Bulletin of Insectology **55** *(1-2): 55-61*

Intraspecific weight variability in Tachinid flies: response of *Pseudogonia rufifrons* to two host species with different size and of *Exorista larvarum* to variations in vital space

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Abstract

The intraspecific size variability of *Pseudogonia rufifrons* Wiedemann was investigated in *Galleria mellonella* L. and in an other smaller factitious host, *Ostrinia nubilalis* (Hübner). The parasitoid puparial weight was found to increase proportionally to that of the host resources (i.e. host pupal weight - cuticle weight) available to it, the heaviest puparia being obtained in the largest hosts that provided the parasitoid with a greater amount of food. Parasitoid puparia from *O. nubilalis* females and *G. mellonella* males, that provided the parasitoid with resources of similar weight, were also of similar size. The larger weight attained by parasitoids in larger hosts may therefore be considered to depend solely on weight and not on other interspecific host differences.

Regardless of host species, sex and weight and of parasitoid sex, less than 50% of available resources were converted by the entomophage into its body mass. It may therefore be assumed that, besides being related to host weight, the parasitoid puparial weight also depends on its intrinsic capability to utilise host tissues.

Tachinid size may also be affected by host volume. The *in vitro* rearing technique was utilised to test the effect of vital space (i.e. mm^3 of volume available per parasitoid) on the growth and development of *Exorista larvarum* (L.). The development of this parasitoid was found to be considerably affected by vital space. In fact, at equal amounts of diet, the number of individuals attaining larval maturity and pupating was significantly lower in 0.38 cm^3 than in 2.27 cm^3 wells, and indeed in the smaller wells no adult was found to emerge. Parasitoid puparial weight was however found not to be affected by vital space.

Key words: tachinid size variability, host size and volume, *Pseudogonia rufifrons*, *Exorista larvarum*, *Galleria mellonella*, *Ostrinia nubilalis*.

Introduction

Parasitoids generally show high intraspecific size variability, which depends on several factors including host species, sex, stage, weight and volume (Salt, 1941). Given that in parasitoids size may be correlated with individual fitness and, in particular, with female fecundity, this characteristic plays a very important role in host-parasitoid relationship (Doutt *et al.*, 1976).

For idiobiotic parasitoids, which attack non-growing or paralysed hosts, large hosts are generally more suitable than small ones in relation to parasitoid size and fitness (Salt, 1940; Arthur and Wylie, 1959; Ueno *et al.*, 1999; Fidgen *et al.*, 2000). Conversely, in koinobiotic parasitoids that attack hosts which continue to feed and grow during the initial phases of parasitism, parasitoid size is especially affected by the growth potential of the host after parasitism (Mackauer, 1986). Hence, the relationship between host and parasitoid size is not necessarily linear (Salt, 1964; Mackauer and Sequeira, 1993; Harvey and Vet, 1997).

In Diptera Tachinidae these issues were investigated using *Steiniella callida* (Meigen). The weight and volume of the puparia resulting from parasitism in the first or second larval instars of the host *Chrysomela populi* L. did not vary appreciably, but considerable dwarfing occurred after parasitization during the second half of the third larval instar of the host (Mellini and Baronio, 1971). Parasitization in the host early prepupal stage also resulted in dwarfing of the parasitoids, the size of which decreased progressively as the age of the host at parasitization increased (Mellini and Baronio, 1972).

Further studies were performed using *Pseudogonia rufifrons* (Wiedemann) (*Gonia cinerascens* Rondani). The biology of this solitary larval-pupal parasitoid, which infests noctuids, has been described by Baronio and Campadelli (1978). *P. rufifrons* was reared on the factitious host *Galleria mellonella* L. (Lepidoptera Galleriidae) in our laboratory for about twenty years. As the factitious host employed was much smaller than the natural ones parasitized by this tachinid, it was deemed advisable to ascertain the parasitoid capability to adapt to the size of *G. mellonella*. Baronio *et al.* (1981) demonstrated that *P. rufifrons* puparium weight and host larva age at the time of parasitization are directly correlated, with parasitoid weight especially depending on the size of the host pupa. Mellini and Campadelli (1982) also investigated the relationship between host and parasitoid weight. Host pupal size was increased by topical treatment with methoprene to last instar larvae and decreased by feeding larvae only with wax. The weight of parasitoid puparia increased proportionally to that of the host pupae until a host weight of 200 mg, increasing however less rapidly in larger hosts. Since the weight attained by *G. mellonella* pupae in standard rearing was usually below 200 mg, it was concluded that *G. mellonella* was an undersized host for *P. rufifrons*.

Parasitoid size may be affected not only by the amount of host resources in terms of weight but also by the host volume available for each entomophage. The relationship of host to parasitoid size has been investi

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† Deceased July 19, 2002

gated with several gregarious oophagous parasitoids, such as *Telenomus fariai* Lima (Rabinovich, 1971), *Trichogramma minutum* Riley (Marston and Ertle, 1973) and *Edovum puttleri* Grissel (Corrigan and Lashomb, 1990). In all these species, vital space (i.e. mm^3 of host egg available per parasitoid) was found to be highly correlated to parasitoid size.

In view of all these considerations, we investigated parasitoid intraspecific size variability in *G. mellonella* L. and in a smaller factitious host, *Ostrinia nubilalis* (Hübner) (Lepidoptera Crambidae), as well as the effects of variations in vital space on the growth and development of another tachinid, *Exorista larvarum* (L.), a polyphagous larval parasitoid of Lepidoptera. Unlike *P. rufifrons*, *E. larvarum* was reared from egg to adult on artificial diets, with adult yields similar to those usually obtained when reared in the host (Mellini and Campadelli, 1995). In view of these results *in vitro* rearing could be utilised to investigate this issue.

Materials and methods

Biological materials. A colony of *P. rufifrons* was established in 1975 from a female collected at Borgo Capanne on the Emilian Apennines (Italy) (Campadelli and Baronio, 1978), while a colony of *E. larvarum* was established in 1992 from adults which had emerged from field-collected larvae of *Lymantria dispar* (L.) (Lepidoptera Lymantriidae) and *Hyphantria cunea* Drury (Lepidoptera Arctiidae) (Coulibaly, unpublished data). Both colonies were maintained in the laboratory using *G. mellonella* as a factitious host. *G. mellonella* larvae were reared on a diet developed by Sehnal (1966) at 30±1°C, 65±5% RH, and in complete darkness. The tachinid adults were kept in plexiglass cages at 26±1°C, 75±5% RH, 16:8 L:D photoperiod, and fed on cotton balls soaked in a honey and water solution. *O. nubilalis* was reared on an artificial diet according to Maini *et al.* (1978).

Response of *P. rufifrons* to variations in host species. *P. rufifrons* microtype eggs were exposed to *G. mellonella* and *O. nubilalis* larvae at the beginning of the last instar. The parasitized larvae were maintained at 30±1°C, 65±5% RH and in complete darkness until pupation. The parasitized pupae, which were easily recognisable from the integumental respiratory funnel induced by the parasitoid second instar larvae, were selected, sexed and kept under the conditions described above until puparium formation. The newly formed puparia were gently removed from host remains. Both the parasitized pupae and the puparia were individually weighed within 24 hours of their formation.

After weighing, the puparia were placed singly into glass tubes. Parasitoid sex was determined at adult emergence. Upon puparium removal, the remains of each host pupa were placed in 10% KOH so as to remove the non-sclerotized parts from the host cuticle, which was then carefully dried and weighed.

The following parameters were considered for statistical analysis:

1. weight of the cuticle of the host pupa
2. weight of host resources available to the parasitoid (= weight of the newly-formed parasitized pupa - weight of the cuticle of the host pupa)
3. puparial weight
4. weight of host remains (= weight of the host resources available to parasitoid - puparial weight)
5. ratio parasitoid weight/host weight (= puparial weight / weight of the host resources available to parasitoid).

All weights were expressed in mg.

Only the data of parasitized pupae that produced a healthy puparium ultimately leading to the emergence of an adult were considered.

The analysed data were collected from 228 *O. nubilalis-P. rufifrons* systems and 236 *G. mellonella-P. rufifrons* systems, each system being considered as a replicate. The data were separately analysed for male and female parasitoids by a 2x2 factorial analysis of variance. The two factors tested were the host species (*O. nubilalis* and *G. mellonella*) and sex (males and females). Means were compared using the Tukey HSD multiple range test where significant difference ($p < 0.05$) occurred.

Response of *E. larvarum* to variations in vital space. This test was performed by rearing *E. larvarum* on the artificial diet developed by Mellini and Campadelli (1995). Two treatments (I and II) in which the diet was distributed in 0.38-cm^3 (I) and in 2.27- cm^3 wells (II) of plastic rearing plates (Nunclon, Denmark) were initially compared . In both treatments about 330 mg of diet were distributed per well to test the parasitoid response to variations in well volume in the presence of the same amount of medium. In treatment I the wells were almost filled up with diet, with air being however present from the beginning of parasitoid development. A further treatment (III) was compared with treatment II only. In treatment III the medium was distributed in 2.27-cm^3 wells as in treatment II but about 560 mg of diet were placed in each well following the standard *in vitro* rearing procedure of *E. larvarum*. Treatment I was finally compared with treatment IV, with 330 mg (I) and 155 mg (IV) of diet per well being distributed in 0.38-cm^3 wells.

In all the treatments of the present study the diet was more than 3.3 mm thick, as recommended Mellini and Campadelli (1996). These authors reported that on thinner layers the artificial rearing of *E. larvarum* was unsuccessful, because the diet tended to dry up, while thicker layers did not positively or negatively affect parasitoid development.

One parasitoid egg was placed in each well according to Bratti and Coulibaly (1995). The plates were then sealed with Parafilm, wrapped in tinfoil and placed in an incubator at 26°C throughout parasitoid development.

The newly formed puparia were gently removed from diet remains. As described above, the puparia were individually weighed within 24 hours of their formation. The diet remains in each well were weighed after removal of the newly formed puparia or of the mature larvae that had died before pupating.

Table 1. Size variability of *Pseudogonia rufifrons* males obtained from *Galleria mellonella* or *Ostrinia nubilalis*, as related to the combination of the factors "host species " and "host sex". Means (± SD) followed by the same letter (uppercase in the same row, lowercase in the same column) are not significantly different (Tukey HSD test, P<0.05).

Parameters	Host species	Host sex		ANOVA results		
		Males	Females	Host species effect	Host sex effect	Interaction
Puparial weight	*O. nubilalis*	(1) 35.3±14.3	(2) 51.2±16	F=78.02 P=0.0000001*	F=47.78 P=0.0000001*	F=0.0003 P=0.99
	G. mellonella	(3) 55.7±19	(4) 71.7±21.8			
Weight of host cuticle	*O. nubilalis*	(1) 3.2±0.9	(2) 4.1±1.2	F=0.21 P=0.65	F=44.21 P=0.0000001*	F=0.58 P=0.45
	G. mellonella	(3) 3.2±1.1	(4) 4.3±1.4			
Weight of host resources	*O. nubilalis*	(1) 81.2±17.2	(2) 108.9±23.4	F=91.7 P=0.0000001*	F=69.8 P=0.0000001*	F=1.6 P=0.21
	G. mellonella	(3) 113.7±35.7	(4) 151.2±39.4			
Ratio Parasitoid weight/Host weight	*O. nubilalis*	(1) 0.42±0.13Aa	(2) 0.48±0.14Ba	F=4.3 P=0.04*	F=1.64 P=0.2	F=6.34 P=0.01*
	G. mellonella	(3) 0.49±0.1Ab	(4) 0.47±0.8Aa			
Weight of host remain	*O. nubilalis*	(1) 49.7±14.6Aa	(2) 58.8±25.1Aa	F=25.5 P=0.000001*	F=27.7 P=0.0000001*	F=4.23 P=0.04*
	G. mellonella	(3) 58.2±21.9Aa	(4) 78.9±24.9Bb			

df= 1, 241

(1) n= 57; (2) n= 63; (3); n= 73; (4); n= 52

The following parameters were considered for result evaluation:

1. percentage of mature larvae observed on the media (= mature larvae/eggs originally placed on the media x 100)
2. percentage of puparia (=puparia/mature larvae x 100)
3. percentage of adult emergence (=adults/puparia x 100)
4. puparial weight (in mg)
5. weight of food remains (in mg)
6. ratio puparial weight/ weight of the original amount of diet (330 or 560 mg)

Four (treatments I and IV) and three (treatments II and III) replicates were performed. Each replicate consisted of 24 eggs (treatments I, II and IV) and 16 eggs (treatment III).

Adult emergence of treatments I and II was compared according to the Kruskal-Wallis non-parametric procedure, as were adult emergence of treatments I and IV and the ratio between the puparial weight and the weight of the original amount of diet of treatments II and III. The other data were analysed by one-way ANOVA. The percentages were transformed for analysis using an arcsine transformation (Mosteller and Youtz, 1961).

Results

Response of *P. rufifrons* to variations in host species. The results are summarised in tables 1-2. The male and female puparial weights were significantly affected by the host species and host sex. The interaction of the two factors was not significant. For the weight of host cuticle of male and female parasitoids no significant effect of host species was found, while the effect of host sex was significant. The interaction of the two factors was significant only for female flies. For the weight of host re sources available to male and female parasitoids the host species and host sex effects were significant, while a significant interaction of host species and host sex was found only for female parasitoids. A significant interaction of the two factors was also found for the ratio between the male parasitoid weights and the relevant host weights. For male flies this parameter was significantly affected by the host species. For the weight of host remains of male and female parasitoids the effect of host species and sex was significant. The interaction of the two factors was also significant.

It has to be pointed out that the larvae of *P. rufifrons* defecate only after reaching maturity (Gardenghi and Mellini, 1990). Thus, the host resources were not spoiled by parasitoid faeces during parasitoid larval development.

Response of *E. larvarum* to variations in vital space. The effect of vital space on parasitoid development is shown in table 3. Parasitoid larvae consumed the same amount of diet both in the small and in the large wells (treatment I and II). In fact, no significant difference was found in the weights of food remains between small and large wells. Notwithstanding, well volume was however seen to considerably affect parasitoid development. Indeed, the percentage of mature larvae was significantly higher in large than in small wells. A very small number of puparia formed throughout the experiment and no adults emerged in the small wells, whereas in the large ones the percentage of puparia and adult emergence was 82.9% and 91.7%, respectively. Among other things this result may be ascribable to air deficiency in the small wells. Despite these differences, puparial weight was not found to be affected by the vital space available to the parasitoids.

Table 2. Size variability of *Pseudogonia rufifrons* females obtained from *Galleria mellonella* or *Ostrinia nubilalis*, as related to the combination of the factors “host species ” and “host sex”. Means (± SD) followed by the same letter (uppercase in the same row, lowercase in the same column) are not significantly different (Tukey HSD test, P<0.05).

Parameters	Host species	Host sex		ANOVA results		
		Males	Females	Host species effect	Host sex effect	Interaction
Puparial weight	*O. nubilalis*	(1) 41±13.1	(2) 57±13.5	F=64.9 P=0.0000001*	F=59.99 P=0.0000001*	F=2.83 P=0.94
	G. mellonella	(3) 57.8±17.4	(4) 82.7±24.1			
Weight of host cuticle	*O. nubilalis*	(1) 3.3±1.4Aa	(2) 4±1Ba	F=0.71 P=0.4	F=32.77 P=0.0000001*	F=4.19 P=0.04*
	G. mellonella	(3) 3.1±1.4Aa	(4) 4.5±1.3Ba			
Weight of host resources	*O. nubilalis*	(1) 88.02±27.5Aa	(2) 113±22.2Ba	F=73.91 P=0.0000001*	F=67.43 P=0.0000001*	F=8.96 P=0.003*
	G. mellonella	(3) 114.8±30.2Ab	(4) 168.4±43.9Bb			
Ratio Parasitoid weight/Host weight	*O. nubilalis*	(1) 0.47±0.1	(2) 0.51±0.96	F=0.69 P=0.41	F=0.37 P=0.54	F=3.61 P=0.06
	G. mellonella	(3) 0.51±0.12	(4) 0.48±0.08			
Weight of host remain	*O. nubilalis*	(1) 48±20.4Aa	(2) 57±18.4Aa	F=29.5 P=0.0000001*	F=34.7 P=0.0000001*	F=9.88 P=0.002*
	G. mellonella	(3) 55.5±20.5Aa	(4) 84.9±27.7Bb			

df= 1, 215

(1) n= 40; (2) n= 68; (3); n= 34; (4); n= 77

Table 3. Effect of variations in well volume on the growth and development of *Exorista larvarum* individually reared *in vitro* in multiwell plates. Both the large and small wells contained 330 mg of artificial diet each. Means (± SD) in a column followed by the same letter are not significantly different (Kruskal-Wallis non parametric test[% adult emergence]; one-way ANOVA [other parameters])

Well volume (cm^3)	Number of replicates	Weight of food remains (mg)	% mature larvae	% puparia	Puparial weight (mg)	% adult emergence
0.38	4	189.3±9.4a	47.9±11.0a	6.9±5a	54.6±3a (1)	0a
2.27	3	170.1±18.3a	75 ±7.2b	82.9±10.7b	55.2±2.6a	91.7±8.3b
H						4.3 (N=6)
F (df)		3.39 (1,5)	14.09 (1,5)	81.62 (1,5)	0.05 (1,4)	
P		0.125	0.013	0.0003	0.835	0.037

(1) Data referred to 3 replicates

Table 4. Growth and development of *Exorista larvarum* individually reared *in vitro* in 2.27-cm^3-volume wells of a multiwell plate. Each well contained 330 mg or 560 mg of artificial diet. Means (± SD) in a column followed by the same letter are not significantly different (Kruskal-Wallis non parametric test [ratio puparial weight/diet weight]; one-way ANOVA [other parameters])

Diet amount (mg)	Number of replicates	Weight of food remains	% mature larvae	% puparia	Puparial weight (mg)	Ratio puparial weight/diet weight	% adult emergence
330	3	170.1±18.3a	75±7.2a	82.9±10.7a	55.1±2.6a	0.17±0.01a	91.7±8.3a
560	3	361.9±49.9b	72.9±1a	63.3±8.3a	57.7±4.3a	0.1±0.01b	87.5±12.5a
H						4.09 (N=6)	
F (df)		0.09 (1,4)	0.07 (1,4)	6.36 (1,4)	0.75 (1,4)		0.36 (1,4)
P		0.78	0.935	0.07	0.435	0.043*	0.583

Table 5. Growth and development of *Exorista larvarum* individually reared *in vitro* in 0.38-cm^3-wells of a multiwell plate. Each well contained 330 mg or 155 mg of artificial diet. Means (± SD) in a column followed by the same letter are not significantly different (Kruskal-Wallis non parametric test [% adult emergence]; one-way ANOVA [other parameters])

Diet amount (mg)	Number of replicates	Weight of food remains (mg)	% mature larvae	% puparia	Puparial weight (mg)	% adult emergence
330	4	189.4±9.4a	47.9±11a	6.9±5a	54.6±3a(1)	0a (1)
155	4	62.5±9.4b	76±1.5b	3.8±7.5a	28.1±4b(2)	16.7±23.6a (2)
H						0.0 (N=5)
F (df)		303.16 (1,6)	11.95 (1,6)	0.2 (1,6)	83.35 (1,3)	
P		0.000002*	0.013*	0.669	0.003*	1

(1) data referred to 3 replicates
(2) data referred to 2 replicates

When parasitoids were reared in large wells containing 330 mg (II) or 560 mg (III) of diet, the weight of food remains was significantly higher and the ratio puparial weight/diet weight significantly lower for the parasitoids provided with the greater amount of medium (table 4). The other parameters, including puparial weight, were not however significantly affected by the quantity of food supplied.

Finally, when parasitoids were reared in the small wells containing 330 mg (I) or 155 mg (IV) of diet puparial weight was significantly lower for the tachinids provided with the smaller amount of food. However, a significantly lower number of larvae reached maturity in the wells containing 330 mg diet. A few puparia formed in both treatments but in the wells containing 330 mg of diet no adults emerged (table 5). Also in this case the result may be partially ascribable to air deficiency in the small wells containing the higher amount of food.

In this tests, the food was spoiled by the parasitoid faeces throughout larval development, as *E. larvarum* larvae release fluid matter from the anal opening beginning from the first instar (Gardenghi and Mellini, 1995).

Discussion

Parasitoids may be considered as predators that develop at the expense of a single victim, whether individually or sharing it with other entomophages belong ing to the same or to a different species. Depending on the host and parasitoid species, the victim may die rapidly or live for some time after parasitization. In the former instance the host-parasitoid relationship is generally simple, whereas in the second complex physiological interactions between the two symbionts occur. The latter is the case with *P. rufifrons* which is dependent on host hormonal balance for its development (Baronio and Sehnal, 1980), whereas *E. larvarum*, the other tachinid investigated in the present study, is independent of the physiology of its host which dies soon after parasitization. *E. larvarum* can hence be easily reared on artificial diets (Mellini *et al.*, 1996; Dindo *et al.*, 1999) unlike *P. rufifrons* (Baronio and Sehnal, 1980; Bratti and Monti, 1988; Mellini *et al*., 1994).

Parasitoid weight depends on the capability of the parasitoid species to exploit the host in order to attain the higher or lower size compatible with its genoma. As the entomophage has to grow inside the host volume, it may be questioned whether parasitoid size depends only on the amount of food available or also on vital space. The size of some species of oophagous parasitoids was found to be affected not only by host volume but also by other factors such as host weight and the parasitoid intrinsic capability to utilise host tissues (Rabinovich, 1971; Marston and Ertle, 1973; Corrigan and Lashomb,1990). According to our findings, the capability of *E. larvarum* to develop up to the pupal stage on an artificial diet was found to depend on the vital space available to the parasitoid. In particular, the comparison of the large versus the small rearing containers filled with the same amount of diet (=330 mg each) showed that the vital space affected the number of the puparia obtained but not their size. Vital space was therefore found to be essential for *E. larvarum* to complete its development. The parasitoid, however, was apparently unable to perceive the volume of its "container" in order to regulate its growth. Both in the large and in the small rearing wells a higher amount of diet was consumed by the parasitoid larvae when a higher quantity of diet was originally placed inside the well. The ratio between puparial weight and diet weight was however lower under these conditions.

The behaviour of *P. rufifrons* was seemingly completely different from that of *E. larvarum*, although the comparison between these two parasitoids is difficult due to their different biology and to the different rearing conditions adopted in the study (i.e. *in vivo* for *P. rufifrons* and *in vitro* for *E. larvarum*). Our findings did however show that vital space also affects the growth of *P. rufifrons* as in small hosts it attained a smaller size and did not even consume all the host tissues at its disposal. In fact, whatever host size, the intrinsic capability of this entomophage to utilise its victim did not exceed 50% of the host weight. In particular, as a consequence of adaptation to host weight, the lowest ratio between parasitoid weight and weight of host resources was recorded in the smallest hosts, i.e. in *O. nubilalis* males. *P. rufifrons* proved therefore to be capable of adapting its size to that of the host in order to complete its development. This adaptation cannot in fact be ascribed to food shortage as in all hosts about 50% host resources were actually not utilised. It may therefore be assumed that *P. rufifrons* is capable of perceiving vital space and hence behave accordingly.

O. nubilalis females and *G. mellonella* males, which provided parasitoids with resources of similar weight, the puparia obtained were also of similar size. Therefore, the larger weight attained by parasitoids in larger hosts may be considered as simply being weight-dependent and not affected by other interspecific host differences. While Sandlan (1982) showed that the size of the ichneumonid parasitoid *Coccygomimus* (*Pimpla*) *turionellae* (L.) was affected by host species factors other than weight, our study confirmed that the heaviest *P. rufifrons* puparia can be obtained from the largest *G. mellonella* pupae, in line with the findings of Baronio *et al.* (1981) and Mellini and Campadelli (1982). Notwithstanding, the male of *G. mellonella* cannot be considered to be such an undersized host for *P. rufifrons* as claimed by Mellini and Campadelli (1982) in their study since the *O. nubilalis* males utilised in our experiments are in fact considerably smaller.

It can therefore be concluded on the basis of our findings that vital space is important for the development of the two parasitoids investigated. In particular, when reared on an artificial diet in small rearing wells *E. larvarum* was often incapable of completing its development because it was unable to perceive and adapt itself to the small size of the rearing container so that it continued growing to its maximum genetically permissible size. Vice versa, *P. rufifrons* proved to be able to perceive the vital space available as in fact it generally consumed only 50% of the host tissue at its disposal.

Acknowledgments

We are grateful to Simon Grenier for reviewing the manuscript and to Edith Ladurner for her assistance in statistical analyses. This work has been supported by the Italian Education, University and Research Ministry (MIUR ex-60%).

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Received September 10, 2002. Accepted December 16, 2002