

See discussions, stats, and author profiles for this publication at: <https://www.researchgate.net/publication/233570222>

Temperature-Dependent Feeding Rates of *Melanoplus sanguinipes* Nymphs (Orthoptera: Acrididae) Laboratory Trials

Article in *Environmental Entomology* · October 1995

DOI: 10.1093/ee/24.5.1291

CITATIONS

42

READS

123

2 authors, including:



Daniel L Johnson

University of Lethbridge

106 PUBLICATIONS 2,696 CITATIONS

SEE PROFILE

Some of the authors of this publication are also working on these related projects:



Analysis of long-term of grasshoppers in Alberta, Canada, 1916-2016 [View project](#)



Potato Psyllid monitoring in Canada, with regard to Lso pathogen, the cause of Zebra Chip [View project](#)

Temperature-Dependent Feeding Rates of *Melanoplus sanguinipes* Nymphs (Orthoptera: Acrididae) in Laboratory Trials

DEREK J. LACTIN AND DAN L. JOHNSON¹

Land Resource Sciences Section, Agriculture and Agri-food Canada Research Centre, Box 3000, Lethbridge, AB, T1J 4B1 Canada

Environ. Entomol. 24(5): 1291-1296 (1995)

ABSTRACT Feeding rates of laboratory-reared *Melanoplus sanguinipes* (F.) nymphs were measured in 3-h trials at 15, 20, 26, 30, 35, 40, or 45°C. Feeding rates increased with temperature to a maximum, then decreased at higher temperatures. Maximum feeding rate occurred at 35°C in 1st and 2nd instars, and at 40°C in 3rd, 4th, and 5th instars. In a subsequent 24-h trial, mean hourly feeding rates at 30, 35, or 40°C agreed with those of the 3-h trials. A linear model was used to describe feeding rates at temperatures at or below that at which rate was maximum, and a nonlinear model was used to describe the feeding rate trends over the full range of experimental temperatures. Using the linear model, estimated low-temperature feeding thresholds ranged from 13.5°C for 2nd instars to 15.9°C for 1st instars. Using the nonlinear model, estimated low-temperature feeding thresholds were near 13°C for all but 3rd instars, for which it was near 8°C; modeled temperatures at which feeding was maximal agreed with measured values, and the modeled upper temperature threshold for feeding was between 45 and 46°C for all instars. The linear and nonlinear models are similar at temperatures below that at which feeding is maximal, but the linear model overestimates feeding at higher temperatures. Application of the feeding rate functions to field conditions requires improved understanding on the determinants of body temperature under field conditions, and on the relationship between feeding and wastage.

KEY WORDS *Melanoplus sanguinipes*, grasshopper, temperature dependence, feeding

GRASSHOPPERS (ORTHOPTERA: ACRIDIDAE) can be serious pests of rangelands and adjoining grain fields. For example, in Alberta during the outbreak in 1985 and 1986, >700,000 ha of agricultural land were treated with insecticides for grasshopper control in each year; the total cost was CAN \$11.8 million (Dolinski and Johnson 1992). In the same period, farm cash receipts for wheat in Alberta totaled CAN \$945 million (Statistics Canada 1991). Given the high value of the crop and the high treatment costs, substantial economic benefits could result from improvements in abilities to make crop protection decisions and to schedule management actions.

Pest control tactics are economically justifiable if the value of the benefit (that is, yield loss averted) exceeds the cost of the pesticide and its application (Stern et al. 1959). One approach to assessing the benefits of various tactics is to couple

models of pest phenology and crop production to simulate yield under various control scenarios. This coupling entails several steps (Bardner and Fletcher 1974), including conversion of insect numbers to feeding rate estimates. Grasshopper models exist that are compatible with this approach (for example, Hewitt and Onsager 1982, Hardman and Mukerji 1982, Hardman et al. 1985, Davis et al. 1992), but their utility is limited because information required to convert pest population data into yield loss estimates are incomplete. Available feeding rates for grasshoppers are either single-temperature values or averages over varying temperatures (Barnes 1955, Smith 1959, Misra and Putnam 1966, Mitchell and Pfadt 1974, Hewitt et al. 1976, Hewitt 1978, Holmberg and Hardman 1984, Johnson and Pavlikova 1986). These results are of limited value because insect feeding rates are temperature dependent (for example, Hammond et al. 1979, Ferro et al. 1985, Logan et al. 1985, Trichilo and Mack 1989, Lactin et al. 1993). Quantification of the temperature dependence of feeding rates by grasshoppers would improve these grasshopper damage models and could thus help rangeland managers and cereal producers to make better-informed grasshopper control decisions.

¹ To whom reprint requests should be addressed

² Unpublished data can be found in "Unpublished appendix for: Holmberg, R. G. and J. M. Hardman. 1984. Relating feeding rates to sex and size in 6 species of grasshoppers (Orthoptera: Acrididae). Canadian Entomologist 116: 597-606." Depository of Unpublished Data, CISTI, National Research Council of Canada, Montreal Road Campus, Ottawa, ON, K1A 0R6, Canada. E-mail CISTI.INFO@NRC.CA

The purpose of this study was to characterize the temperature dependence of feeding rates of nymphal *Melanoplus sanguinipes* (F.) on spring wheat. *M. sanguinipes* is an oligophagous species distributed throughout the grassy regions of much of North America (Vickery and Kevan 1983).

Materials and Methods

All measurements were made in growth chambers at constant temperatures (Conviron, Controlled Environments, Pembina, ND 58271). Photophase was produced using four 20-W cool fluorescent lights. Relative humidity in the chambers was 30–60%.

Grasshopper nymphs were reared from eggs obtained in the laboratory from adult grasshoppers collected from field margins the previous August. Nymphs were reared in white-painted wood and glass rearing cages (40 by 40 by 30 cm), equipped with 40-W light bulbs, in rooms with full-spectrum (Vitalite) fluorescent bulbs at a diel cycle of 16:8 (L:D) h and an air temperature of $\approx 25^{\circ}\text{C}$. Insect body temperature was probably near air temperature during scotophase, but because grasshopper actively thermoregulate, body temperature was probably greater than air temperature during photophase.

For rearing and experimentation, insects were fed foliage from young wheat plants, *Triticum aestivum* 'Norstar', grown in vermiculite in a greenhouse. Plants were in the pretiltering stage, and were ≈ 15 cm tall when used. While in the rearing cages, insects were provisioned with live wheat growing in sod in plastic containers (20 by 30 by 5 cm). The sod with wheat was replaced as necessary.

For each trial, nymphs were collected from the rearing cages, sorted by instar and held at 26°C in 22 ml shell vials with a small amount of wheat foliage for 20–30 min. Insects were transferred to their nominal feeding temperatures (15, 20, 26, 30, 35, 40, or 45°C , measured in the chamber) by moving them through the intermediate temperatures, holding them in each for 20–30 min. This graduated transfer was adopted to minimize shock responses to sudden temperature change.

For the feeding measurements, the insects were transferred to clear plastic food cups with dome lids (parts No. TS9 and DL620, Solo Cup, Urbana, IL), which enclosed a volume of 330 ml. The number of insects per cup was adjusted according to instar: 5 were used for 1st and 2nd instars, 3 for 3rd instars, 1–3 for 4th instars, and 1 or 2 for 5th instars. The number of replicates of the instars varied, depending on availability. At each temperature in each trial, 4–6 (mode: 5) control cups containing only wheat leaves were included.

Short-Duration Trials. In short-duration trials, the insects were confined to cups for ≈ 3 h. Thirteen trials were conducted; in 6, insects were placed in 15, 20, 26, 30, and 35°C or 26, 30, 35,

40, and 45°C ; in 7, insects were placed at 4 of these temperatures, either $15\text{--}30^{\circ}\text{C}$ or $26\text{--}40^{\circ}$ excluding 30°C . To approximately balance overall numbers of insects tested at each temperature, fewer insects per trial were assigned to temperatures $20\text{--}30^{\circ}$, which appeared in more trials than did other temperatures.

During the 20 min in which the insects in vials were adapting to the nominal rearing temperature, a known weight of wheat foliage was placed in each food cup. A cluster sample of wheat leaves was cut at the 1st node, then sufficient subsamples were drawn to provision all cups. Subsamples of ≈ 200 mg were weighed to 1 mg and assigned randomly to cups.

Insects were transferred from the vials to the cups, left for ≈ 3 h at the nominal temperature, then removed from the cups. At each temperature, the times at which each trial started and finished were each measured to the nearest 5 min. The remaining foliage was dried at 60°C for ≥ 18 h, then weighed to 1 mg.

Feeding rate was measured from the difference in dry leaf mass over the interval. Initial dry mass of the leaf samples fed to the insects was estimated by multiplying the initial fresh mass by the mean dry:wet mass ratio of the matched controls. Total dry mass removed was estimated by subtracting the measured final dry mass of the leaf samples from the estimated initial dry mass. To obtain (milligrams of dry mass) per hour per insect, this amount was divided by confinement interval multiplied by the number of insects surviving. Nymphs which died were assumed not to have eaten during the trial.

The temperature dependent trend in feeding rate in the short-duration trials was described in 2 ways. A linear regression (PROC REG, SAS Institute 1989) was fitted to means weighted by sample size (n -weighted) over the range of temperatures in which the feeding rate response appeared approximately linear ($\leq 35^{\circ}\text{C}$ for 1st and 2nd instars; $\leq 40^{\circ}\text{C}$ for 3rd to 5th instars).

A nonlinear function (equation 1) (Lactin et al. 1995), was used to describe feeding rates over the full range of experimental temperatures:

$$r(T) = e^{\rho T} - e^{\left[\rho T_{\max} \frac{(T_{\max} - T)}{\Delta} \right]} + \lambda, \quad (1)$$

where $r(T)$ is the mean feeding rate at temperature T ; ρ describes the acceleration of the function from the low-temperature threshold to the optimal temperature; λ is the asymptote to which the function tends at low temperatures; T_{\max} is the supraoptimal temperature at which $r(T) = \lambda$; and Δ is approximately the range of temperatures between the value at which the function starts to descend, and T_{\max} . Although the fitted function can be < 0 , the feeding estimate was constrained to be ≥ 0 . Equation 1 is a modification of a widely used model of temperature dependent rate phenomena in arthropods (Logan et al. 1976).

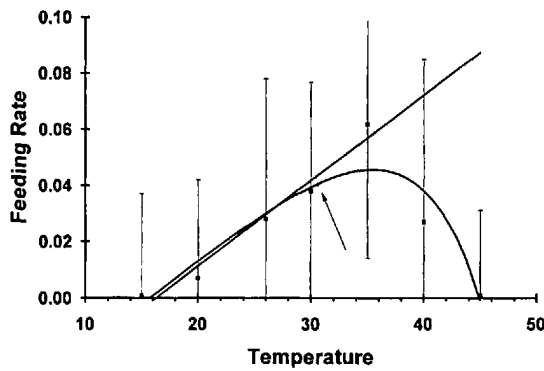


Fig. 1. Feeding rates of 1st-instar *M. sanguinipes* (milligrams of dry mass per hour per insect) plotted against temperature (°C). Squares, mean rate in 3-h trials; diamond, accented by arrow, mean hourly rate from Holmberg and Hardman (unpublished data). Bars are ± 1 SEM. Straight line is linear fit to rates at temperatures $\leq 35^\circ\text{C}$; solid curve is output of equation 1 fit to all data.

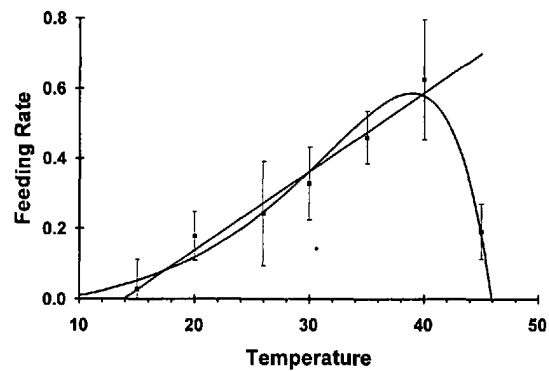


Fig. 3. Feeding rates of 3rd-instar *M. sanguinipes* (milligrams of dry mass per hour per insect) plotted against temperature (°C). Squares, mean rate in 3-h trials; diamond, mean hourly rate from Holmberg and Hardman (unpublished data). Bars are ± 1 SEM. Straight line is linear fit to rates at temperatures $\leq 40^\circ\text{C}$; solid curve is output of equation 1 fit to all data.

Equation 1 was fitted separately for each instar, using iterative nonlinear regression (PROC NLIN, SAS Institute 1989) applying the Marquardt algorithm to n -weighted means by temperature. Lactin et al. (1995) provide the partial derivatives which this algorithm requires. Fitted curves were considered acceptable if a subsequent linear regression of predicted values on observed means had an intercept not significantly different from 0 and a slope significantly >0 but not significantly different from 1.

Long-Duration Trial. To assess whether the results of the short-term trial are applicable to long-term exposures, nymphs of 2nd, 4th, and 5th stadia were held for 24 h at 30, 35, and 40°C. The experimental protocol was the same as that of the short-duration trials except that cups contained three 2nd instars, or a single 4th or 5th instar, and

$\approx 1,500$ mg of wheat leaves. Initial sample sizes were 5, 7, and 10 cups for 2nd, 4th, and 5th instars, respectively, at each temperature.

Results

Short-Duration Trials. Feeding rates were successfully measured in all instars at all temperatures (Figs. 1–5). In several cases where the feeding rate was small, the standard error of the feeding rate estimate includes 0. Sample sizes are given in Table 1. The response of feeding rate to temperature was nonlinear over the full range of temperatures, although for all instars, there was a range of temperatures in which the rate function was approximately linear. Table 2 lists parameter estimates from the linear regressions of feeding rate in the

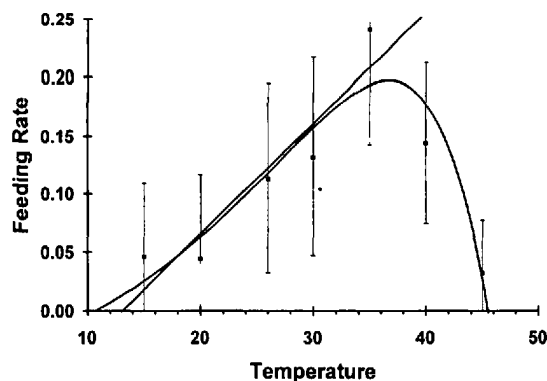


Fig. 2. Feeding rates of 2nd-instar *M. sanguinipes* (milligrams of dry mass per hour per insect) plotted against temperature (°C). Squares, mean rate in 3-h trials; diamond, mean hourly rate from Holmberg and Hardman (unpublished data). Bars are ± 1 SEM. Straight line is linear fit to rates at temperatures $\leq 35^\circ\text{C}$; solid curve is output of equation 1 fit to all data.

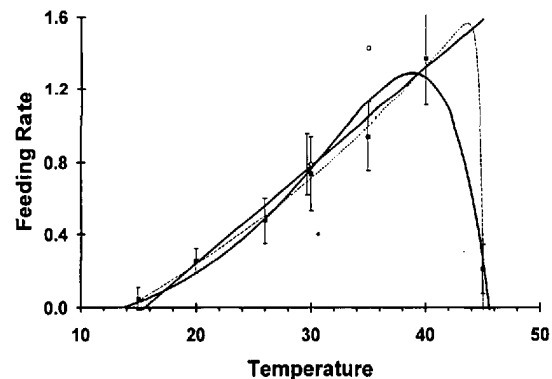


Fig. 4. Feeding rates of 4th-instar *M. sanguinipes* (milligrams of dry mass per hour per insect) plotted against temperature (°C). Squares, mean rate in 3-h trials; circles, mean rate in 24-h trials; diamond, mean hourly rate from Holmberg and Hardman (unpublished data). Bars are ± 1 SEM; those for 24-h trial are offset to the left. Straight line is linear fit to rates at temperatures $\leq 40^\circ\text{C}$; solid curve is output of equation 1 fit to all data.

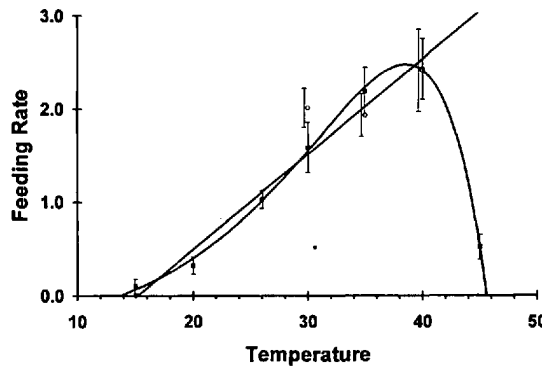


Fig. 5. Feeding rates of 5th-instar *M. sanguinipes* (milligram of dry mass) per hour per insect plotted against temperature (°C). Squares, mean rate in 3-h trials; circles, mean rate in 24-h trials; diamond, mean rate from Holmberg and Hardman (unpublished data). Bars are ± 1 SEM; those for 24-h trial are offset to the left. Straight line is linear fit to rates at temperatures $\leq 40^\circ\text{C}$; solid curve is output of equation 1 fit to all data.

temperature ranges in which the response was approximately linear. The linear regression lines are included in Figs. 1–5.

Equation 1 was fitted successfully to feeding rate data for all instars. The best-fit curve for 4th instars (Fig. 4, broken line) differed from those for the other instars: it was less sigmoid at suboptimal temperatures, had a higher estimated optimum temperature and a much narrower range of supraoptimal temperatures in which the feeding rate diminished. The solid curve in Fig. 4 was fitted by restricting ρ to between 0.10 and 0.14, a range chosen based on the values of this parameter in 3rd and 5th instars; this approach adopts the interpretation of ρ as a “composite Q10 value for critical enzyme-catalyzed, biochemical reactions” (Logan et al. 1976) and further assumes that this value should be similar among instars. In all cases, including both lines for 4th instars, the fitted curves were acceptable. Parameter estimates of the nonlinear models are given in Table 3. Because the curve is extremely sensitive to rounding error, 6 decimal places are given.

The mean dry: fresh ratio of the control leaves in the 3-h trials was 0.124 (SEM = 0.0002, $n = 249$),

Table 1. Sample sizes used to estimate feeding rates of *M. sanguinipes* nymphs

Temp, °C	Sample size by instar ^a				
	1st	2nd	3rd	4th	5th
15	19, 94	9, 45	7, 21	17, 40	21, 23
20	13, 65	9, 44	8, 23	13, 31	19, 20
26	16, 78	15, 72	11, 32	17, 41	25, 30
30	13, 60	12, 58	9, 26	14, 34	21, 23
25	9, 41	12, 55	9, 27	11, 27	13, 17
40	8, 40	10, 43	10, 30	10, 26	16, 20
45	8, 39	10, 46	10, 30	12, 32	17, 22

^a Number of food cups, number of insects.

Table 2. Parameter estimates ± 1 SE from linear regressions of *M. sanguinipes* feeding rate on temperature

Instar	Intercept	Slope	F	r ²
1	-0.046 \pm 0.01	0.003 \pm 0.000	78.6**	0.96
2	-0.13 \pm 0.06	0.010 \pm 0.002	20.8*	0.87
3	-0.32 \pm 0.05	0.023 \pm 0.002	150.4**	0.97
4	-0.80 \pm 0.13	0.052 \pm 0.004	129.7**	0.97
5	-1.54 \pm 0.20	0.101 \pm 0.007	194.2**	0.98

For 1st and 2nd instars, temperatures $>35^\circ$ were deleted; for 3rd to 5th instars, temperatures $>40^\circ$ were deleted (see text). Degrees of freedom are 1, 3 for 1st and 2nd instars and 1, 4 for other instars. *, $P < 0.05$; **, $P < 0.01$.

and did not differ significantly among trials or among temperatures within trials (analysis of variance, $P > 0.05$). Therefore, a fresh mass consumption estimate can be obtained from the dry mass consumption estimate (equation 1) by dividing by 0.124.

Long-Duration Trial. In the 24-h feeding trials, moulting by insects during the measurement period reduced sample sizes. In all cups containing

Table 3. Parameter estimates ± 1 SE, for the nonlinear model (equation 1) of temperature-dependent feeding rates of *M. sanguinipes* nymphs

Parameter	Estimate	r ²
1st instar		
ρ	0.003071 \pm 0.001485	0.85
T_{\max}	59.938198 \pm 9.971111	
Δ	6.019770 \pm 4.787918	
λ	-1.048824 \pm 0.026407	
2nd instar		
ρ	0.100652 \pm 0.048802	0.83
T_{\max}	46.568421 \pm 2.973679	
Δ	9.869060 \pm 4.619492	
λ	-0.070286 \pm 0.161050	
3rd instar		
ρ	0.138661 \pm 0.028747	0.99
T_{\max}	46.121811 \pm 0.810252	
Δ	7.191102 \pm 1.462689	
λ	-0.047941 \pm 0.121183	
4th instar (solid line)		
ρ	0.140000 \pm 0.023093	0.97
T_{\max}	45.918344 \pm 0.593276	
Δ	7.096624 \pm 1.121367	
λ	-0.196457 \pm 0.201722	
4th instar (broken line)		
ρ	0.025272 \pm 0.000567	0.99
T_{\max}	45.247485 \pm 0.010045	
Δ	0.331435 \pm 0.000000	
λ	-1.421121 \pm 0.036023	
5th instar		
ρ	0.132072 \pm 0.006000	0.99
T_{\max}	46.063044 \pm 0.175208	
Δ	7.434967 \pm 0.299394	
λ	-0.463347 \pm 0.118183	

Table 4. Feeding rates of *M. sanguinipes* nymphs on Norstar wheat in 24-h trials

Temp. °C	Number of insects ^a	Feeding rates ^b
	4th instar	
30	7, 6	0.79 ± 0.17
35	7, 1	1.43 ± —
40	7, 0	— ± —
	5th instar	
30	10, 10	2.01 ± 0.21
35	10, 10	1.93 ± 0.23
40	10, 10	2.41 ± 0.44

^a Initial, final.^b Milligrams dry mass per hour per insect. —, non-estimable.

2nd instars, 1 or more of the insects moulted at all temperatures. Among 4th instars, 1 moulted at 30°C, 6 at 35°C and 7 at 40°C. None of the 5th instars moulted. Data for cups in which 1 or more of the insects moulted during the trial were discarded. Sample sizes and mean feeding rates for these trials, where estimable, are given in Table 4. Mean feeding rates and standard errors are included in Figs. 4 and 5.

Discussion

In the 3-h trials, the feeding rate response to temperature was clearly nonlinear and asymmetrical for all instars. Feeding rates increased with temperature to a maximum, then decreased at higher temperatures.

A linear model approximated the feeding function adequately if mean rates at temperatures above that at which feeding was maximal were disregarded. Estimates of the low-temperature threshold for feeding, obtained algebraically from the linear regression parameters, were 15.9, 13.5, 14.1, 15.3, and 15.2°C for 1st to 5th instars, respectively. At temperatures above that at which feeding was maximal, the linear approximation overestimated feeding rates.

A nonlinear model (equation 1) described feeding rates over the full range of experimental temperatures. Estimates of upper and lower threshold temperatures for feeding were obtained graphically. The low-temperature threshold estimates from the nonlinear model were 15.8, 10.7, 8.4, 13.7, and 13.7°C for 1st to 5th instars, respectively. The threshold given for 4th instars is for the model with the estimate of ρ restricted; for the unrestricted case, the threshold was 13.9°C. There is no apparent trend over instars in the low-temperature threshold for feeding, but the uncertainty of these estimates is large because at low temperatures the variance of the feeding rate estimates as proportion of the mean was greater than at high temperatures. The optimum temperature for feeding was lower for 1st and 2nd instars (measured optima 35°C, modeled optima 35.4 and 36.6°C, respectively) than for the 3rd to 5th instars (measured optima

40°C, modeled optima 39.0°C for 3rd instar and 38.6°C for 5th instar; for 4th instars the modeled optima were 38.8°C [ρ estimate restricted; solid curve] and 43.6°C [ρ estimate not restricted; dotted curve]). Estimates of the upper threshold for feeding were between 44.9 and 45.9°C for all instars. In nature, acridids elevate body temperature behaviorally when insolation is sufficient (Stower and Griffiths 1966) and the maximum amount by which body temperature can exceed air temperature increases with body mass (Digby 1955). The trend in feeding rate optima might be an evolutionary response to this apparent constraint on the ability to increase body temperature.

Holmberg and Hardman (1984) measured feeding rates of *M. sanguinipes* at 30.6°C. Converted from 24-h totals, their mean feeding rate measurements were 0.04, 0.10, 0.14, 0.40, and 0.51 mg/h for 1st to 5th instars, respectively (R. G. Holmberg and J. M. Hardman, unpublished data²). These values are included in Figs. 1–5. At 30°C in the current study, the measured mean rates were 0.04, 0.13, 0.33, 0.74, and 1.58 mg/h for 1st to 5th instars, respectively. These results agree for the 1st instar, but for later instars, our measurements exceed those of Holmberg and Hardman (unpublished data) by increasing amounts. These differences in feeding rate estimates do not result from differences in feeding rate in long- and short-duration trials, because the results of our 24-h trials are consistent with those of our 3-h trials. The differences probably result from differences in experimental methods. Holmberg and Hardman (1984) confined their insects in vertical cylindrical paper containers with opaque sides and a screen ceiling; container volumes were 90 ml for insects <1 cm long (that is, 1st to 3rd instars) and 1 liter for larger insects (that is, 3rd to 5th instars). Grasshoppers are strongly positively phototactic, and probably spent a large portion of their time at the illuminated top of the cage, that is, away from the food; this response would have reduced their time spent feeding, and hence their average feeding rate. Furthermore, when the grasshoppers chose to leave the well-lighted end to feed, they were obliged to locate the food first, and we suspect that the time required to do so averaged greater for larger insects than for small ones, because larger insects tended to be confined in larger arenas than were small insects.

Application of our feeding rate functions to field conditions will require at least 2 considerations. The 1st is that feeding rates are a function of body temperature, which in insects, including acridids, can be very different from air temperature (Stower and Griffiths 1966, May 1979); therefore, information is required on *M. sanguinipes* body temperatures in the field. This information may also determine whether the linear or nonlinear model should be used in feeding rate estimation: if behavioral thermoregulation results in body temperatures being frequently near the optimum for

feeding, the nonlinear model is recommended. The 2nd consideration is that feeding damage may be amplified by wastage, in which the leaf apical to the feeding site is clipped off. This effect is particularly important in monocots. The relationship between wastage and feeding is not well understood, and should be quantified before these feeding rate functions can be used under field conditions.

Acknowledgments

We thank Z. D. Becker, N. Michaud, R. C. Andrews, D. Drader, R. Feniuk, T. Danyk, G. D. Inglis, and E. Pavlik for assistance. T. J. Lysyk, D. S. Yu, and H. McMenamin reviewed earlier drafts of the manuscript. This project was funded in part by grants from the Alberta Agricultural Research Institute and the Nat Christie Foundation, through the University of Lethbridge. This is contribution 3879484 of the Lethbridge Research Centre.

References Cited

- Bardner, R. S., and R. E. Fletcher.** 1974. Insect infestations and their effect on yield: a review. *Bull. Entomol. Res.* 64: 141-160.
- Barnes, O. L.** 1955. Effect of food plants on the lesser migratory grasshopper. *J. Econ. Entomol.* 48: 119-124.
- Davis, R. M., M. D. Skold, J. S. Berry, and W. P. Kemp.** 1992. The economic threshold for grasshopper control on public rangelands. *J. Agric. Res. Econ.* 17: 56-65.
- Digby, P. S. B.** 1955. Factors affecting the temperature excess of insects in sunshine. *J. Exp. Biol.* 32: 279-298.
- Dolinski, M. G., and D. L. Johnson.** 1992. Feasibility of long-term grasshopper management. Farming for the Future, Final report Project #88-0323. Alberta Agriculture, Edmonton.
- Ferro, D. N., J. A. Logan, R. H. Voss, and J. S. Elkinton.** 1985. Colorado potato beetle (Coleoptera: Chrysomelidae) temperature-dependent growth and feeding rates. *Environ. Entomol.* 14: 343-348.
- Hammond, R. B., L. P. Pedigo, and F. L. Poston.** 1979. Green cloverworm leaf consumption on greenhouse and field soybean leaves and development of a leaf consumption model. *J. Econ. Entomol.* 72: 714-717.
- Hardman, J. M., and M. K. Mukerji.** 1982. A model simulating the population dynamics of the grasshoppers (Acrididae) *Melanoplus sanguinipes* (Fabr.), *M. packardii* Scudder and *Camnula pellucida* Scudder. *Res. Popul. Ecol.* 24: 276-301.
- Hardman, J. M., W. A. Charnetski, and M. K. Mukerji.** 1985. A model simulating grasshopper damage to wheat planted in infested stubble. *J. Appl. Ecol.* 22: 373-394.
- Hewitt, G. B.** 1978. Reduction of western wheatgrass by the feeding of two rangeland grasshoppers, *Aulocara elliotti* and *Melanoplus infantilis*. *J. Range Manage.* 31: 419-421.
- Hewitt, G. B., and J. A. Onsager.** 1982. A method of forecasting potential losses from grasshopper feeding on northern mixed prairie forages. *J. Range Manage.* 31: 53-57.
- Hewitt, G. B., W. H. Bursleson, and J. A. Onsager.** 1976. Forage losses caused by the grasshopper *Aulocara elliotti* on shortgrass rangeland. *J. Range Manage.* 29: 376-380.
- Holmberg, R. G., and J. M. Hardman.** 1984. Relating feeding rates to sex and size in six species of grasshoppers (Orthoptera: Acrididae). *Can. Entomol.* 116: 597-606.
- Johnson, D. L., and E. Pavlikova.** 1986. Reduction of consumption by grasshoppers (Orthoptera: Acrididae) infested with *Nosema locustae* Canning (Microsporida: Nosematidae). *J. Invertebr. Pathol.* 48: 232-238.
- Lactin, D. J., N. J. Holliday, and L. L. Lamari.** 1993. Temperature dependence and constant-temperature diel aperiodicity of feeding by Colorado potato beetle larvae (Coleoptera: Chrysomelidae) in short-duration laboratory trials. *Environ. Entomol.* 22: 784-790.
- Lactin, D. J., N. J. Holliday, D. L. Johnson, and R. Craigen.** 1995. Improved rate model of temperature dependent development by arthropods. *Environ. Entomol.* 24: 68-75.
- Logan, J. A., D. J. Wollkind, S. C. Hoyt, and L. K. Tanigoshi.** 1976. An analytic model for description of temperature-dependent rate phenomena in arthropods. *Environ. Entomol.* 5: 1133-1140.
- Logan, P. A., R. A. Casagrande, H. H. Faubert, and F. A. Drummond.** 1985. Temperature-dependent development and feeding of immature Colorado potato beetles, *Leptinotarsa decemlineata* (Say) (Coleoptera: Chrysomelidae). *Environ. Entomol.* 14: 275-283.
- May, M. L.** 1979. Insect thermoregulation. *Ann. Rev. Entomol.* 24: 313-349.
- Misra, S. D., and L. G. Putnam.** 1966. The damage potential of the grasshopper, *Camnula pellucida* (Scudd.) (Orthoptera: Acrididae) on pastures and ranges in Canada. *Indian J. Entomol.* 28: 224-233.
- Mitchell, J. E., and R. E. Pfadt.** 1974. A role of grasshoppers in a shortgrass prairie ecosystem. *Environ. Entomol.* 3: 358-360.
- SAS Institute.** 1989. SAS/STAT user's guide, 4th ed., vol. 2. SAS Institute, Cary NC.
- Smith, D. S.** 1959. Utilization of food plants by the migratory grasshopper, *Melanoplus bilituratus* with some observations on the nutritional value of the plants. *Ann. Entomol. Soc. Am.* 52: 674-680.
- Statistics Canada.** 1991. Agriculture economics statistics, catalogue 21-603. Statistics Canada, Ottawa, ON.
- Stern, V. M., R. F. Smith, R. van den Bosch, and K. S. Hagen.** 1959. The integrated control concept. *Hilgardia* 29: 81-101.
- Stower, W. J., and J. F. Griffiths.** 1966. The body temperature of the desert locust (*Schistocerca gregaria*). *Ent. Exp. Appl.* 9: 127-178.
- Trichilo, P. J., and T. P. Mack.** 1989. Soybean leaf consumption by the soybean looper (Lepidoptera: Noctuidae) as a function of temperature, instar, and larval weight. *J. Econ. Entomol.* 82: 633-638.
- Vickery, V. R., and D. K. McE. Kevan.** 1983. A monograph of the orthopteroid insects of Canada and adjacent regions, vol. 11. Lyman Entomological Museum and Research Laboratory Memoir no. 13, McGill University, Ste. Anne de Bellevue, PQ.

Received for publication 30 November 1994; accepted 10 May 1995.