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Theory for quantitative inheritance of behavior in a protelean parasitoid, *Muscidifurax raptorellus* (Hymenoptera: Pteromalidae)

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Abstract. Two races of *Muscidifurax raptorellus* Kogan & Legner (Hymenoptera: Pteromalidae) reveal combinations of extranuclear and chromosomal inheritance for the quantitative trait, gregarious oviposition. In the first extranuclear phase prior to chromosomal inheritance, unknown substances transferred at mating cause a portion ($\leq 1/2$) of the intensity of a particular quantitative trait present in the males' genome to be expressed phenotypically in the inseminated ♀♀ within an hour of mating. The ability to change the adult female's expression of the quantitative character, either positively or negatively, challenges accepted views of polygenic loci, and it is suggested that such loci may not be inherited, but rather another group of genes which have the capability to switch on or off the loci. Such genes may influence DNA methylation of the loci controlling oviposition behavior. All polygenic loci may be perpetually present for a given quantitative trait in all individuals of both races, but they are either activated or inactivated by substances under the control of another group of genes. An enhanced significance for haploid males is indicated through an ability to activate expressions of part of their own genetic make-up within their own generation, which may quicken natural selection and the pace of evolution.

INTRODUCTION

Studies in quantitative inheritance of behavior in the protelean polyphagous hymenopteran parasitoid (Askew, 1971; Reuter, 1913) *Muscidifurax raptorellus* Kogan & Legner (Hymenoptera: Pteromalidae), have shown a typical pattern for gregarious oviposition such as that found generally in plants and animals (Gardner & Snustad, 1984; Goodenough, 1984; Lande, 1981; Legner, 1987, 1988a,b,c). In *M. raptorellus* quantitative behavior expressed as gregarious oviposition (> one individual developed per host) is obviously controlled by polygenic loci where there is a difference in degree among related individuals. The greater number of loci determining the trait, the more continuous the variation (Legner 1991a), and as the number of loci determining this trait increases, the proportion of extreme phenotypes among progeny decreases (Legner, 1991a). F_1 and F_2 populations tend to display the same average value for gregarious expression, and the range of phenotypes for the F_2 is usually greater than in the F_1 (Legner, 1991a). Estimates of gene number, made on the basis of variances in P_1, F_1, F_2 and backcrossed progeny, and by observing behavior in second and third order backcrosses, ranged from two to 19 (Legner, 1991a), but at least eight loci were believed to be actively segregating for this characteristic (Legner, 1991a). Estimates of the coefficient of heritability in the broad sense based on parental and F_1 and F_2variances indicated that variability of gregarious

behavior in the constant experimental environment was influenced > 60% by genotypic factors, while offspring-parent regression gave estimates of > 38% (Legner, 1991a).

Although experiments support the existence of recombinant ♂♂ and chromosomal inheritance, and minimize extranuclear inheritance of gregarious behavior in progeny (Legner, 1991b), certain extranuclear influences on first-mated ♀♀ are evident (Legner, 1989a,b). Males are capable of changing a virgin females' oviposition phenotype upon mating, by transferring unknown substances (Legner, 1987, 1988a). Females with the solitary genotype express gregarious oviposition behavior after mating with ♂♂ possessing the gregarious genotype, and ♀♀ with the gregarious genotype reduce the intensity of their gregarious behavior after mating with ♂♂ of the solitary genotype. The intensity differs depending on the respective genetic composition of the mating pair (Legner, 1989a).

The extranuclear phase to inheritance is examined in greater detail through increased replication and dissection of hosts for parasitoid eggs and segregation of Peruvian and Chilean maternal lines, in an attempt to clarify the nature of the genetic loci controlling gregarious oviposition in this species.

MATERIALS AND METHODS

PARENTAL STOCK. Parental parasitoid cultures were obtained from 25 mated ♀♀ each of the Peruvian (solitary) and Chilean (gregarious) races of *Muscidifurax raptorellus* in mass-cultured stock (Legner, 1991a). The genus is known to attack Muscidae polyphagously (Legner et al., 1967; Legner & Olton, 1971). Parasitoids were perpetuated for 12 generations in 500-cc screened polystyrene containers with ca. 500 randomly mated ♀♀ parasitoids ovipositing on 2,000 *Musca domestica* L. puparia for 48-h. Electrophoretic analyses had established extremely low levels of variability in the mass-cultured founder stock, especially when compared to later field-collected wild cultures (Kawooya, 1983; Legner, 1991a). Parasitoids used to start the original colonies were thought to possess only a fraction of the gene pool of wild parental populations (Kawooya, 1983). However, Hymenoptera generally show lower genetic variability than other insect orders (Crozier, 1971, 1975; Metcalf et al., 1975; Kawooya, 1983).

EXPERIMENTAL DESIGN. Single 1-day-old ♀♀ of the inbred solitary Peruvian and gregarious Chilean cohorts of *M. raptorellus* (Legner, 1987) were randomly isolated in screened polystyrene vials (46-cm^2), with a basal area of 7 cm^2. They remained virgins or were individually mated for one day to ≤ 1-day old ♂♂ secured at random from cultures of the opposite race, to produce an F_1 generation of virgin ♀♀. Backcrosses of the first order were made to randomly chosen ♂♂ from the respective parental populations. Mating partners for the crosses were chosen at random from parasitoids that emerged in gelatin capsules. Backcrosses of the 2nd and 3rd orders also were performed in each line with 30 replicate ♀♀ to create a variety of genotypes for assessing the relationship between the intensity of behavioral expression and genotype.

Each virgin ♀♀ was supplied daily for 16 days with 20–24 to 30-h-old puparia of *Musca domestica* L. (6.4 ± 0.5mm × 2.8 ± 0.2 mm), distributed randomly over the vial base. Flies were reared to pupation using commercial CSMA^R medium. Parasitization at this host density and in this time period, and environment at 25.5 ± 1°C, 50% ambient RH, was found adequate for the measurement of polygenic traits (Legner, 1987, 1988a).

Two separate maternal lines were established by (1) mating Peruvian ♀♀ to Chilean ♂♂ and (2) mating Chilean ♀♀ to Peruvian ♂♂. There were 30 replicate ♀♀ examined in each parental population, and 30 replicates of F_1 progeny in each line. For the Peruvian line, there were 30 backcrosses each to Peruvian and Chilean ♂♂ parents. In the Chilean line, there were 30 backcrosses each to Peruvian and Chilean ♂♂ parents.

Parasitoids were allowed to oviposit in host puparia for 24-h at 25.5 ± 1°C, 55% RH and a 13L : 11D photoperiod of ca. 269 lux irradiance at table level. Light was supplied by fluorescent lamps. Puparia in each of 20 random replicates were dissected after the 24-h exposure in order to determine the number of

eggs laid. Progeny sex ratios were estimated from 10 additional replicates that were allowed to incubate until adult parasitoid emergence.

The total number of eggs laid and the number of hosts in which parasitoids oviposited more than one egg and associated variances were estimated for each parental and hybrid cohort, by the response of individual replicate ♀♀.

Experiments were conducted with replicates arranged in a completely random design in space and time. Analyses of variance were performed on the expression of individual ♀♀ transformed to the $\sqrt{(X + 1/2)}$ for hosts parasitized and arcsin $\sqrt{(\% + 1/2)}$ for percentage of hosts parasitized gregariously (Steel & Torrie, 1980). Duncan's (1955) new multiple range tests were performed on the transformed data, with significance tested at $P \leq 0.05$. Data of the percentage of hosts sustaining gregarious oviposition were plotted with trend curves generated by Harvard Graphics 2.13.

RESULTS AND CONCLUSIONS

Virgin Peruvian and Chilean ♀♀, and virgin hybrids and progeny of several backcrosses demonstrated the typical precise correlation of gregarious behavior with the expected genomic fraction for both maternal lines (Table 1 and Fig. 1). Reciprocal crosses of both

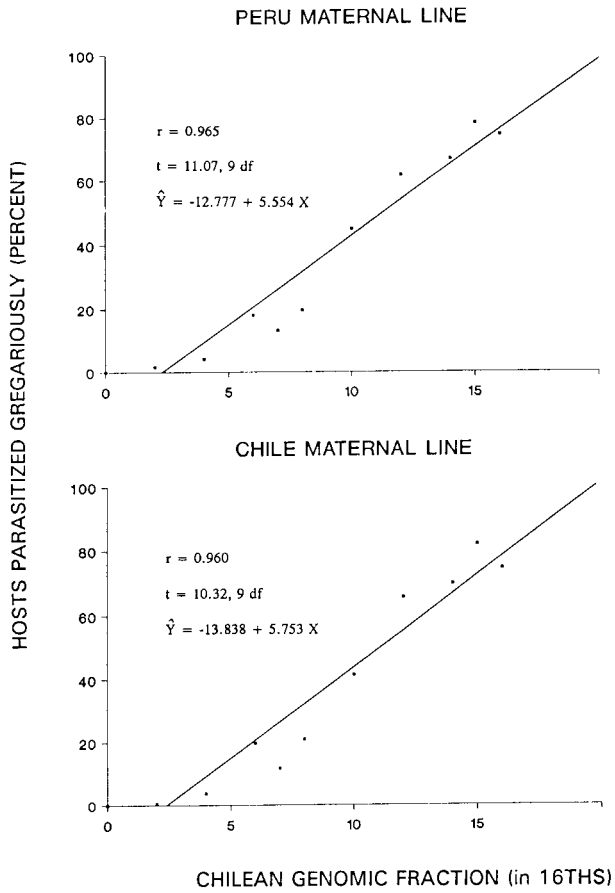

Fig. 1. Proportion of *Musca domestica* puparia parasitized gregariously for each expected fraction of the *Muscidifurax raptorellus* genome that is Chilean in origin, with Peruvian and Chilean maternal lines shown separately. Each point represents the average of 20 replicate ♀♀.

races produced hybrids expressing only a portion (< 1/3rd) of the gregarious behavior of the Chilean race, showing the partial dominance of the solitary oviposition trait (Figs 2, 3). Estimations of progeny that emerged from 10 incubated replicates revealed sex ratios of 75.4–83.3% ♀♀ from mated mothers and all ♂♂ from virgin mothers.

TABLE 1. Average daily number of hosts parasitized and gregarious ovipositions in parental F_1 and backcross cultures of *Muscidifurax raptorellus*, where 20 females oviposit continuously 25 ± 1°C, 55% RH on 20 *Musca domestica* puparia daily for 16 days.[1]

Parasitoid genotype	Avg. No. per ♀♀ per day (stand.-error)[2]		
	♀ genomic fraction of Chilean origin	Hosts parasitized	Gregarious ovipositions (%)
P_1			
Chile ♀ (virgin)	16/16	3.72[a] (1.37)	74.3[a] (3.7)
Chile ♀ w/ Chile ♂	16/16	4.43[ab] (0.59)	79.4[a] (2.1)
Chile ♀ w/ Peru ♂	16/16	5.35[ab] (0.69)	55.6[b] (1.7)
Peru ♀ (virgin)	0/16	6.97[b] (0.59)	0[g]
Peru ♀ w/ Peru ♂	0/16	6.32[b] (0.52)	0[g]
Peru ♀ w/ Chile ♂	0/16	7.43[b] (0.58)	8.2[e]
F_1 Hybrids			
(Chile ♀ × Peru ♂)♀ (virgin)	8/16	7.08[b] (0.53)	20.9[c] (1.2)
(Chile ♀ × Peru ♂)♀ w/ Peru ♂	8/16	7.31[b] (0.61)	8.1[c] (0.5)
(Chile ♀ × Peru ♂)♀ w/ Chile ♂	8/16	7.21[b] (0.47)	41.7[b] (1.5)
(Peru ♀ × Chile ♂)♀ (virgin)	8/16	6.54[b] (0.41)	19.5[c] (1.1)
(Peru ♀ × Chile ♂)♀ w/ Peru ♂	8/16	6.68[b] (0.78)	10.5[de] (1.1)
(Peru ♀ × Chile ♂)♀ w/ Chile ♂	8/16	6.25[ab] (0.62)	41.6[b] (2.1)
First Backcross Progeny			
[(Chile ♀ × Peru ♂)♀ × Chile ♂]♀ (virgin)	12/16	3.69[a] (0.92)	65.5[ab] (4.7)
[(Chile ♀ × Peru ♂)♀ × Chile ♂]♀ w/ Chile ♂	12/16	7.17[b] (0.47)	65.3[ab] (3.0)
[(Chile ♀ × Peru ♂)♀ × Chile ♂]♀ w/ Peru ♂	12/16	6.00[ab] (0.67)	27.7[bc] (2.4)

TABLE 1 (continued).

Parasitoid genotype	Avg. No. per ♀♀ per day (stand.-error)[2]		
	♀ genomic fraction of Chilean origin	Hosts parasitized	Gregarious ovipositions (%)
[(Chile ♀ × Peru ♂)♀ × Peru ♂]♀ (virgin)	4/16	3.79[a] (0.78)	3.65[ef] (0.7)
[(Chile ♀ × Peru ♂)♀ × Peru ♂]♀ w/ Chile ♂	4/16	7.05[b] (0.33)	22.1[c] (1.5)
[(Chile ♀ × Peru ♂)♀ × Peru ♂]♀ w/ Peru ♂	4/16	5.81[ab] (0.35)	1.5[ef] (0.1)
[(Peru ♀ × Chile ♂)♀ × Peru ♂]♀ (virgin)	4/16	4.00[ab] (0.33)	4.1[ef] (0.3)
[(Peru ♀ × Chile ♂)♀ × Peru ♂]♀ w/ Chile ♂	4/16	5.85[ab] (0.37)	29.7[bc] (2.4)
[(Peru ♀ × Chile ♂)♀ × Peru ♂]♀ w/ Peru ♂	4/16	5.54[b] (0.46)	2.5[ef] (0.4)
[(Peru ♀ × Chile ♂)♀ × Chile ♂]♀ (virgin)	12/16	4.09[ab] (0.21)	61.5[ab] (3.3)
[(Peru ♀ × Chile ♂)♀ × Chile ♂]♀ w/ Chile ♂	12/16	7.13[b] (0.30)	67.9[ab] (2.1)
[(Peru ♀ × Chile ♂)♀ × Chile ♂]♀ w/ Peru ♂	12/16	5.30[b] (1.06)	44.2[b] (2.5)
Second Backcross Progeny			
[[(Chile ♀ × Peru ♂)♀ × Chile ♂]♀ × Chile ♂]♀ (virgin)	14/16	6.10[b] (0.31)	69.6[ab] (1.5)
[[(Chile ♀ × Peru ♂)♀ × Chile ♂]♀ × Chile ♂]♀ w/ Chile ♂	14/16	7.96b (0.38)	68.2[ab] (0.7)
[[(Chile ♀ × Peru ♂)♀ × Chile ♂]♀ × Chile ♂]♀ w/ Peru ♂	14/16	5.94[ab] (0.45)	34.9[bc] (3.4)
[[(Chile ♀ × Peru ♂)♀ × Chile ♂]♀ × Peru ♂]♀ (virgin)	6/16	5.74[ab] (1.41)	19.6[c] (1.7)
[[(Chile ♀ × Peru ♂)♀ × Peru ♂]♀ × Chile ♂]♀ (virgin)	10/16	6.13[b] (0.75)	41.3[b] (3.2)
[[(Chile ♀ × Peru ♂)♀ × Peru ♂]♀ × Peru ♂]♀ (virgin)	2/16	4.78[ab] (1.20)	0.4[fg] (0.2)
[[(Peru ♀ × Chile ♂)♀ × Peru ♂]♀ × Chile ♂]♀ (virgin)	10/16	7.55[b] (0.41)	44.8[b] (2.3)
[[(Peru ♀ × Chile ♂)♀ × Peru ♂]♀ × Peru ♂]♀ (virgin)	2/16	6.41[b] (0.49)	1.6[ef] (0.4)
[[(Peru ♀ × Chile ♂)♀ × Chile ♂]♀ × Chile ♂]♀ (virgin)	14/16	6.41b (0.62)	66.6[ab] (2.0)
[[(Peru ♀ × Chile ♂)♀ × Chile ♂]♀ × Chile ♂]♀ w/ Peru ♂	14/16	6.55[b] (1.16)	34.7[bc] (0.7)
[[(Peru ♀ × Chile ♂)♀ × Chile ♂]♀ × Chile ♂]♀ w/ Chile ♂	14/16	5.80[b] (0.87)	76.6[a] (1.2)

TABLE 1 (continued).

Parasitoid genotype	Avg. No. per ♀♀ per day (stand.-error)[2]		
	♀ genomic fraction of Chilean origin	Host parasitized	Gregarious ovipositions (%)
[[(Peru ♀ × Chile ♂)♀ × Chile ♂]♀ × Peru ♂]♀ (virgin)	6/16	6.76[b] (0.75)	8.7[e] (1.1)
Third Backcross Progeny			
[[[(Chile ♀ × Peru ♂)♀ × Chile ♂]♀ × Chile ♂]♀ × Chile ♂]♀ (virgin)	15/16	7.05b (0.44)	81.8[a] (1.0)
[[[(Chile ♀ × Peru ♂)♀ × Chile ♂]♀ × Chile ♂]♀ × Peru ♂]♀ (virgin)	7/16	7.02b (1.12)	11.6[de] (0.9)
[[[(Peru ♀ × Chile ♂)♀ × Chile ♂]♀ × Chile ♂]♀ × Peru ♂]♀ (virgin)	7/16	6.42b (2.05)	13.1[de] (1.1)
[[[(Peru ♀ × Chile ♂)♀ × Chile ♂]♀ × Chile ♂]♀ × Chile ♂]♀ (virgin)	15/16	7.12b (0.59)	78.0[b] (1.2)

[1] Table derived from Legner (1988a) with 10 additional replicates.

[2] Values within a column followed by the same letter are not significantly different ($P \leq 0.05$; Duncan's [1955] multiple range test). Analyses performed on expressions of individual females transformed to $\sqrt{(X + 1/2)}$ for hosts parasitized and arcsin $\sqrt{(\% + 1/2)}$ for percentage data.

A significant positive heterosis expressed as increased numbers of parasitized hosts was evident in F_1 hybrids and certain backcrossed progeny (Table 1) as previously observed (Legner, 1989a). Females changed their oviposition behavior significantly soon after mating (< 24 h) (Figs 2, 3). Mating a Peruvian ♀♀ of solitary heritage to a Chilean ♂♂ caused her to lay eggs gregariously in some hosts, while Peruvian ♂♂ of solitary heritage significantly reduced the magnitude of gregarious behavior of Chilean ♀♀ with whom they mated (Figs 2, 3). Mating hybrid ♀♀ with ♂♂ from either the solitary or gregarious population similarly caused a decrease or increase in gregarious behavior (Figs 2, 3). For example, if an F_1 (Chile ♀ × Peru ♂) virgin ♀, demonstrating 20.9% gregarious oviposition and possessing 8/16th of the Chilean genome, was mated to a Chilean ♂, she thereafter oviposited gregariously in 41.7% of hosts; and her virgin ♀♀ offspring, with 12/16th of the Chilean genome, demonstrated 65.5% gregarious behavior (Fig. 4). On the other hand, if the F_1 virgin ♀ mated with a Peruvian ♂, she oviposited gregariously in only 8.1% of hosts, and her virgin ♀♀ progeny, with 4/16th of the Chilean genome, demonstrated only 3.6% gregarious behavior. The same pattern was obtained in other matings shown in Figs 2–4. A summary of these responses for 16 oviposition days is shown in Fig. 4.

The degree of behavioral change in the mated mother and her progeny differed for the Chilean and Peruvian ♂. When mated to a Chilean ♂, increases in gregarious oviposition were determined by the ♀♀ genome. Thus, the more genes for gregarious oviposition in the ♀♀ genome, the less influence a Chilean ♂ had on her behavior. However, the "diluting" influence that a Peruvian ♂, with an apparent absence of genes for gregarious oviposition, had on the ♀ with whom he mated and her progeny, was independent of her genome (Figs 2–4).

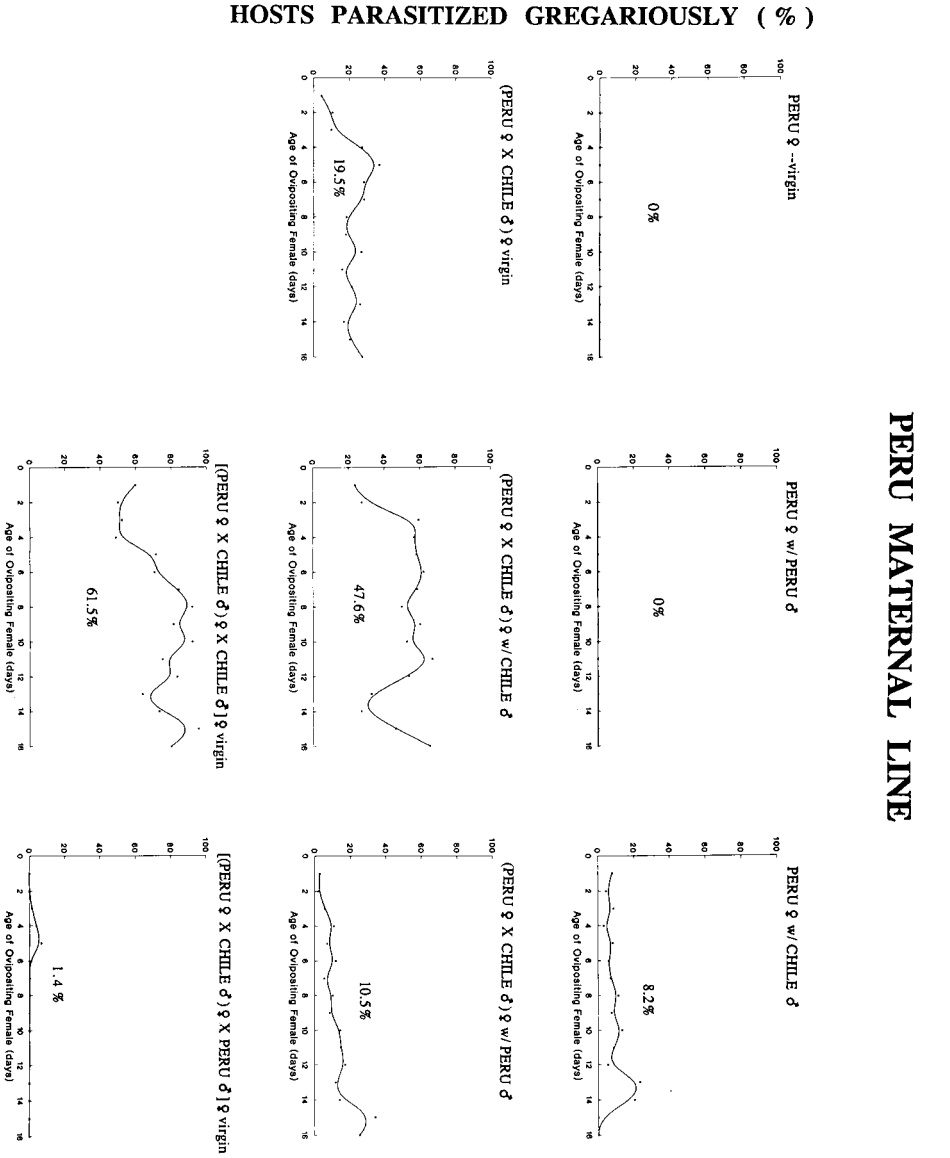

Fig. 2. Daily gregarious oviposition in the Peruvian line of *Muscidifurax raptorellus* Kogan & Legner, showing expression in the P_1, F_1 and first backcross progeny, where 20 females oviposit continuously at 25 ± 1°C, 55% RH, on 20 *Musca domestica* puparia daily for 16 days. Each point represents the average of surviving females.

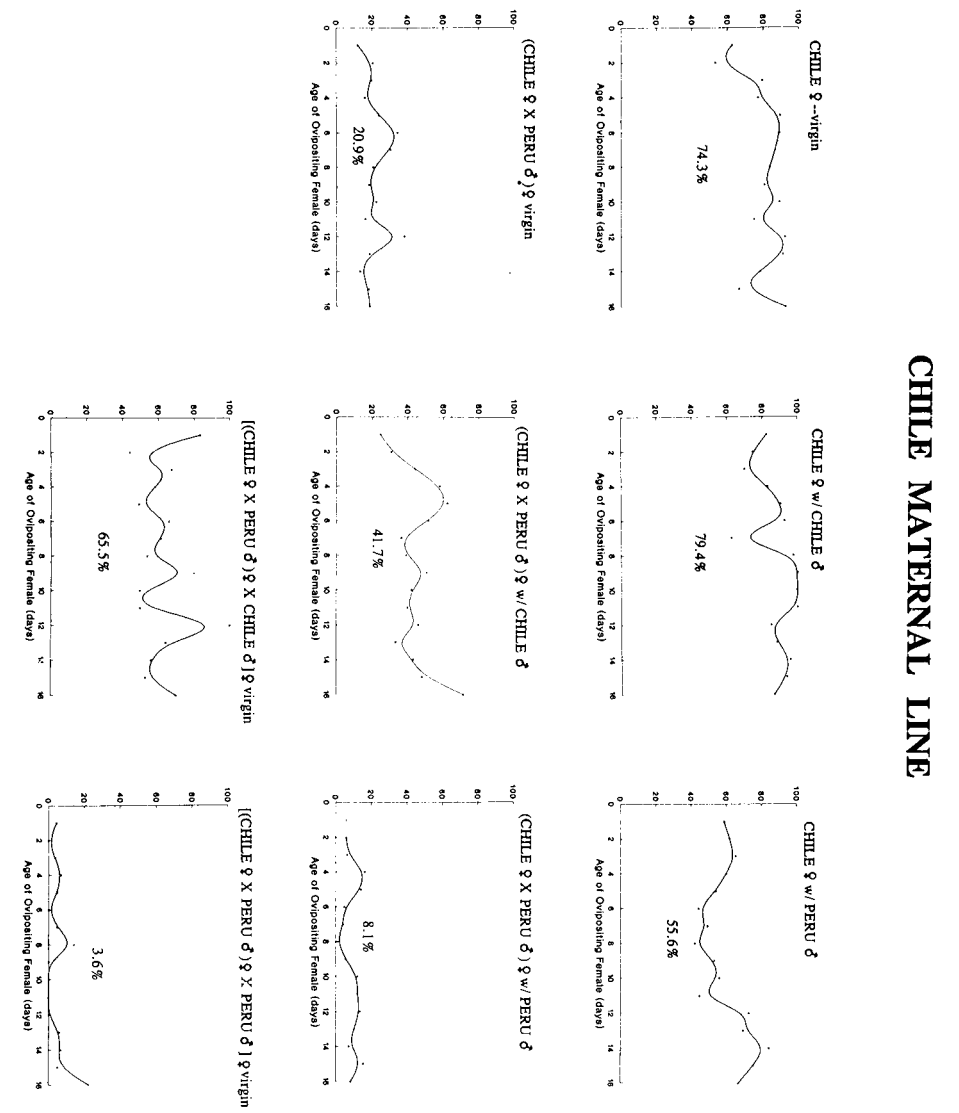

Fig. 3. Daily gregarious oviposition in the Chilean line of *Muscidifurax raptorellus* Kogan & Legner, showing expression in the P_1, F_1 and first backcross progeny, where 20 females oviposit continuously at 25 ± 1°C, 55% RH, on 20 *Musca domestica* puparia daily for 16 days. Each point represents the average of surviving females.

The novel aspect of this process is that the mated ♀ receives a stimulus after mating with the Peruvian ♂, which expresses his genome for the "absence" of gregarious genes. A code for "solitariness" is present in Peruvian ♂♂ that reduces the magnitude of gregarious oviposition behavior in mated ♀♀. However, as in the previous case with Chilean ♂♂, the behavioral change is less than that which will be exhibited by resulting progeny. Behavioral changes after mating are permanent, there being no reversion in behavior following a second mating with a ♂ of the opposite race. Signals are sent to a ♀ from the ♂ within an hour of mating, obviously via the sperm or seminal fluid; these signals partially express the code of the male's genes. The male's genes are then inherited by the progeny in a manner typical of polygenic inheritance. Such a stepwise inheritance has been termed "accretive inheritance." As only a *portion* of the polygenic controlled expression surfaces in the mother-to-be, *before* appearance of her progeny, exposure of this trait to natural

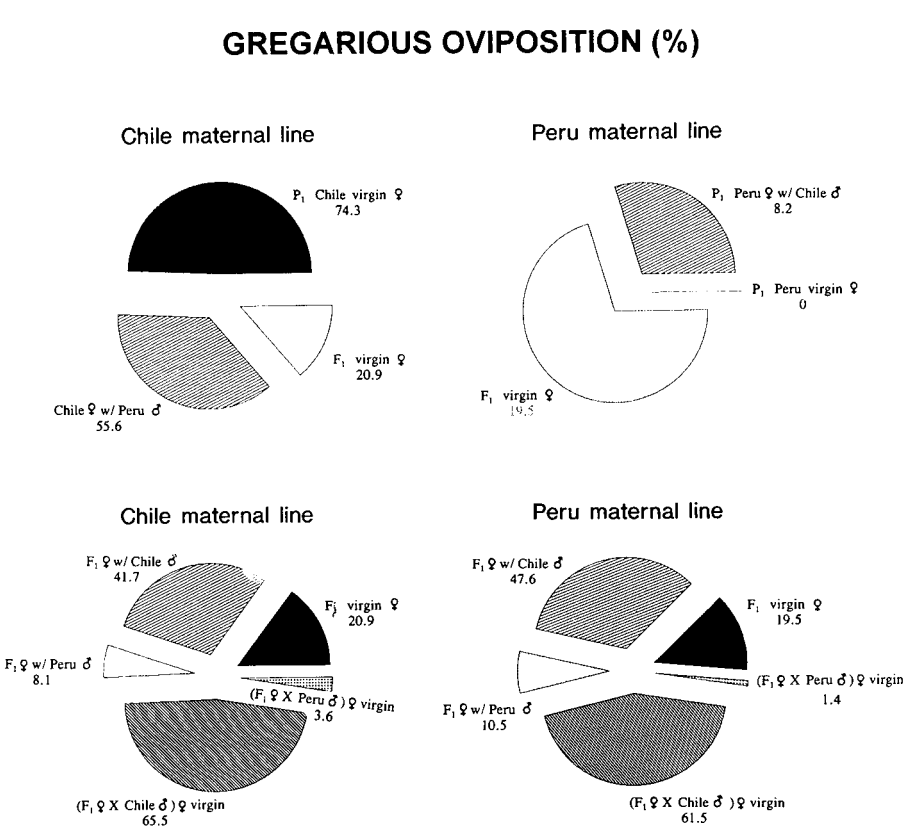

Fig. 4. Averaged total gregarious oviposition for the 16 days shown in Figs 2, 3, in Peruvian and Chilean lines of *Muscidifurax raptorellus* Kogan & Legner. Expressions are shown for P_1, F_1 and first backcross progeny, where 20 females oviposit continuously at 25 ± 1°C, 55% RH, on 20 *Musca domestica* puparia daily for 16 days.

selection begins with *caution*, and the kind of genes involved have been termed "wary" (Legner, 1989a).

An enhanced significance for haploid males is indicated through their ability to activate expressions of part of their own genetic make-up *within their own generation*, which could *quicken the pace of evolution* by allowing natural selection for carried traits to begin to act in the *parental* generation. Although the usual haploid origin of males in Hymenoptera has been regarded as a possible means to rid populations of undesirable recessive traits (see Dobzhansky, 1951), it is obvious that many important characteristics such as host searching, parasitization and fecundity are expressed only in diploid females. The *M. raptorellus* results reveal a passive means of expressing male traits within the male's own generation. Therefore, if the above mentioned wary genes occur more generally in Hymenoptera, their presence might account partially for the rapid evolution thought to occur in certain groups of the order (Gordh, 1975, 1979; Hartl, 1972, Legner, 1989a).

In applied biological control, the ability of ♂♂ parasitoids to activate part of their own genetic make-up *within their own generation* in ♀♀ with whom they mate also places greater importance on liberated ♂♂ during inundative or inoculative release strategies. Certain desirable racial characteristics may be conveyed directly to unmated ♀♀ already resident in the environment.

The combination of extranuclear and chromosomal inheritance witnessed in this species challenges accepted views of polygenic loci. Such loci actually may not be inherited, but rather another group of genes which act to *switch on* or *off* the loci. These genes may influence DNA methylation of the polygenic loci controlling oviposition behavior in a manner described for other organisms by Bird (1992). The picture thus envisioned is that all polygenic loci may be perpetually present for a given quantitative trait in all individuals of both races, but they are activated or inactivated by substances under the control of another group of genes. The fact that the substances transferred at mating cause only partial change in the female's phenotype may be related to the haploid origin of males, which translates to a male possessing only one half the number of genes as his mate. Assuming that the diploid virgin female's genetic make-up determines how many polygenic loci are turned on or off, the addition of more phenotype-changing substances from her haploid mate through insemination would not be expected to change her existing phenotype to the same extent as chromosomal inheritance in the ensuing diploid female progeny.

Because quantitative inheritance in *M. raptorellus* follows the general pattern witnessed in most animals and plants, it is tempting to envision a similar genetic system for other organisms. Certainly the kind of environmental uniformity and experimental replication possible in the *M. raptorellus* case has not been readily attainable with other systems; and extranuclear expressions occur only after the first mating. However, such an assumption is unwarranted at this time, and the superimposed second genetic system visualized for this species way well be confined to it alone.

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REFERENCES

ASKEW R.R. 1971: *Parasitic Insects.* Amer. Elsevier Publ. Co., Inc., New York, 316 pp.

BIRD A. 1992: The essentials of DNA methylation. *Cell* **70**: 5–8.

CROZIER R.H. 1971: Heterozygosity and sex determination in haplodiploidy. *Amer. Nat.* **105**: 399–412.

CROZIER R.H. 1975: *Animal Cytogenetics 3, Insecta 7, Hymenoptera.* Gebrüder Borntträger, Berlin, 95 pp.

DOBZHANSKY T. 1951: *Genetics and the Origin of Species. 3rd ed.* Columbia Univ. Press, New York, 364 pp.

DUNCAN D.B. 1955: Multiple range and multiple F tests. *Biometrics* **11**: 1–41.

GARDNER E.J. & SNUSTAD D.P. 1984: *Principles of Genetics. 7th e*d. John Wiley & Sons, New York, 648 pp.

GOODENOUGH U. 1984: *Genetics. 3rd ed.* Saunders College Publ. Co., New York, 894 pp.

GORDH G. 1975: Some evolutionary trends in the Chalcidoidea (Hymenoptera) with particular reference to host preference. *J. New York Entomol. Soc.* **83**: 279–280.

GORDH G. 1979: *Catalog of Hymenoptera in America North of Mexico. Vol. I.* Smithsonian Institution Press, Washington, D.C., pp. 734–748.

HARTL D.L. 1972: A fundamental theorem of natural selection for sex linkage arrhenotoky. *Amer. Nat.* **106**: 516–524.

KAWOOYA J.K. 1983: *Electrophoretic discrimination of species of the Muscidifurax (Hymenoptera: Pteromalidae) complex.* Ph.D. Dissertation, Univ. of Illinois, Urbana. 133 pp.

LANDE R. 1981: The minimum number of genes contributing to quantitative variation between and within populations. *Genetics* **99**: 541–553.

LEGNER E.F. 1987: Inheritance of gregarious and solitary oviposition in Muscidifurax raptorellus Kogan & Legner (Hymenoptera: Pteromalidae). *Canad. Entomol.* **119**: 791–808.

LEGNER E.F. 1988a: Muscidifurax raptorellus (Hymenoptera: Pteromalidae) females exhibit post mating oviposition behavior typical of the male genome. *Ann. Entomol. Soc. Amer.* **81**: 524–527.

LEGNER E.F. 1988b: Quantitation of heterotic behavior in parasitic Hymenoptera. *Ann. Entomol. Soc. Amer.* **81**: 567–681.

LEGNER E.F. 1988c: Hybridization in principal parasitoids of synanthropic Diptera: the genus Muscidifurax (Hymenoptera: Pteromalidae). *Hilgardia* **56**(4): 1–36.

LEGNER E.F. 1989a: Wary genes and accretive inheritance in Hymenoptera. *Ann. Entomol. Soc. Amer.* **82**: 245–249.

LEGNER E.F. 1989b: Phenotypic expressions of polygenes in Muscidifurax raptorellus (Hym.: Pteromalidae), a synanthropic fly parasitoid. *Entomophaga* **34**: 37–44.

LEGNER E.F. 1991a: Estimations of number of active loci, dominance and heritability in polygenic inheritance of gregarious behavior in Muscidifurax raptorellus (Hymenoptera: Pteromalidae). *Entomophaga* **36**: 1–18.

LEGNER E.F. 1991b: Recombinant males in the parasitic wasp Muscidifurax raptorellus (Hymenoptera: Pteromalidae). *Entomophaga* **36**: 173–181.

LEGNER E.F. & OLTON G.S.: Distribution and relative abundance of dipterous pupae and their parasitoids in accumulations of domestic animal manure in the southwestern United States. *Hilgardia* **40**(14): 505–35.

LEGNER E.F., BAY E.C. & WHITE E.B. 1967: Activity of parasites from Diptera: Musca domestica, Stomoxys calcitrans, Fannia canicularis, and F. femoralis at sites in the Western Hemisphere. *Ann. Ent. Soc. Amer.* **60**: 638–51.

METCALF R.A., MARTIN J.C. & WHITT G.S. 1975: Low levels of genetic heterozygosity in Hymenoptera. *Nature* **257**: 792–794.

REUTER O.M. 1913: *Lebensgewohnheiten und Instinkte der Insekten.* Friedlander, Berlin. 488 pp.

STEEL R.G.D. & TORRIE J.H. 1980: *Principles and Procedures of Statistics, 2nd ed.* McGraw-Hill, New York, 633 pp.

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