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Infestation Procedures and Heritability of Characters Used to Estimate Ear Damage Caused by Second-Brood European Corn Borer (*Ostrinia nubilalis*, Hübner) on Corn¹

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Abstract. Procedures for forced field infestation of maize with European corn borer egg masses, placed to simulate possible natural ovipositional sites and to emphasize damage to the ear, were compared. A growth chamber procedure using excised ears and a free-choice (preference) infestation procedure were also used. Forced infestation in the field permitted infestation at a uniform relative maturity and uniform development of borers from time of infestation to evaluation. An ear-and-leaf infestation procedure appeared to be the most appropriate for simultaneous evaluation of kernel damage and stalk tunneling. Estimated heritabilities, using this procedure on 2 segregating populations, were 0.71 and 0.84 for kernel damage and 0.39 and 0.79 for stalk tunneling. Phenotypic correlations among 3 ear damage criteria were noted ($r = 0.42$ to 0.46). Evaluation based on kernel damage alone, excluding cob tunneling and number of surviving larvae, was considered sufficient. There was no evidence that kernel damage was influenced by level of stalk tunneling.

The value of the sweet corn crop, extent and cost of chemical control to prevent losses, and the development of laboratory

rearing techniques (4) have stimulated research on the use of artificial infestation to simulate oviposition by the second brood of the European corn borer. In grain corn, studies of resistance to the second brood have emphasized stalk tunneling and sheath and collar damage (4). Because ear damage has more direct importance in sweet corn losses, a reexamination of infestation techniques and redefinition of damage characters was undertaken.

Pounders et al. (8) infested sweet corn using a modification of the method described by Pesho et al. (7) for grain corn: during anthesis, pairs of egg masses at the near hatch stage were pinned to the lower midrib surface of the primary ear leaf and to one leaf each immediately above and below the ear. Plants were evaluated for husk penetrations and for sheath, collar, stalk, shank, silk, and kernel damage.

Andrew and Carlson (1) and Carlson and Andrew (2) placed 4 egg masses in the whorl to simulate first brood infestation

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³Egg masses were produced in the laboratory of H. C. Chiang, University of Minnesota, Department of Entomology, Fisheries and Wildlife.

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and 4 egg masses under the husk near the tip of the developing shoot to simulate second brood infestation. Husk and ear tip damage were rated on 4-point scales based on number of tunnels and damage to the 5 cm below the apex, respectively. Tunnels were counted on the remainder of the ear. Tip rating was combined with ear tunnel count to obtain an ear damage index.

Shehata et al. (12) developed a controlled environment (growth chamber) technique for evaluating sweet corn ears for second brood resistance. At silking, ears were excised, trimmed to within 2.5 cm of the cob tip, and artificially infested in the silks at this cut tip with 5 freshly hatched larvae. The infested ears were placed individually in clear polyethylene bags which were closed (tied) and suspended in a controlled environment chamber for 2 weeks. Evaluation was made for larval weight, number of surviving larvae, and number of 4th and 5th instar larvae.

Our objectives were to investigate: 1) phenotypic and genotypic variability in resistance to ear damage and stalk tunneling, 2) the relationship among 3 ear damage characters and stalk tunneling, 3) the relative usefulness of 4 forced infestation procedures for identifying superior genotypes, and 4) the relationship between forced and free-choice infestation procedures.

Materials and Methods

Experiment #1. In 1976, a random sample of 63 F₃ families derived from a commercial sweet corn hybrid ('Green Giant Code 4') were evaluated for second brood resistance. These were planted in a randomized complete block design with 4 replications. The 0.9 × 6.1 m single-row plots were thinned to 20 plants, divided into 3 subplots of 5 plants each, with single plants serving as borders between the subplots and 1 or 2 plants used as border material at the ends of each whole plot. In this and all subsequent experiments, plants were established in early to mid-May plantings at St. Paul, Minnesota, and were grown under normal cultural conditions with supplemental irrigation.

Three infestation procedures, 2 involving infestation in the field and 1 employing a growth chamber, were used: ear-and-leaf (EL), ear-only (EO), and tip of excised ears in the growth chamber (GC). These were randomly assigned to subplots. EL was a modification of the procedure used by Pounders et al. (8). Beginning at the onset of silking in each entry, pairs of black-headed egg masses³ were pinned, with a 3-day interval between sites: 1) through the lower midrib on the leaf above the ear at a distance of 2.5 to 5 cm from the collar, 2) through the midrib on the upper surface of the ear leaf 2.5 to 5 cm from the collar, and 3) through the husk at the ear tip so that the young larvae would be in contact with the silk. Infested ears were covered with ear bags to prevent bird damage.

To standardize plant and larval development during the period of infestation, evaluation was made when approximately 278 heat units (°C), calculated as the mean daily temperature above a 10° base, had accumulated. Evaluation was made for: 1) extent of damage to the kernels, where 0 = none, 1 = 1-5, 2 = 6-15, 3 = 16-30, and 4 = >30 damaged kernels; 2) extent of cob tunneling, where damage was scored as cm of tunneling in multiples of 2.5 cm, where any tunnel under 2.5 cm was scored one point; 3) number of larvae and pupae within the husk, on the ear, and in the cob; and 4) extent of tunneling in the stalk and shank, where every penetration was scored 1 point and every 2.5 cm of tunneling beyond 2.5 cm from the penetration site was scored an additional point.

EO was similar to EL except that plants were infested only at the ear tip. Infestation was at the same time as the ear tip infestation of EL. Evaluations were also similar except that no evaluation of stalk tunneling was made.

As a modification of the growth chamber procedure of Shehata et al. (12), ears from each entry were harvested 6 days after the entry started to silk. The husk was trimmed to 2.5 cm beyond the ear tip and split about 7.5 cm to expose the ear

tip. Hatching egg masses were placed on a shelf edge from which the larvae were allowed to suspend themselves. Five larvae were placed on each ear tip. The husk was loosely folded back over the ear tip. Hence, the larvae were in close proximity to the ear tip, the silk, and the husk. Each infested ear was then placed in a 15 × 10 × 36 cm polyethylene bag. These bags were tied and suspended in growth chambers maintained at a 16/8 hr light/dark cycle under 8.6 klx of fluorescent light. Two chambers were used with 2 of the replicates in each chamber. Chamber #1 was maintained at 27°/21° during the light/dark cycle and chamber #2 was maintained at a constant 24°. After 10 days the ears were removed and evaluated for no. of larvae and larval development (instar).

Data were analyzed to investigate the relationship among damage characters and to compare potential response to selection following the different infestation procedures. Phenotypic correlation coefficients were calculated, using F₃ family means, to provide an indication of possible relationships among damage characters. Genotypic correlations (9) between kernel damage and stalk tunneling were calculated. Analyses of variance were used to determine if significant differences could be detected among F₃ families for the various characters following the 3 infestation procedures. F₃ family means for the damage characters were regressed on days to silk and accumulated heat units. Heritabilities, based on F₃ family means, were calculated using the components of variance method (6). We attached 95% confidence limits (3) to provide a measure of the sampling variation associated with these heritability estimates.⁴

Experiment #2. Sixteen F₄ families, derived by single seed descent from random F₂ plants of the cross 'I453' (sugary inbred) × 'B52' (stalk tunneling resistant dent inbred), were evaluated for kernel damage and stalk tunneling following each of 3 forced infestation procedures: 1) the ear-and-leaf (EL), 2) the ear-only (EO), and 3) a leaf-only procedure (LO) involving infestation only at the 2 leaf sites described for EL. The 3 procedures were randomly assigned to whole plots within each of 18 replications, and the 16 F₄ families were randomly assigned to 0.6m single plant subplots 4 rows spaced 0.9m apart.

All egg masses were pinned to a given plant on the same day, with infestation of each family made when 90% of the plants of that family had silked. Kernel damage was scored as the number of kernels damaged by larval feeding. Stalk tunneling was scored as previously described. Cob tunneling and number of larvae surviving on the ear were not recorded. To investigate the effect of stalk tunneling on kernel damage, kernel damage from EL was regressed on kernel damage from EO and stalk tunneling from LO.

Experiment #3. The 16 F₄ families described in Experiment #2 were further evaluated in an adjacent plot in which free choice infestation under a 7.3 × 7.3 × 2.4 m screen cloth cage was used. Plots consisted of single plants spaced 0.3 × 0.9 m in a randomized complete block design with 11 replications. The cage was set in place when the plants were at the 4-leaf stage.

When the first silks emerged, a corrugated ring containing approximately 200 pupae was suspended 0.6 m above the ground at the center of the cage. Five 0.6 × 0.6 m squares of crabgrass in the cage provided additional shelter for the moths. After 400 heat units (°C) had accumulated, the plants were evaluated for kernel damage and stalk tunneling as described in Experiment #2. In addition, the length of the longest husk flag leaf and the number of egg masses (empty cases) on the 3 leaves proximal to the ear were recorded.

Results and Discussion

Experiment #1. Significant variation ($P \leq 1\%$) was observed among the 63 F₃ families derived from 'Green Giant Code 4' for all damage characters in both EL and EO (Table 1). In GC,

Table 1. Means standard deviations, and heritability estimates of 63 F₃ families derived from 'Green Giant Code 4', (Experiment #1).

Character ^z	Infestation procedure	F ₃ family means			
		Grand mean (\bar{X})	Standard deviation ($s_{\bar{p}}$) ^y	Heritability (%) (\hat{H}) ^x	95% confidence interval ^w
Kernel damage	Ear-and-leaf (EL)	3.01	0.45**	71	54-82
Kernel damage	Ear-only (EO)	2.19	0.61**	57	32-73
Cob tunneling	Ear-and-leaf (EL)	3.61	1.55**	66	46-79
Cob tunneling	Ear-only (EO)	2.44	1.30**	55	28-71
Number of larvae	Ear-and-leaf (EL)	1.56	0.57**	63	40-76
Number of larvae	Ear-only (EO)	1.07	0.48**	38	0-60
Number of larvae	Growth chamber (GC)	2.89	0.39*	31	0-56
Mean instar	Growth chamber (GC)	4.74	0.12	31	-28-49
Stalk tunneling	Ear-and-leaf (EL)	39.55	6.02**	39	24-61

^zRating scales: Kernel damage; 1 (no damage) to 5 (30+ kernels damaged). Cob tunneling: cm in multiples of 2.5. Stalk tunneling: 1 point for each penetration and 1 additional point for each 2.5 cm of tunneling beyond 2.5 cm from the penetration site.

$$y_{s_{\bar{p}}} = \sqrt{\frac{MS \text{ families}}{4}}$$

$$x_{\hat{H}} = \frac{s_{\bar{G}}^2}{s_{\bar{p}}^2} = \frac{(MS \text{ families} - MS \text{ error})/4}{s_{\bar{p}}^2}$$

^wLower 95% confidence limit = $1 - F_{\alpha} \frac{MS \text{ error}}{2 MS \text{ families}} = 1 - 1.60 \frac{MS \text{ error}}{MS \text{ families}}$, and upper 95% confidence limit = $1 - F_1 - \frac{\alpha}{2}$

$$\frac{MS \text{ error}}{MS \text{ families}} = 1 - 0.64 \frac{MS \text{ error}}{MS \text{ families}}$$

*, **Variation among families significant at the 5% and 1% levels, respectively.

Table 2. Phenotypic correlation coefficients among characters for 63 F₃ families derived from 'Green Giant Code 4' (Experiment #1).

Character	Ear-and-leaf procedure (EL)			Ear-only procedure (EO)		Growth chamber (GC)
	Kernel damage	Cob tunneling	Number of larvae	Kernel damage	Cob tunneling	Mean instar
Cob tunneling	.46			.57		
Number of larvae	.44	.42		.50	.40	.24
Stalk tunneling	.46	.42	.44			

significant variation ($P \leq 5\%$) was observed among the F₃ families for number of surviving larvae but not for mean larval instar, perhaps because most larvae had reached the 5th instar. Had the material been evaluated earlier, differences, as reported by Shehata et al. (12) using other material, might have been observed.

The lower 95% confidence intervals were greater than zero for damage character in EL and EO except for number of larvae in EO, and were not greater than zero for the GC characters. The 95% confidence intervals suggest that heritabilities do not differ between EL and EO for kernel damage and stalk tunneling but was greater following EL for number of larvae.

The phenotypic correlation coefficients for F₃ families among the 4 damage characters evaluated in EL and EO were all moderate (Table 2). The correlation between number of surviving larvae and mean larval instar in GC was low. The phenotypic correlation for F₃ families for kernel damage between EL and EO was disappointingly low (Table 3), was higher for cob tunneling, and was low for number of surviving larvae. The correlations between the two GC characters and the characters evaluated in the EL and EO were all low. GC did not increase heritability relative to infestation in the field to provide a greater opportunity for selection gain. Since resistance to

kernel feeding has direct economic value in sweet corn, it could be used as the sole character, with limited correlated gain expected for cob tunneling and number of larvae (cobs are discarded and larvae can be floated off during processing). We prefer EL to EO because it also encourages sheath and collar feeding and permits subsequent evaluation for stalk tunneling resistance. We attribute the low correlation for kernel damage between these two procedures ($r = 0.23$) to the relatively small phenotypic standard deviations of family means in this material. In EL, the regressions on days to silk were significant ($P \leq 1\%$) for kernel damage and for stalk tunneling (Table 4). The slopes are negative in both, indicating that there was less damage in later maturing families. Since both were evaluated within a narrow range of accumulated heat units, their subsequent regression on heat units was not significant ($P \geq 5\%$).

Experiments #2 and #3. Significant differences ($P \leq 5\%$) were observed among the 16 F₄ families for both kernel damage and stalk tunneling in separate analyses of the 3 forced infestation procedures (Table 5). Correlations among F₄ families for the 3 infestation procedures were moderate to high for both characters (Table 6).

The procedures involving infestation on the ear (EL and EO) differed ($P \leq 1\%$) in the amount of kernel damage (Table 5)

Table 3. Phenotypic correlation coefficients among procedures for 63 F₃ families derived from 'Green Giant Code 4' (Experiment #1).

Character	Between ear-and-leaf (EL) and ear-only (EO)	Between ear-and-leaf (EL) and growth chamber (GC)		Between ear-only (EO) and growth chamber (GC)	
		No. of larvae	Mean instar	No. of larvae	Mean instar
		Kernel damage	.23	-.09	-.06
Cob tunneling	.61	-.06	.08	.09	.12
Number of larvae	.35	-.17	-.28	-.06	-.12
Stalk tunneling		-.01	-.18		

Table 4. Regression of family means for kernel damage and stalk tunneling on days to silk and accumulated heat units at time of evaluation of 63 F₃ families derived from 'Green Giant Code 4' (Experiment #1) and 16 F₄ families derived from 'I453' x 'B52' (Experiments #2 and 3).

Experiment no. (and procedure)	Source	df	Mean squares	
			Kernel damage	Stalk tunneling
Experiment #1 (ear-and-leaf)	Due to regression on:	2		
	Days to silk	1	1.31**Z	350.64**Y
	Heat units	1	0.05 ns	90.32 ns
	Deviation from regression	60	0.18	30.06
Experiment #2 (ear-and-leaf)	Due to regression on:	2		
	Days to silk	1	600.80 ns	43.10 ns
	Heat units	1	0.06 ns	0.13 ns
	Deviation from regression	13	244.50	10.00
Experiment #3 (free-choice)	Due to regression on:			
	Days to silk	1	307.00 ns	0.58 ns
	Deviation from regression	14	243.10	12.65

**Significant at the 1% level.

Zb₀ = 9.72, b₁ = -1.21.

Yb₀ = 14.94, b₁ = -19.81.

and, on average, differed ($P \leq 1\%$) from the procedure involving infestation only on the leaves (LO). Similarly, the 2 procedures involving infestation on the leaves (EL and LO) differed ($P \leq 1\%$) in the amount of stalk tunneling and, on average, differed ($P \leq 1\%$) from the procedure involving infestation only on the ear (EO). Freshly hatched larvae can suspend themselves with larval silk and potentially be carried to adjacent plants by wind. Our results indicate that stalk tunneling was concentrated on plants on which the egg masses had been pinned. Hence, air movement did not randomize the distribution of larvae among infestation procedures (whole plots).

Significant variation ($P \leq 1\%$) was also observed among the 16 F₄ families for both kernel damage and stalk tunneling after the free-choice (caged) infestation (Table 5). Correlations of F₄ families for both kernel damage and stalk tunneling between the free-choice and the forced infestation procedures were not strong (Table 6). The highest correlations were observed between the free-choice and EL.

Significant differences ($P \leq 5\%$) among families were also observed in the free-choice procedure for length of flag leaves and no. of egg masses as counted on the underside of the 3 leaves proximal to the ear.

The relatively large heritabilities for stalk tunneling in this material (Table 5) compared to the families derived from 'Green Giant Code 4' (Table 1) reflect the fact that a susceptible inbred ('I453') and a highly resistant inbred ('B52') were

used as parents, with considerable variation expected among randomly derived F₄'s; such variability was not necessarily expected among F₃ families derived from 'Green Giant Code 4'.

Flag leaf length was highly heritable, as expected (Table 5). The estimated heritabilities for kernel damage and stalk tunneling were also relatively large, suggesting that this material should be quite responsive to selection. As with the F₃ families derived from 'Green Giant Code 4', the 95% confidence intervals suggest that heritabilities do not differ among the infestation procedures for kernel damage. However, the estimated heritability for EO is less than the lower 95% confidence limits for EL and LO, suggesting that leaf infestation improved our potential response to selection for resistance to stalk tunneling.

The regressions of kernel damage and stalk tunneling on days to silk and accumulated heat units were not significant ($P \geq 5\%$, Table 4). This suggests that, unlike the 'Green Giant Code 4' derived families, there was no tendency for later maturing families to be relatively more resistant.

In the analysis to determine the extent to which stalk tunneling affected the kernel damage observed in EL, much of the variability among F₄ families for kernel damage could be accounted for by the regression on kernel damage in EO ($P \leq 1\%$, Table 7). The subsequent regression of kernel damage on stalk tunneling in LO was not significant. This indicates that phenotypic differences for kernel damage in EL could not be explained in part as a function of the increased stalk

Table 5. Means standard deviations, and heritability estimates of 16 F₄ families derived from 'I453' × 'B52', (Experiments #2 and #3).

Character ^Z	Infestation procedure	F ₄ family means			
		Grand mean (X)	Standard deviation (s _p) ^Y	Heritability (H̄) ^X	95% confidence interval ^W
Kernel damage	Ear-and-leaf (EL)	42.3	15.9**	84	61-92
Kernel damage	Ear-only (EO)	33.4	11.4**	71	28-85
Kernel damage	Leaf-only (LO)	21.2	8.5**	76	40-87
Kernel damage	Free-choice (FC)	26.2	15.7**	83	58-91
Stalk tunneling	Ear-and-leaf (EL)	8.4	3.3**	79	49-89
Stalk tunneling	Ear-only (EO)	4.1	1.5*	42	-40-70
Stalk tunneling	Leaf-only (LO)	7.1	3.8**	85	64-92
Stalk tunneling	Free-choice (FC)	8.6	3.6**	72	32-85
Flag leaf length (cm)	Free-choice (FC)	9.2	5.4**	95	87-97
# of egg masses	Free-choice (FC)	0.6	0.8**	73	34-86

^ZRating scales: Kernel damage; number of damaged kernels. Stalk tunneling; 1 point for each penetration and 1 additional point for each 2.5 cm of tunneling beyond 2.5 cm from the penetration site.

$$y_{s_p} = \sqrt{\frac{MS \text{ families}}{r}}; r = 18 \text{ for EL, EO, and LO}; r = 12 \text{ for FC.}$$

$$x\hat{H} = \frac{s_G^2}{s_p^2} = \frac{(MS \text{ families} - MS \text{ error})/r}{s_p^2}$$

^WLower 95% confidence limit = $1 - F_{\alpha} \frac{MS \text{ error}}{2 MS \text{ families}}$, and upper 95% confidence limit = $1 - F_1 - \frac{\alpha MS \text{ error}}{2 MS \text{ families}}$

*, **Variation among families significant at the 5% and 1% levels, respectively.

Table 6. Phenotypic (and genotypic) correlation coefficients among infestation procedures for kernel damage and stalk tunneling, and between kernel damage and stalk tunneling for infestation procedures (16 F₄ families derived from 'I453' × 'B52', Experiments #2 and #3).

Character	Kernel damage			Stalk tunneling			Between kernel damage and stalk tunneling
	Ear-&-leaf infestation (EL)	Ear-only infestation (EO)	Leaf-only infestation (LO)	Ear-&-leaf infestation (EL)	Ear-only infestation (EO)	Leaf-only infestation (LO)	
Ear-&-leaf infestation (EL)							.43 (.47)
Ear-only infestation (EO)	.66			.60			.55 (.86)
Leaf-only infestation (LO)	.75	.74		.86	.62		.54 (.62)
Free-choice (FC)	.46	.22	.37	.36	.10	.21	.18 (.23)

Table 7. Regression of kernel damage from ear-and-leaf infestation on kernel damage from ear-only infestation and stalk tunneling from leaf-only infestation, for 16 F₄ families derived from 'I453' × 'B52'.

Source	df	Mean squares
Attributable to regression		
(of kernel damage from ear-and-leaf infestation on:)	2	
Kernel damage from ear-only infestation	1	1657.03**
Stalk tunneling from leaf-only infestation	1	101.61
Deviation from regression	13	155.47
Total	15	

**Significant at the 1% level.

tunneling which results from this procedure. It is possible that ear resistance may be affected if stalk tunneling is extensive (e.g., scores of 50 or more), because ear stress may result from stalk damage. If kernel size is reduced and amount of material consumed by feeding larvae remains constant, the kernel damage rating is expected to be increased by stalk tunneling. Our data do not suggest such an effect. Guthrie et al. (5) attributed a reduction in kernel size and consequently yield, to sheath and collar feeding, rather than to stalk and shank tunneling, because grain development is nearly complete by the time 5th instar larvae move into the stalk and shank.

With the free-choice procedure, a moderate phenotypic correlation was observed between kernel damage and number of egg masses on plants but not between stalk tunneling and

Table 8. Phenotypic correlation coefficients among characters measured in the free-choice (caged) environment (days to silk are from the ear-and-leaf infestation procedure) for 16 F₄ families derived from 'I453' × 'B52'.

	Days to silk	Length of flag leaves	Number of egg masses	Kernel damage
Length of flag leaves	-.24			
Number of egg masses	.36	-.26		
Kernel damage	.29	.16	.63	
Stalk tunneling	-.06	.61	-.01	.18

number of egg masses (Table 8). Results from the forced infestation procedures indicated a positive relationship between no. of egg masses pinned to the plants and extent of both kernel damage and stalk tunneling (i.e., egg masses pinned to the ears increased kernel damage and egg masses pinned to the leaves increased stalk tunneling). In the free-choice environment, the correlation between kernel damage and number of egg masses further suggests that kernel damage may be anticipated, in part, as a function of the preference that may exist for a genotype as an ovipositional site. However, the lack of correlation between stalk tunneling and number of egg masses is not consistent with this interpretation.

Scott et al. (11) observed that plants shedding pollen are preferred for oviposition. In our experimental design we expected that pollen would be carried by the wind and would be equally available on all plants. A positive, but weak, relationship was observed between days to silk and number of egg masses, i.e., oviposition was slightly greater on later silking genotypes (Table 8). As in EL, no negative relationship was observed between either kernel damage or stalk tunneling and days to silk in the free-choice procedure (Table 4).

A moderate correlation was observed between stalk tunneling and length of flag leaves (Table 8), but we can offer no biological explanation. Windels and Chiang (13) reported that the proportion of egg masses observed on husk flag leaves is related to the size of these leaves and suggested that kernel damage might be greater on genotypes with larger flag leaves. We did not observe such a relationship (Table 8).

The phenotypic correlation observed between kernel damage and stalk tunneling was moderate for EL (Table 6), slightly stronger for EO and LO, but very low in the free-choice procedure. Comparable genotypic correlations were obtained (Table 6). Implications about pleiotropism or linkage of genes conditioning resistance are conflicting because of the moderate

to high genotypic correlations in the forced infestation procedures and the low genotypic correlation in the free-choice procedure.

In summary, we conclude that: 1) evaluation based on kernel damage and not including cob tunneling and number of surviving larvae is justified, and 2) EL is appropriate for evaluating germplasm for both kernel damage and stalk tunneling resistance. The advantages of EL over previously reported methods is that it permits infestation at a uniform relative maturity and permits uniform development of borers from time of infestation to time of evaluation.

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