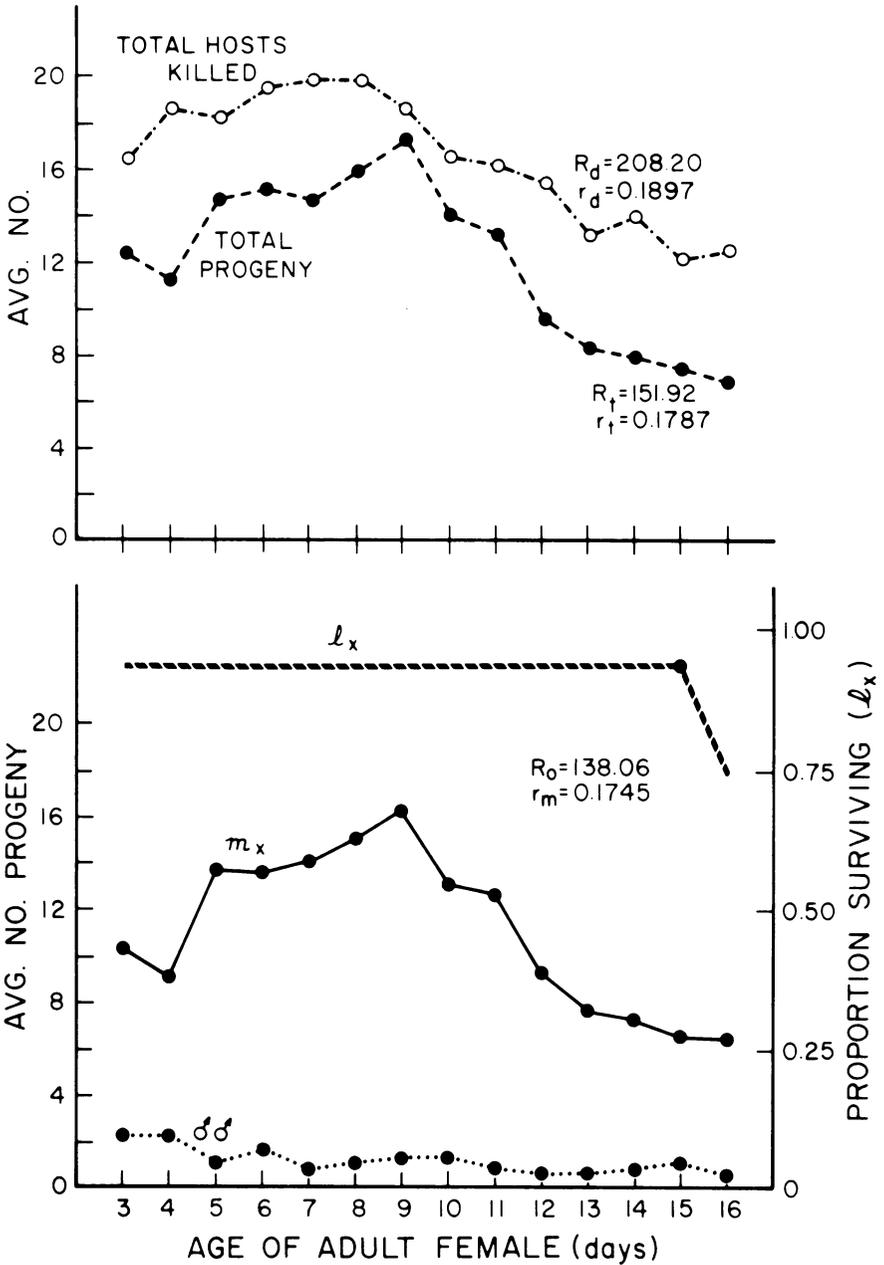


Fig. 1b. Denver, Colorado population of *Muscidifurax zaraptor*.

Muscidifurax zaraptor NEW MEXICO-(P-I)

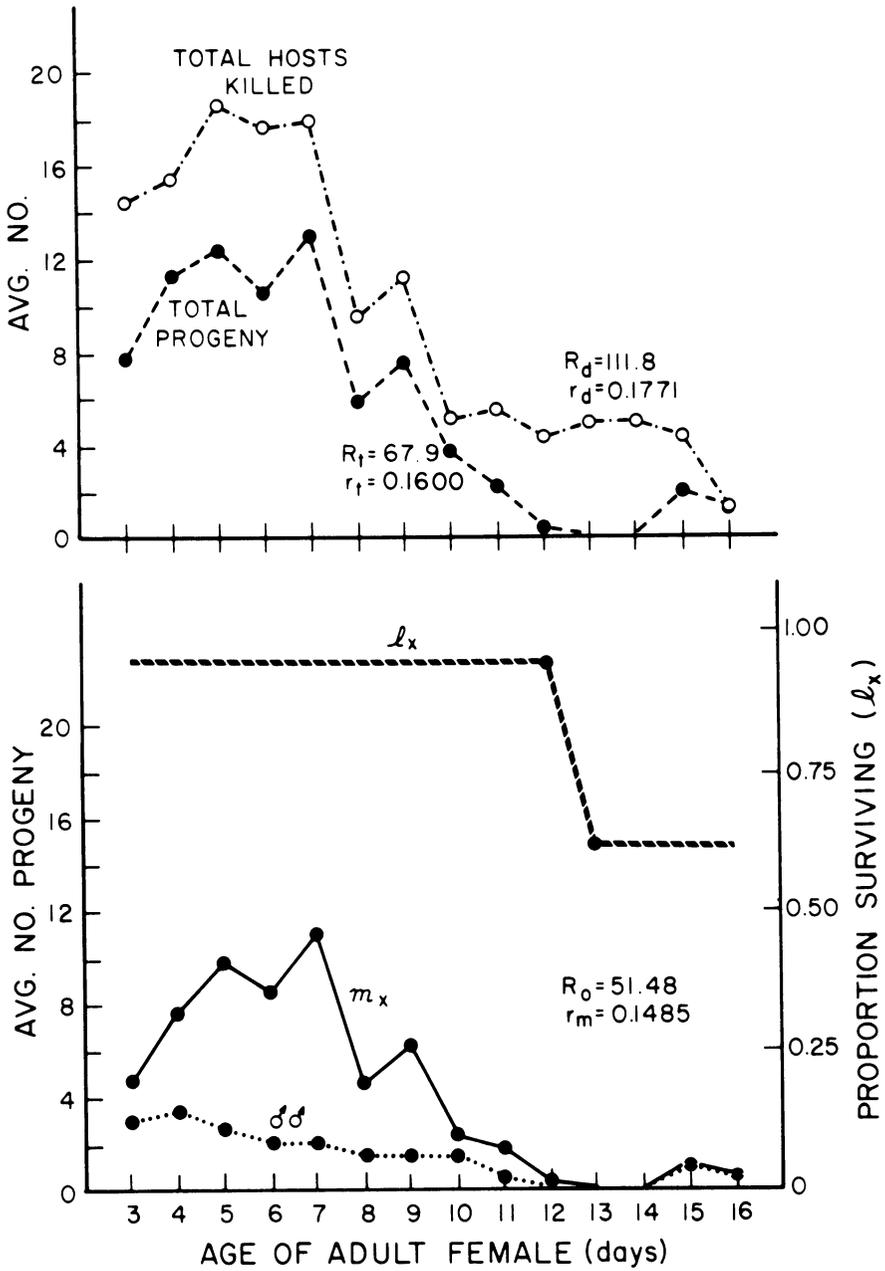


Fig. 1c. Las Cruces, New Mexico population of *Muscidifurax zaraptor*.

Muscidifurax zaraptor NEBRASKA-(P-I)

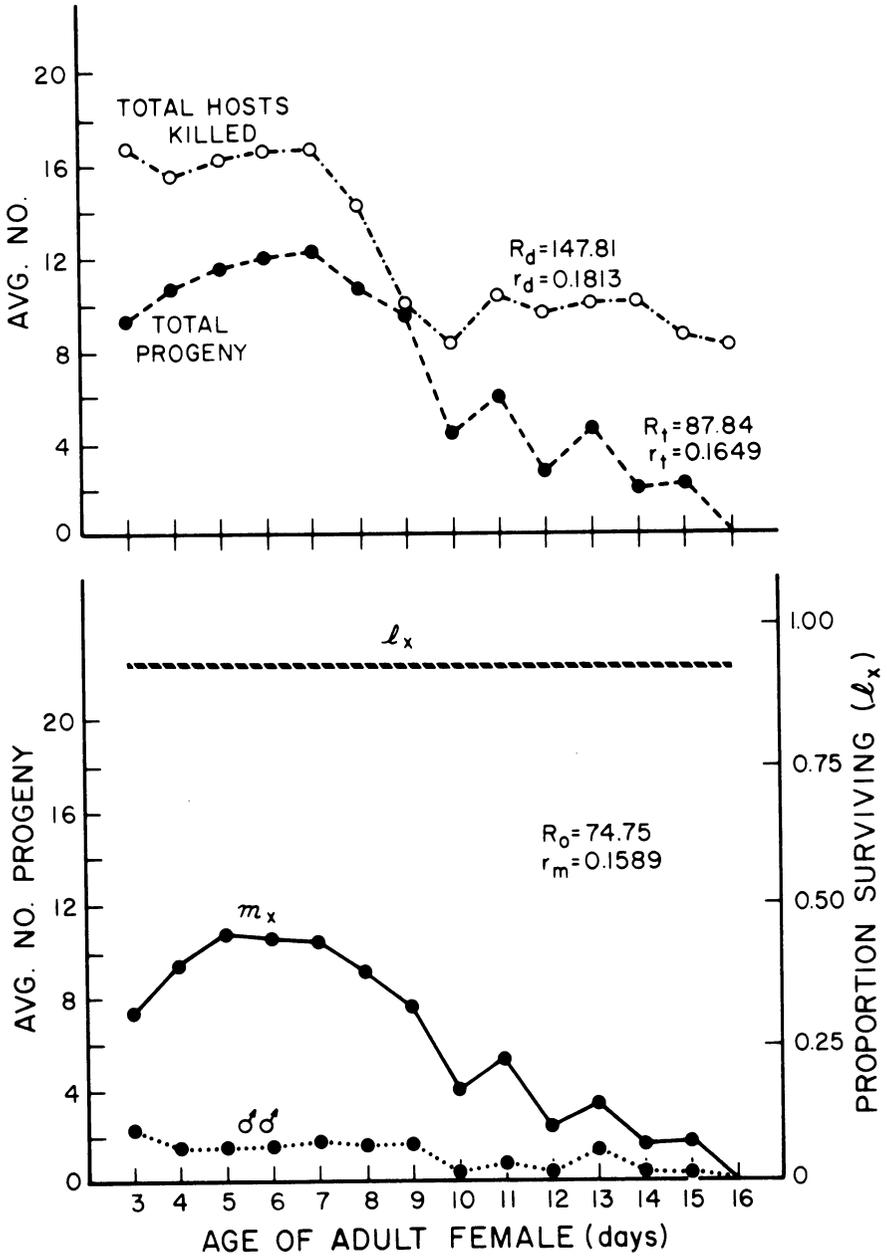


Fig. 1d. Lincoln, Nebraska population of *Muscidifurax zaraptor*.

Muscidifurax raptor ISRAEL-(P-1)

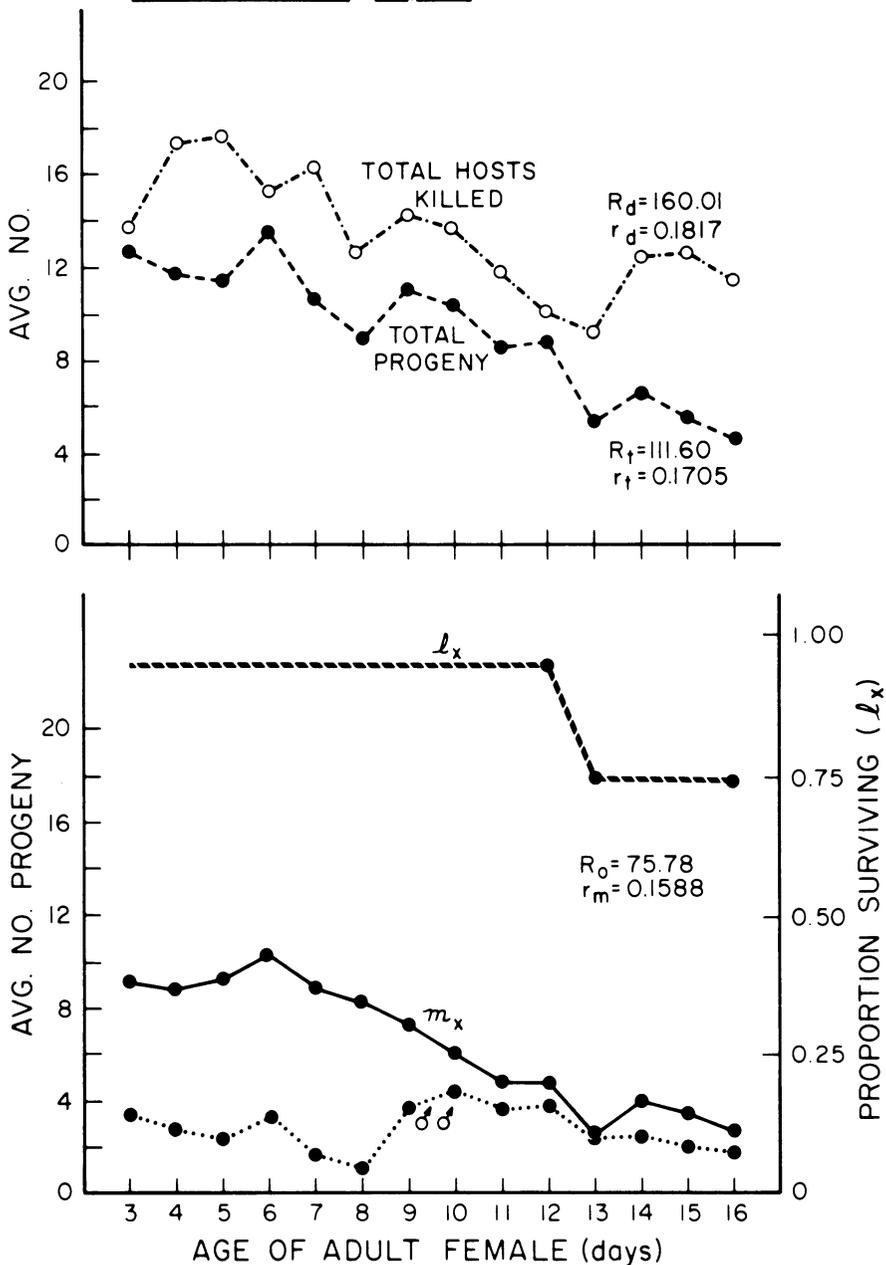


Fig. 1e. Rehovot, Israel population of *Muscidifurax raptor*.

Muscidifurax raptor NORTH CAROLINA- (P-I)

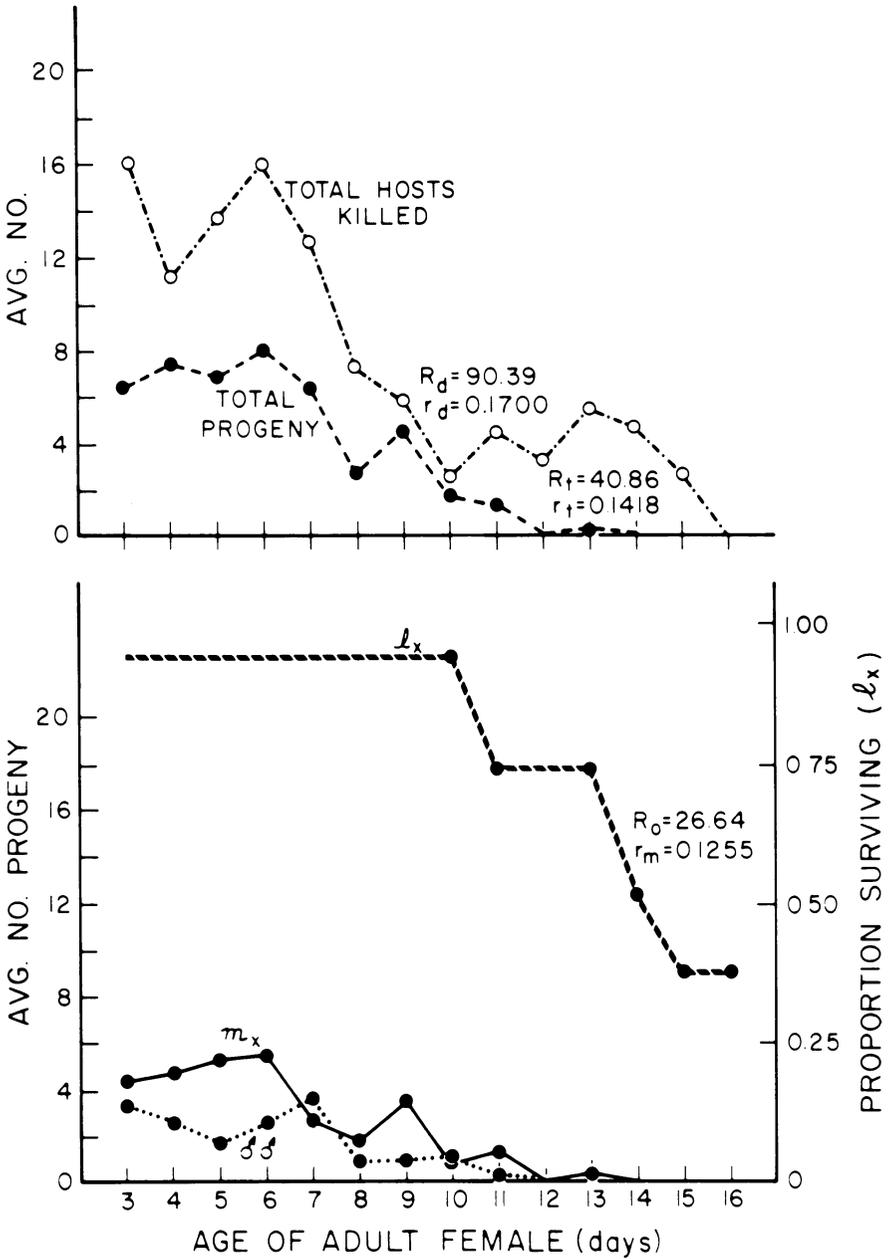


Fig. 1f. Raleigh, North Carolina population of *Muscidifurax raptor*.

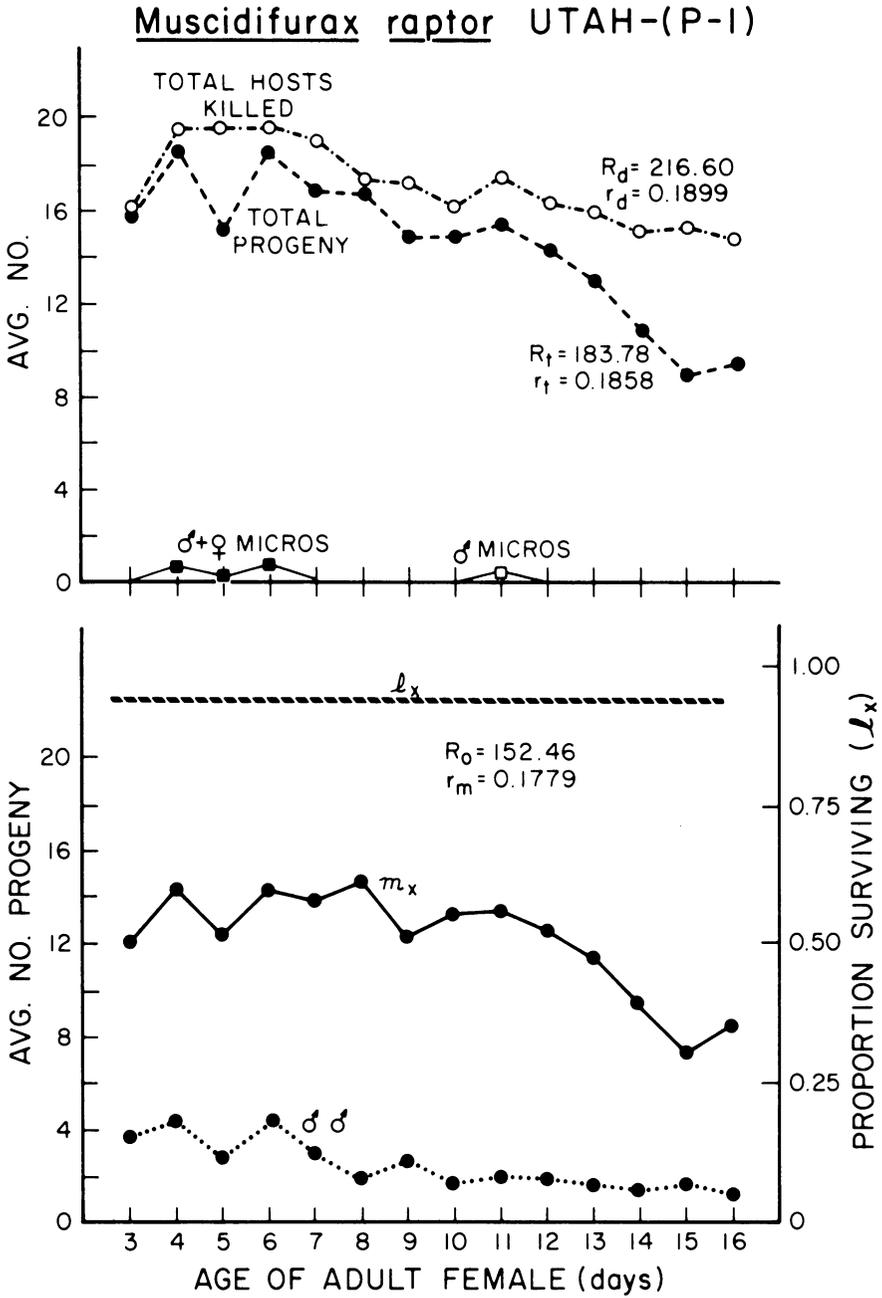


Fig. 1g. Huntsville, Utah population of *Muscidifurax raptor*.

Muscidifurax raptor CALIFORNIA 1976-(P-I)

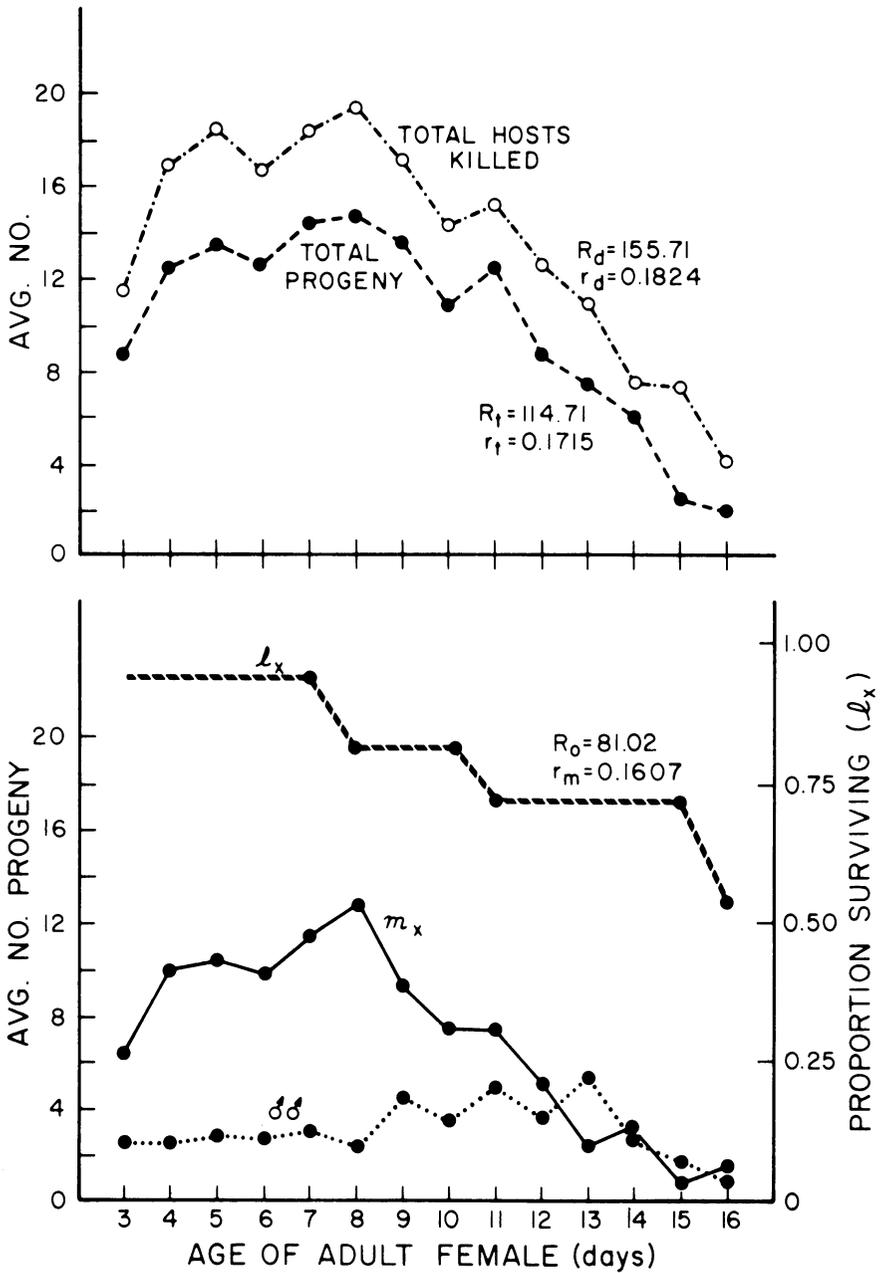


Fig. 1h. Riverside, California population of *Muscidifurax raptor*.

Muscidifurax raptorellus CHILE-(P-I)

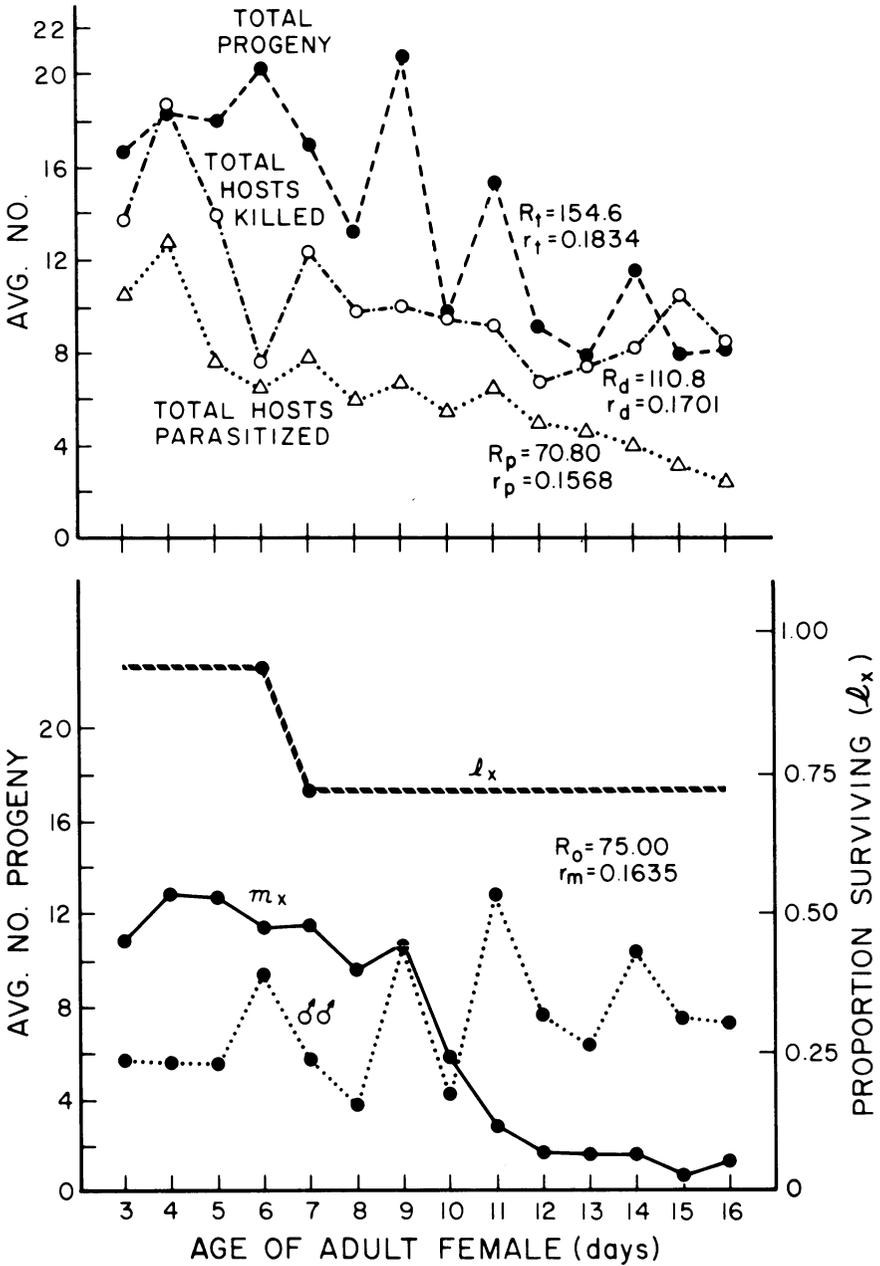


Fig. 1i. Quillota, Chile population of *Muscidifurax raptorellus*.

Muscidifurax raptorellus PERU-(P-I)

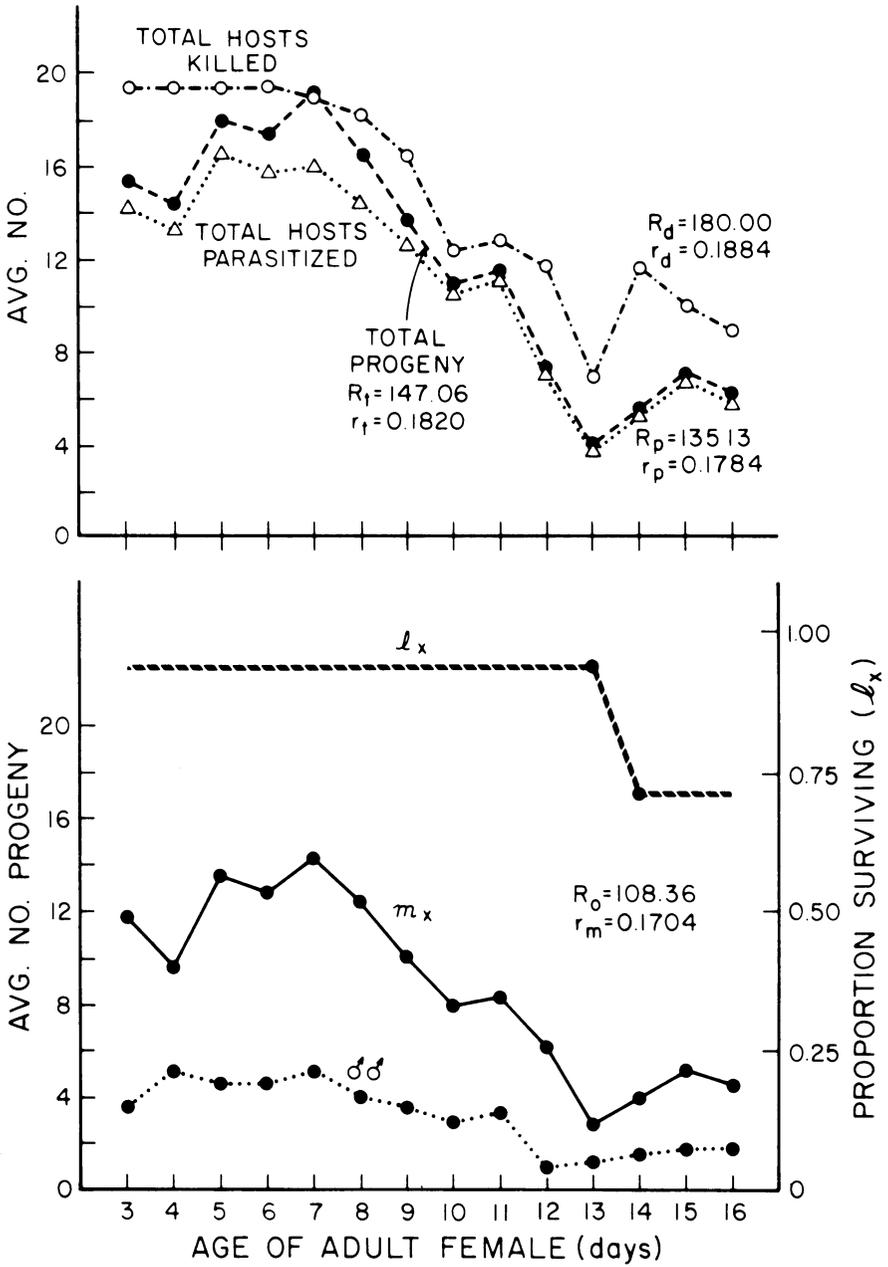


Fig. 1j. La Molina, Peru population of *Muscidifurax raptorellus*.

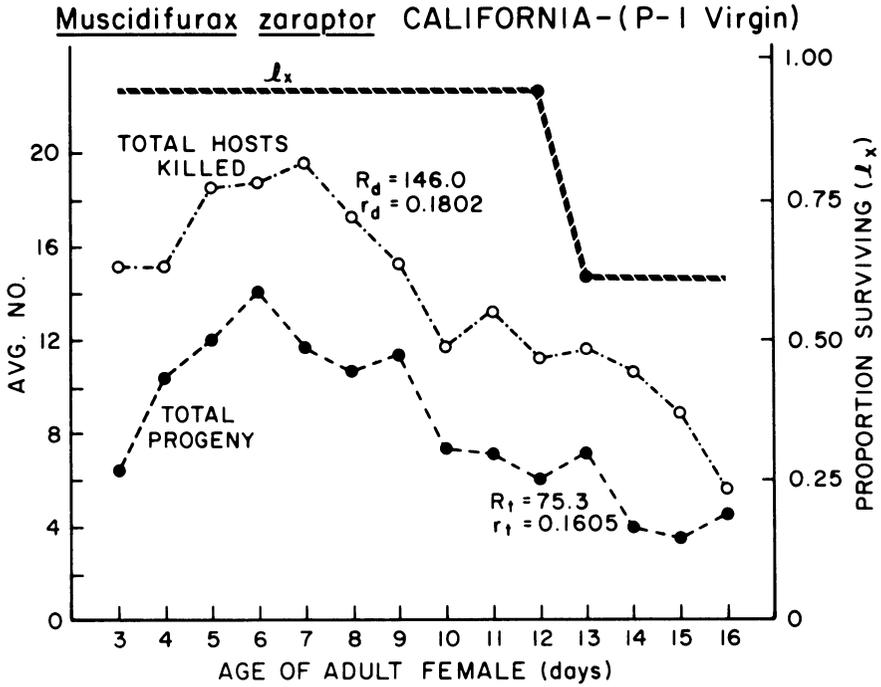


Fig. 2. Survival rate ( $l_x$ ), total progeny production ( $t_x$ ) and host destruction ( $d_x$ ) for 10 virgin arrhenotokous females ovipositing continuously at  $25.5^\circ \pm 1^\circ\text{C}$  and 55% RH; this is also fig. 2a. Riverside, California population of *Muscidifurax zaraptor*.

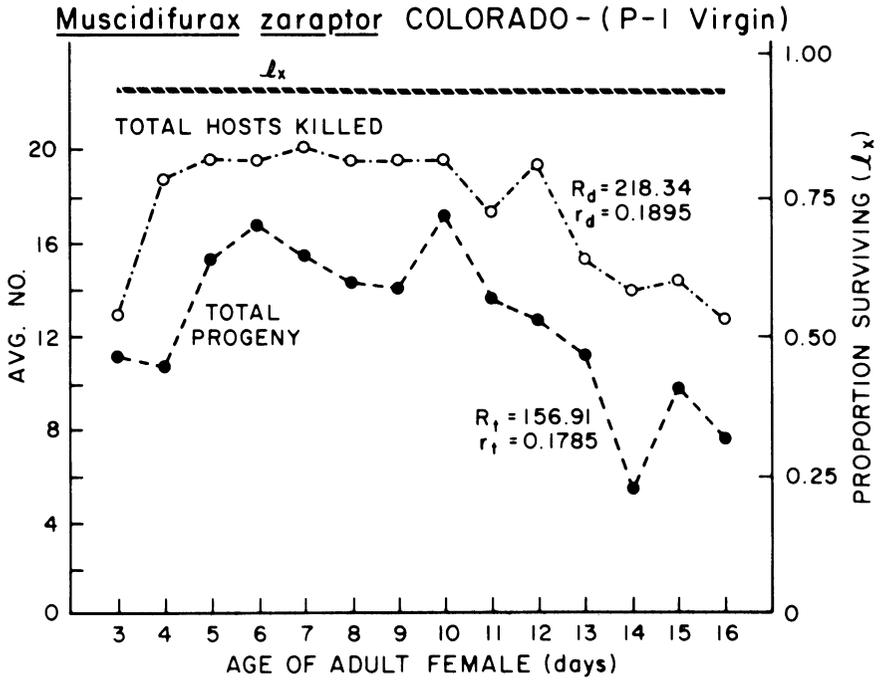


Fig. 2b. Denver, Colorado population of *Muscidifurax zaraptor*.

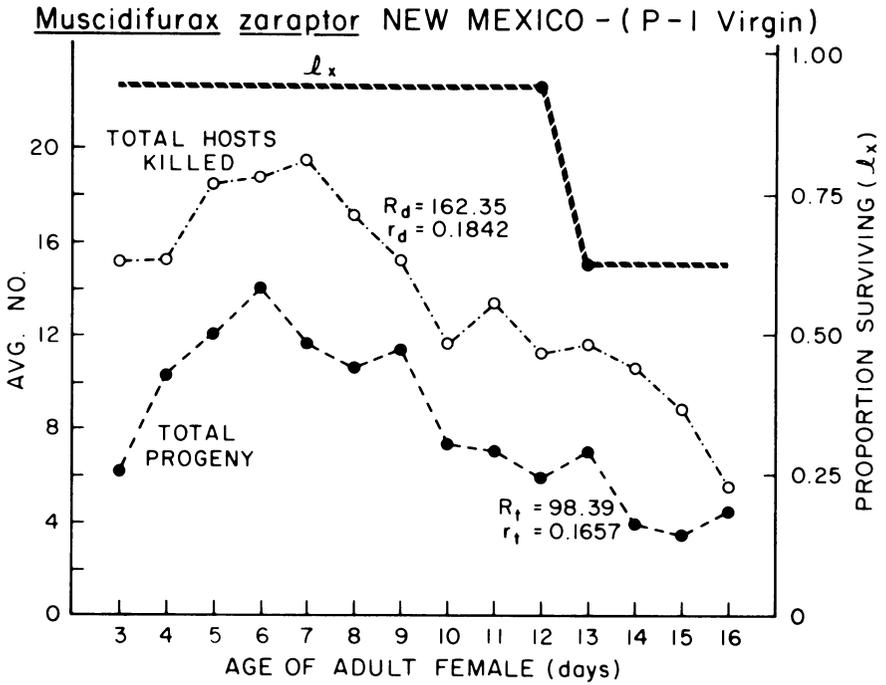


Fig. 2c. Las Cruces, New Mexico population of *Muscidifurax zaraptor*.

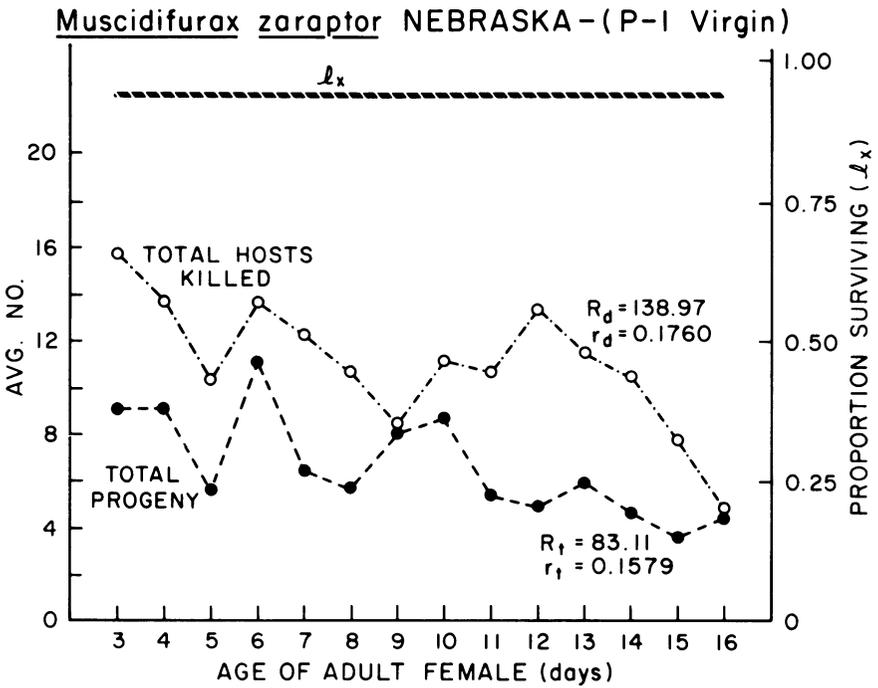


Fig. 2d. Lincoln, Nebraska population of *Muscidifurax zaraptor*.

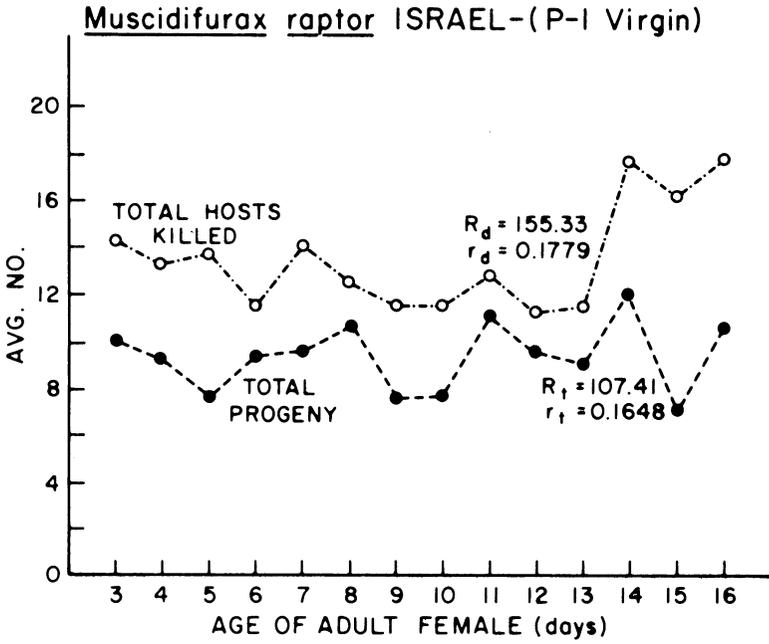


Fig. 2e. Rehovot, Israel population of *Muscidifurax raptor*—[70% survival].

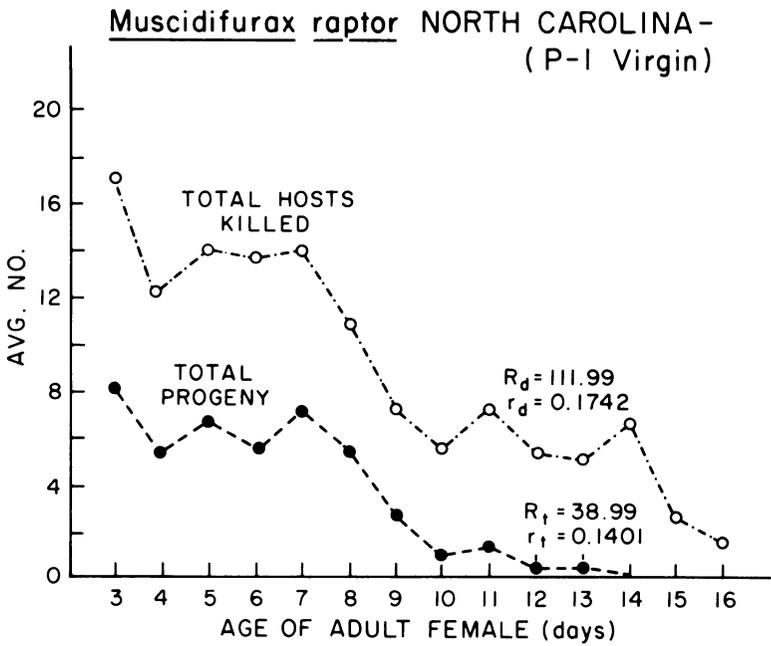


Fig. 2f. Raleigh, North Carolina population of *Muscidifurax raptor*—[100% survival].

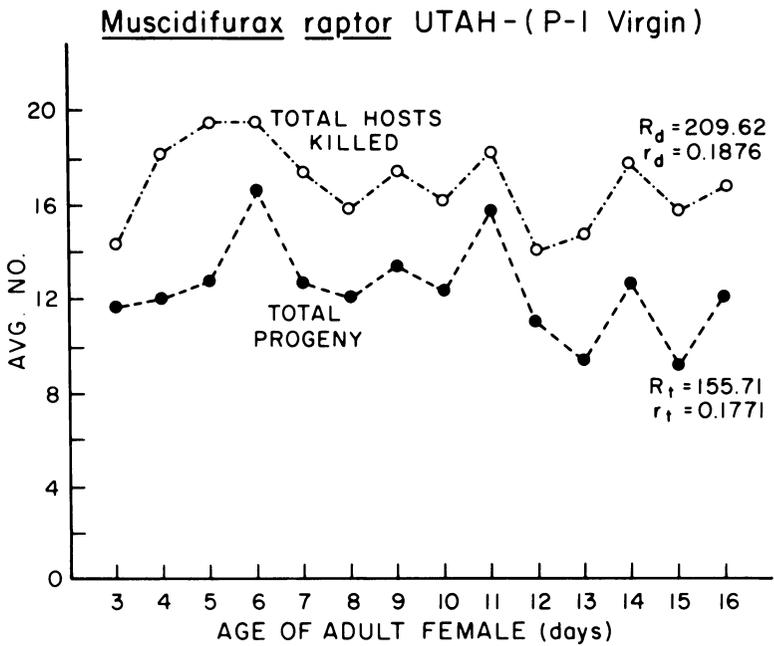


Fig. 2g. Huntsville, Utah population of *Muscidifurax raptor*—[100% survival].

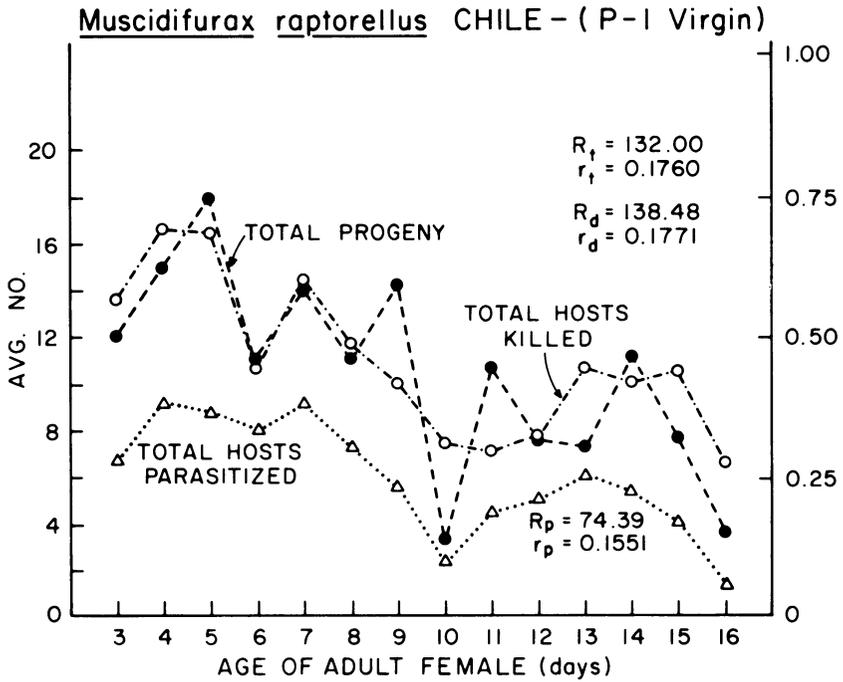


Fig. 2h. Quillota, Chile population of *Muscidifurax raptorellus*—[40% survival].

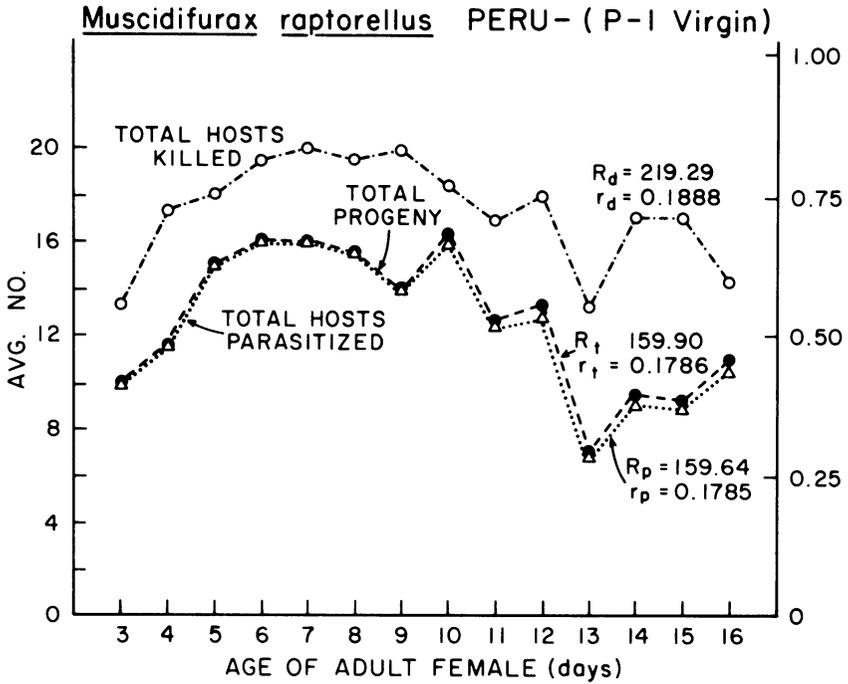


Fig. 2i. La Molina, Peru population of *Muscidifurax raptorellus*—[50% survival].

Muscidifurax uniraptor PUERTO RICO 1965-(P-I)

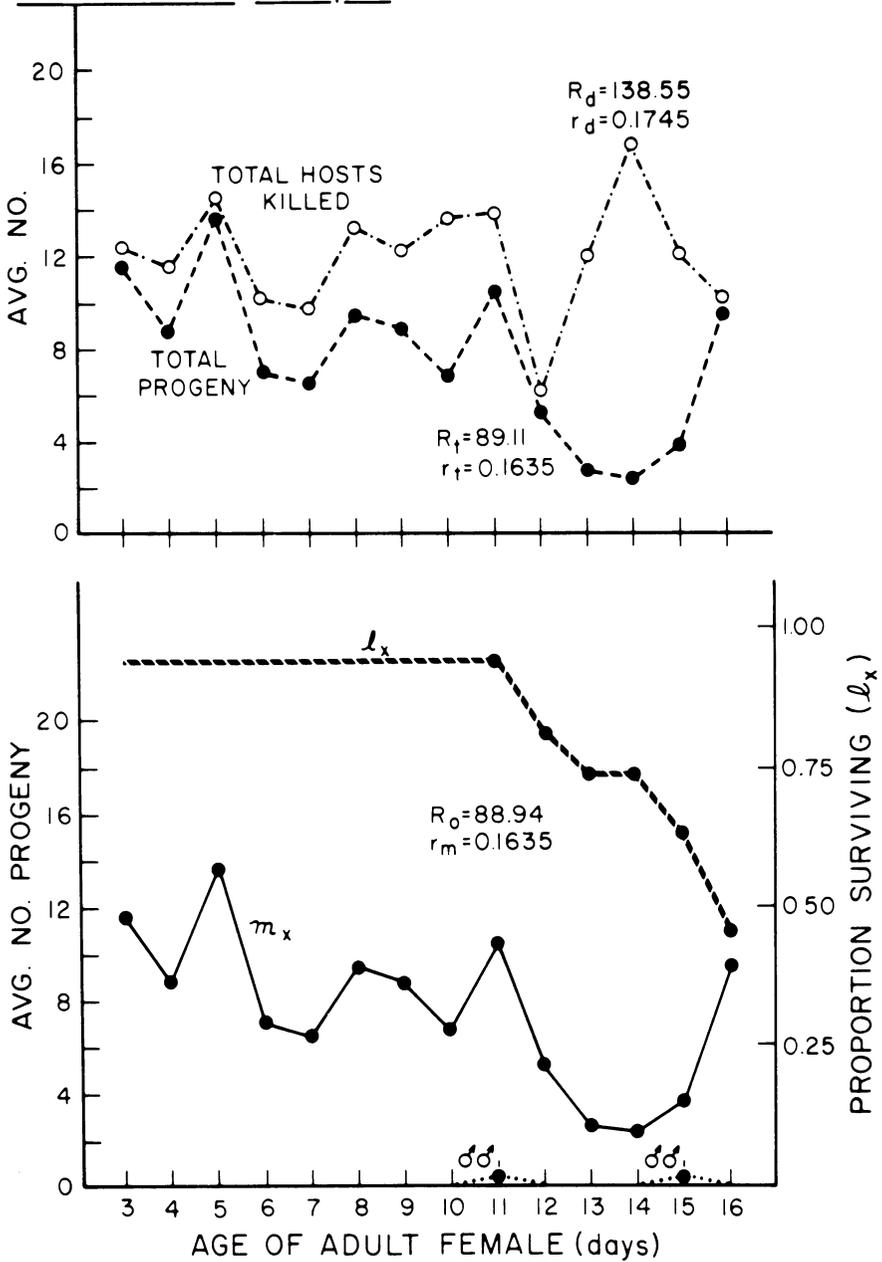


Fig. 3. Survival rate ( $l_x$ ), daily fecundity ( $m_x$ ), total progeny production ( $t_x$ ) and host destruction ( $d_x$ ) for 10 virgin thelytokous females ovipositing continuously at  $25.5^\circ \pm 1^\circ\text{C}$  and 55% RH; this is also fig. 3a. 1965 Cayey, Puerto Rico isolate of *Muscidifurax uniraptor*.

Muscidifurax uniraptor PUERTO RICO 1981-(P-I)

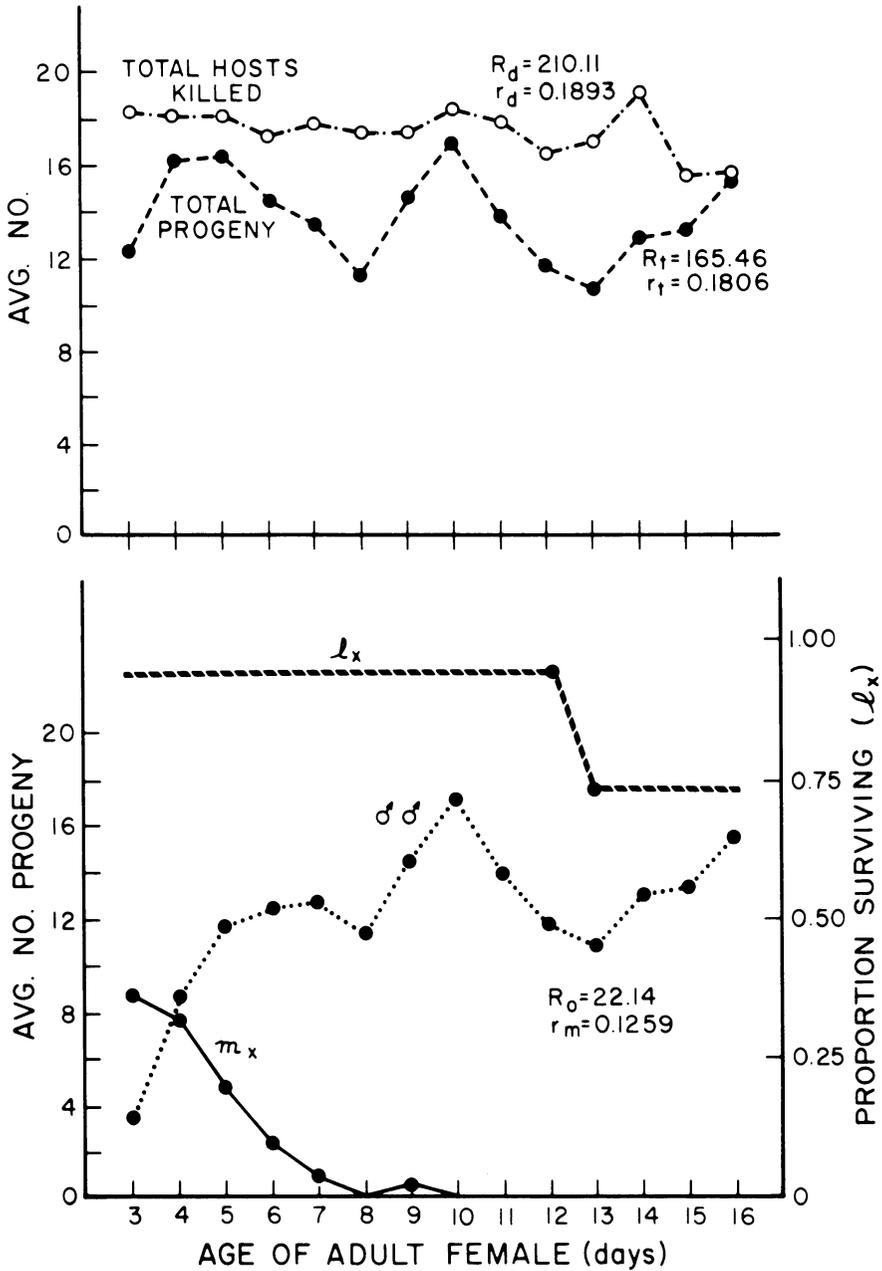


Fig. 3b. 1981 Cayey, Puerto Rico isolate of *Muscidifurax uniraptor*.

## CONCLUSIONS

These results show a clear rationale for preintroduction assessments of parasitoid populations, and are in agreement with previous authors' disposition to elevate exotic natural enemy importation into a solid scientific base (Coppel and Mertins 1977; Legner 1986a). However, in addition to reproductive and host destruction behavior, other attributes such as habitat-searching capacity, and response at varied temperatures, relative humidities, and host densities should ideally be included in such assessments before sensible conclusions may be drawn on whether or not to introduce a new parasitoid species or population. However, long term harmful effects of mixing populations of the same species would probably not occur since weaker hybrids should be eliminated by competition with the numerically larger resident populations.

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