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David B. Taylor
USDA-ARS & University of Nebraska-Lincoln, dave.taylor@ars.usda.gov

Roger D. Moon
University of Minnesota, St. Paul, rdmoon@umn.edu

Darrell R. Mark
University of Nebraska-Lincoln

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Economic Impact of Stable Flies (Diptera: Muscidae) on Dairy and Beef Cattle Production

DAVID B. TAYLOR,[1] ROGER D. MOON,[2] AND DARRELL R. MARK[3]

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ABSTRACT Stable flies, *Stomoxys calcitrans* (L.), are among the most damaging arthropod pests of cattle worldwide. The last estimate of their economic impact on United States cattle production was published 20 yr ago and placed losses at $608 million. Subsequently, several studies of effects of stable flies on beef cattle weight gain and feed efficiency have been published, and stable flies have become increasingly recognized as pests of cattle on pasture and range. We analyzed published studies and developed yield-loss functions to relate stable fly infestation levels to cattle productivity, and then estimated the economic impact of stable flies on cattle production in the United States. Four industry sectors were considered: dairy, cow-calf, pastured stockers, and feeder cattle. In studies reporting stable fly infestation levels of individual herds, median annual per animal production losses were estimated to be 139 kg of milk for dairy cows, and 6, 26, and 9 kg body weight for preweanling calves, pastured stockers, and feeder cattle, respectively. The 200,000 stable flies emerging from an average sized winter hay feeding site reduce annual milk production of 50 dairy cows by an estimated 890 kg and weight gain of 50 preweanling calves, stockers, or feeder cattle by 58, 680, or 84 kg. In 2009 dollars, the value of these losses would be $254, $132, $1,279, or $154, respectively. Using cattle inventories and average prices for 2005–2009, and median monthly infestation levels, national losses are estimated to be $360 million for dairy cattle, $358 million for cow-calf herds, $1,268 million for pastured cattle, and $226 million for cattle on feed, for a total impact to U.S. cattle industries of $2,211 million per year. Excluded from these estimates are effects of stable flies on feed conversion efficiency, animal breeding success, and effects of infested cattle on pasture and water quality. Additional research on the effects of stable flies on high-production dairy cows and nursing beef calves is needed to increase the reliability of the estimates.

KEY WORDS *Stomoxys*, production loss, dairy, beef, grazing cattle

Stable flies, *Stomoxys calcitrans* (L.), are serious pests of humans and animals worldwide. Biting stable flies reduce the productivity of livestock, cause pain and suffering in companion animals, and disrupt human recreation. Stable flies are also competent vectors of microbial and metazooan pathogens (Berberian 1938, Dikmans 1950, Riordan 1972, Morgan and Miller 1976, Golovanov et al. 1977, Mellor et al. 1987). Although none are currently problematic in North America (Moon 2009), several pathogens are expanding their ranges and may emerge as important North American disease agents in the future. Currently, the primary effect of stable flies on cattle is reduced production.

Stable flies affect cattle in a variety of ways. They reduce grazing time and stimulate defensive behaviors such as foot stomping, head throwing, skin twitching, and tail switching (Dougherty et al. 1993, 1994; Mullens et al. 2006). Time spent bedded down decreases with increasing stable fly populations (Vitela et al. 2006, 2007) and cattle frequently "bunch" in response to attack (Bishopp 1913, Campbell and Hermanussen 1971, Berry et al. 1983, Wieman et al. 1992). Bunching increases heat stress and risk of injury while animals jockey for position (Wellman 1973, Campbell et al. 1993).

Several estimates of the economic impact of stable flies on cattle have been published (Table 1). Loss estimates (in 2009 dollars) for cattle industries in the United States increased from $152 million (Hyslop 1938) to $930 million (Byford et al. 1992), due in part to changes in cattle inventories, values of dairy and beef products, and scientific understanding of effects of stable flies on cattle. Six studies of effects on confined beef cattle (Catangui 1992; Wieman et al. 1992, Campbell et al. 1993; Catangui et al. 1993, 1995, 1997), and one study of effects on stocker cattle (Campbell et al. 2001) have been published since 1992, and results

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[1] Corresponding author: USDA, Agricultural Research Service, Agroecosystem Management Research Unit, and Department of Entomology, University of Nebraska, Lincoln, NE 68583 (e-mail: dave.taylor@ars.usda.gov).

[2] Department of Entomology, University of Minnesota, St. Paul, MN 55108.

[3] Department of Agricultural Economics, University of Nebraska, Lincoln, NE 68583.

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Table 1. Estimates of economic impact of stable flies on cattle industries in the U.S.

Source of estimate	Dollars, millions	
	Original	2009[a]
Hyslop, 1938	10	152
USDA, 1954	20	160
USDA, 1965	142	967
Drummond et al., 1981	398	939
Drummond, 1987	428	808
Kunz et al., 1991	432	680
Byford et al., 1992	608	930
Present study[b]	—	2,211

[a] Adjusted for inflation, using U.S. Department of Labor, Bureau of Labor Statistics, Inflation Calculator (http://www.bls.gov/data/inflation_calculator.htm).

[b] Based upon the absolute loss model.

of those studies remain to be incorporated into loss estimates. Furthermore, before the 1980s, stable flies were considered to be primarily pests of confined dairy and beef cattle, but subsequent observations indicate stable flies are also important pests of pastured cattle (Hall et al. 1982, Campbell et al. 2001).

Increased populations of stable flies associated with pastured cattle have been attributed to the recently adopted practice of using stationary large round hay bale feeders to provide hay for pastured cattle during winter (Broce et al. 2005). In spring, accumulations of hay and animal wastes around these feeders are excellent substrates for the development of stable fly larvae (Talley et al. 2009, Taylor and Berkebile 2011).

Given recent publications on the effects of stable flies on stocker and feeder cattle, and the association of stable flies with hay feeding sites for pastured cattle, we developed a model to estimate economic impact of stable flies on cattle. The model is based on yield-loss functions relating stable fly infestation levels to cattle productivity. The model is explicit and dynamic, and can be modified as additional research data become available and commodity values and herd inventories change in the future. We illustrate the model's predictions by using it to estimate (1) annual losses for animals in individual locations where stable fly populations have been described, (2) losses caused by stable flies emanating from characterized winter hay feeding sites, and (3) national losses to dairy and beef producers in the United States, based on commodity values and inventories of dairy, cow-calf, stocker, and feeder cattle.

Materials and Methods

Definitions, descriptions, and units for variables and constants used to estimate effects of stable flies on dairy and beef cattle industries are summarized in Table 2.

Yield-Loss Functions. A key component of estimating the economic value of injury due to any pest is a yield-loss function, $y = f(x)$, the relationship between abundance of the pest (x) and associated loss in quantity and quality of saleable product (y). For dairy cows, we assume the primary loss is reduced average daily milk production, ΔADM, and primary losses to growing beef calves, yearling stockers, and feeder cattle are reduced average daily gain, ΔADG.

Table 2. Variables and constants used to estimate production losses caused by stable flies in dairy and beef industries

Abbreviation	Meaning	Units
A	Area of winter hay feeding debris site	m^2
ADG	Average daily gain, per growing animal	Kg hd^{-1} d^{-1}
ΔADG	Absolute difference in ADG, treated and untreated herds	Kg hd^{-1} d^{-1}
%ADG	Relative difference in ADG	% fly-free ADG
ADM	Average daily milk production, per cow	Kg hd^{-1} d^{-1}
ΔADM	Absolute difference in ADM, treated and untreated herds	Kg hd^{-1} d^{-1}
%ADM	Relative difference in ADM	% fly-free ADM
$\overline{D}$	Mean density of stable flies emerging from larval substrate	No. per m^2 d^{-1}
e_0	Expectation of life of an adult stable fly at emergence	Days (d)
LC	No. stable flies per animal front leg (=WBC ÷ 2.81)	Number
L_S	Economic loss in sector s (dairy, cow-calf, stocker, feeder)	US dollars ($)
m	Daily mortality rate	Proportion per d
ME	Metabolic energy	Megajoules (MJ)
ME_F	Energy to produce 1 kg flesh	Megajoules
ME_M	Energy to produce 1 kg milk	Megajoules
N_S	Number of animals in sector s	Number
V_S	Value of product, milk or live wt, in sector s	US dollars ($) kg^{-1}
WBC	No. flies per whole animal body (=LC × 2.81)	Number

Historically, stable fly abundance was indexed by mean whole body counts (WBCs), i.e., the average number of stable flies on the entire bodies of chosen animals. More recently, abundance has been indexed by mean leg count (LC), the average number of flies on the visible halves of both front legs, from brisket to hoof, when viewed from a single angle (Berry et al. 1983). Because most recent studies of cattle responses to stable flies report LCs, this metric was used throughout the present analysis.

Yield-loss functions were estimated from published, quantitative studies of dairy and beef cattle. Admissible studies were field experiments where investigators altered stable fly infestation levels by insecticidal control or augmentative release on otherwise matching groups of animals. Studies where subject animals were infested with appreciable numbers of biting flies other than stable flies were excluded. Reported WBCs were converted to LCs by dividing WBCs by 2.81, the average ratio of flies on the entire body to those on one front leg (Berry et al. 1983).

Effects of stable flies in each study were calculated as absolute difference (y = ΔADM or ΔADG) between the performance of animals in a fly-free reference group and a matching group with reported numbers of flies. Performance of reference animals was extracted directly from descriptions of fly-free control groups if available, or estimated by linear or curvilinear extrapolation to projected ADM or ADG at LC = 0 if fly-free controls were not available. Effects were also quantified in relative terms (y = %ADM or %ADG), where losses were expressed as percentages of the reference group's performance. Repeated measures of performance and fly abundance in the same study were averaged to obtain single values for the full study period. Results from replicated treatment groups (if available) were averaged before comparison with controls. Finally, when multiple experiments were presented in the same report, they were treated independently. All experiments were weighted equally, regardless of duration or numbers of animals.

To characterize a yield-loss function for animals in each industry sector, we graphed change in daily production against corresponding LCs. When four or more cases were available, we fit a quadratic regression, $y = b_0 + b_1x + b_2x^2$ and tested for curvature by comparing b_2 against zero with a t-test. When curvature was apparent, we used nonlinear regression to fit a 2-parameter exponential curve,

$$y = b_0\,[1 - \exp(b_1 \times \text{LC})] \qquad [1]$$

where b_0 is an asymptote that represents maximum loss, and b_1 is slope at $y = b_0/2$ and $\text{LC} = -\ln(0.5)/b_1$ (see Catangui et al. 1997, Jonsson and Mayer 1999). When curvature was not apparent, we fit simpler linear and zero-intercept models to characterize responses. Subsets of data were analyzed for consistency of regression lines by analysis of covariance (ANCOVA), using dummy variables to code for the different subsets, and testing for interactions between subgroups and regression slopes. Model parameter estimates and goodness-of-fit statistics were derived with nls and lm procedures in R (R Development Core Team 2010).

Metabolic Equivalence. Jonsson and Mayer (1999) proposed that biting flies deprive their hosts of a fixed amount metabolic energy (ME) regardless of animal type. If true, then a single yield-loss function could describe the effects of biting flies on all cattle sectors in terms of the amount of ME required to produce a unit of product. To determine if yield-loss functions for different production sectors could be consolidated, we converted measures of milk loss and growth loss into their ME equivalents, 5.24 megajoules (MJ) per kg of 4% fat corrected milk and 35.9 MJ per kg live-weight gain (National Research Council [NRC] 1988, Jonsson and Mayer 1999). We then compared yield-loss functions for dairy, stockers and feeder cattle with a general F statistic to test the significance of the reduction in residual mean square error (RMSE) when yield-loss functions were fit separately versus one model fit to data for the three sectors combined.

Estimated Production Losses. The effects of stable flies on dairy or beef cattle were estimated by calculating daily production losses as a function of estimated stable fly infestation levels and then totaling those daily losses over a year to calculate annual loss per animal. Dollar losses per animal were extrapolated to local herds or national totals by multiplying annual product loss per animal by number of animals, and converting saleable product to equivalent dollar values at time of sale. Formally,

$$L_s = V_s \times N_s \times \sum_{t=1}^{n} f_s(\text{LC}_t) \qquad [2]$$

where L_s is total \$ loss; s is an index for industry sector (d = dairy, c = cow-calf, s = stocker or f = feeder); V_s is annual average dollar value of milk or live sale weights for calves, feeders or fat cattle; N_s is number of animals; and $f_s(\text{LC}_t)$ is a sector-specific yield-loss function relating average leg count in time interval t to average daily loss in milk production or body growth. A dynamic version of equation 2 was produced using Microsoft Excel, and is available from the senior author.

Individual Locations. Descriptions of seasonal stable fly abundance (LC) on untreated herds in different industry sectors and geographic locations were compiled from published and unpublished reports. Leg counts from individual locations were extracted from tables or figures, averaged by month within year, and then monthly means were averaged by month across years if multiple years were available. The resulting series of monthly means were then used to calculate annual losses per animal at corresponding locations, using equation 2, with V_s and N_s each set to 1.0.

Losses at Hay Feeding Sites. A similar approach was used to estimate losses caused by stable flies developing in winter hay feeding sites as recently described by Broce et al. (2005), Talley et al. (2009), and Taylor and Berkebile (2011). Infestation levels on cattle resulting from flies emerging from a larval developmental site was estimated as

$$\text{LC} = \frac{A \times \overline{D} \times e_0}{N_s \times 108 \times 2.81} \qquad [3]$$

where A is total m^2 of the site, $\overline{D}$ is mean number of adults emerging per meter square per day, e_0 is expectation of life for newly emerged adults, and N_s is the number of cattle exposed to flies from the site. The constant 108 is the ratio of number of adult flies on or around cattle to number on the animals' bodies at any instant (Berry et al. 1981), and 2.81 is the ratio of flies on bodies to flies per front leg (Table 2). Representative parameter values were derived from published studies of hay feeding sites (Broce et al. 2005, Talley et al. 2009, Taylor and Berkebile 2011). LCs over the period of emergence were estimated with equation 3, and then substituted into equation 2 to sum sector-specific yield loss (Table 3) over time for exposed cattle.

National Losses. Phenological patterns in stable fly abundance varied among locations (Table 4). To derive a model infestation pattern representative of a national average, we ranked monthly mean LCs within each study from highest to lowest and then calculated median LCs for each of the 12 ranked levels across studies.

Values of milk, calves, and stocker cattle (V_s) for 2005–2009 were obtained from Milk Production, Disposition, and Income (2005–2009) Summary (USDA-NASS 2006a-2010a) and Agricultural Prices

Table 3. Coefficients and summary statistics for absolute and relative yield-loss functions for different types of cattle

Type	Response[a]	Model no.[b]	Form[c]	Regression coefficients						SE_{est}	df	Adj R^2
				b_0	SE	b_1	SE	b_2	SE			
Dairy	ΔADM	1a	Quad	0.13	0.15	0.16	0.06	0.01	0.01	0.33	27	0.86
		1b	Line	0.01	0.10	0.22	0.02	—	—	0.33	28	0.86
		1c*	No-int	—	—	0.22	0.01	—	—	0.33	29	0.95
	%ADM	1d*	No-int	—	—	2.26	0.10	—	—	3.38	29	0.95
Calf	ADG	2a	Quad	0.86	0.01	0.36	0.03	−0.12	0.03	0.03	2	0.98
		2b	Exp-1	1.05	0.02	0.27	0.02	—	—	0.02	3	0.99
	ΔADG	2c*	Exp-2	0.24	—	0.06	—	—	—	—	—	—
	%ADG	2d*	Exp-2	22.52[d]	—	0.06	—	—	—	—	—	—
Stocker	ADG	3a	Quad	1.29	0.06	−0.18	0.05	0.02	0.01	0.04	3	0.91
	ΔADG	3b*	Exp-1	0.52	0.08	−0.40	0.12	—	—	0.04	4	0.86
	%ADG	3c*	Exp-1	40.63	6.10	−0.40	0.12	—	—	3.09	4	0.86
Feeder	ΔADG	4a	Quad	0.11	0.02	0.12	0.11	−0.01	0.11	0.11	17	0.00
		4b	Line	0.08	0.04	0.01	0.01	—	—	0.11	18	0.01
		4c	No-int	—	—	0.01	0.01	—	—	0.12	19	0.01
		4d*	Exp-1	0.15	0.06	−0.15	0.14	—	—	0.11	18	0.01
	%ADG	4e	Quad	6.99	1.48	11.66	6.64	0.08	6.64	6.64	17	0.05
		4f	Line	4.05	2.17	0.26	0.14	—	—	6.45	18	0.11
		4g	No-int	—	—	0.46	0.10	—	—	6.86	19	0.49
		4h*	Exp-1	13.26	5.87	−0.08	0.07	—	—	6.64	18	0.10

[a] ADG, avg daily gain (kg hd^{-1} d^{-1}); ΔADG, absolute loss as difference between ADGs by noninfested and infested animals; %ADG, relative loss as percentage of ADG by noninfested animals.
[b] Models with asterisk (*) were used to derive national loss estimate for given type of animal. Dependent variable (x) is mean leg count (LC), unless noted otherwise.
[c] Quad, $y = b_0 + b_1x + b_2x^2$; Line, $y = b_0 + b_1x$; No-int, $y = b_1x$; Exp-1, $y = b_0 \times (1 - \exp[b_1x])$; Exp-2, $y = b_0 \times (\exp[b_1x] - 1)$.
[d] $b_0 = 100(\text{model 2c's } b_0)/1.05$ kg d^{-1}.

(2005–2008) Summaries (USDA-NASS 2006b-2009b). Because the 2009 Agricultural Prices Summary was not available, 2009 calf and stocker cattle prices were obtained from Agricultural Prices (February 2010, USDA-NASS 2010b). Fed cattle prices were from the 2005–2009 Annual Meat Trade Review (USDA-AMS 2005–2009). Cattle inventories (N_s) for 1 January 2005–2009 were from the January Cattle report (USDA-NASS 2005d-2009d). Commodity values were converted to 2009 dollars using the U.S. Department of

Table 4. Seasonal abundance of stable flies on non-treated dairy and beef herds in different cattle industry sectors, compiled from published and unpublished studies, and resulting estimates of annual losses in commodity mass and value per animal, calculated from monthly leg counts and absolute loss method

Sector	Location[b]	Source	Average monthly leg count (LC)[a]								Annual loss	
			Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Kg	$ US[c]
Dairy	Alberta (D)	Lysyk 1993[d]			0.1	1.1	3.6	2.3	0.2		49	14
	California (D)	Mullens and Meyer 1987[e]	0.5	6.2	17.2	2.6	1.8	1.7	1.5	0.9	229	65
	Illinois (P)	Bruce and Decker 1958[f]		3.4	6.4	8.8	9.8	10.4	5.9	0.0	299	85
	New York (P)	D. A. Rutz, unpubl.[g]	0.0	0.0	1.0	1.4	1.7	1.3	0.9		42	13
Cow-calf	Minnesota (P)	RDM, unpubl.[h]		0.0	10.8	15.2	9.4	3.3	0.4		24	56
	Nebraska (P)	DBT, unpubl.[i]		0.0	4.7	6.7	0.9				6	14
	Nebraska (P)	D. R. Berkebile, unpubl.[j]		1.4	2.1	1.4	0.5	2.7	0.1	0.2	4	10
Stocker	Nebraska	G. J. Brewer, unpubl.[k]			1.2	3.9	1.1	0.3			26	48
Feeder	Nebraska (D)	McNeal and Campbell 1981[l]		1.7	4.2	3.0	1.6				6	11
	Nebraska (D)	Skoda et al. 1991[m]		1.3	8.6	7.1	4.6	1.9	1.4		11	21
	Nebraska (D)	Thomas et al. 1990[n]		4.9	23.9	23.4	15.9	4.9	1.4		19	34
	Nebraska (D)	Thomas et al. 1996[o]			6.1	6.6	3.2				7	13

[a] Average leg counts assumed to be zero in early spring and late autumn, except as noted below.
[b] (P) = cattle in pasture, (D) = drylot.
[c] At 2009 prices.
[d] Four dairies per year, 1989–1991.
[e] Six dairies per year, 1985–1986. Jan, LC = 0.5; Feb, LC = 0.5; Mar, LC = 0.5; Dec, LC = 0.3.
[f] Eight dairies per year, 1955–1957.
[g] One dairy per year, 2000–2002, Varna, NY.
[h] One herd per year, 1988–1991, Morris, MN.
[i] One herd, 2010, Ithaca, NE.
[j] One herd, 2007, Ithaca, NE.
[k] One herd per year, 2008–2010, North Platte, NE.
[l] In total, 27 feedlots 1976, 35 feedlots 1977, and 16 feedlots 1978, all implementing sanitation programs, North Platte, NE.
[m] One feedlot, 1986; three feedlots 1987.
[n] One feedlot per year, 1984–1985.
[o] Two uncleaned feedlots per year for 2 yr.

Labor, Bureau of Labor Statistics, Inflation Calculator (http://www.bls.gov/data/inflation_calculator.htm).

Numbers of dairy cows and feeder cattle were reported directly in the inventories. Numbers of calves were calculated by dividing numbers of beef cows having calved by 2, because it takes ≈6 mo for a calf to reach 500 lb (197 kg) and transition to a stocker. Numbers of stocker cattle on pasture were calculated by adding number of Other Heifers >500 lb and Steers >500 lb together and then subtracting the number of cattle on feed.

Results and Discussion

Yield-Loss Functions. *Dairy Cattle.* We found 11 studies of effects of stable flies on dairy cattle, but most were not suitable for formal analysis; time-matched controls were lacking (Bishopp 1913, Morgan and Bailie 1980), fly control treatments were likely to have harmed the cows (Freeborn et al. 1925, 1928; Shaw and Atkeson 1943), cows were housed in artificial situations (Freeborn et al. 1925, Regan and Freeborn 1936, Miller et al. 1973), or cows were infested with other fly species in addition to stable flies (Granett and Hansens 1956, 1957; Cheng and Kesler 1961; Morgan and Bailie 1980).

The two remaining studies involved commercial dairies in Illinois (Bruce and Decker 1947, 1958). In the first study, milk production was ≈20% higher in cows sprayed with DDT and Rhothane than in control cows sprayed with small amounts of repellent pyrethrins and thiocyanates. Increases in milk production from fly control were greater in poorly managed herds than in better managed herds provided with nutritional supplements. Unfortunately, herds in these studies were infested with both stable flies and horn flies, and control methods reduced the abundance of both species, so yield losses could not be attributed solely to stable flies.

In the second study, Bruce and Decker (1958) achieved horn fly control on whole commercial dairy farms from June through September by treating replacement heifers and dry cows "not involved in production data." The authors then used lactating cows in adjacent pastures to examine benefits of stable fly control. In split herd studies, lactating cows in two herds in each of 3 yr were subdivided, and then one subherd was treated daily with a repellent. In the same 3 yr, whole milking herds at 5–7 dairies per year were treated with variably effective repellents. Lactation rates for each of the 30 subherds and whole herds were expressed as percent reductions in butterfat production compared with levels in the same herds in May or June (before stable flies became active). Stable fly abundance was reported as WBCs.

To derive a dairy yield-loss function, we converted percentage reductions in butterfat levels to 4% adjusted whole milk equivalents, using 1 June production levels of 0.39 kg hd^{-1} d^{-1} for butterfat and 9.7 kg hd^{-1} d^{-1} for whole milk, as reported for comparable herds in Bruce and Decker (1947). Estimated loses were then plotted against corresponding fly densities

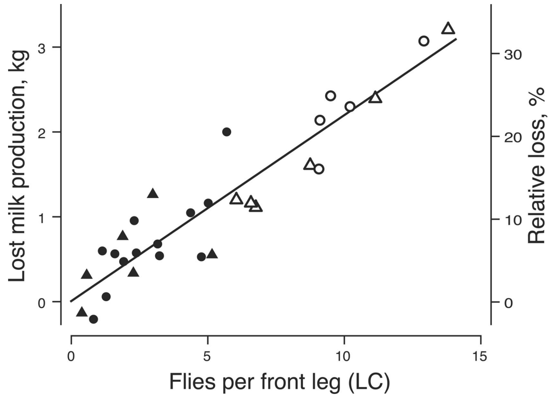

Fig. 1. Absolute and relative yield-loss functions for dairy cattle, adapted from Bruce and Decker (1958). Each point represents one subherd or whole herd in one summer, 1955–1957; filled triangles, treated subherds, open not treated, filled circles treated whole herds, open not treated. Line is least squares fit to all data combined, forced through origin (Table 3, models 1c).

(Fig. 1), and analyzed for homogeneity among treated and nontreated subgroups. Loss functions fit to the different subsets were statistically indistinguishable (test for separate versus combined quadratic regressions: $F = 0.96$; df = 9, 18; $P = 0.50$). Curvilinearity was not significant in the combined relation (Table 3, model 1a; $t = 1.09$, df = 27, $P = 0.28$), and the intercept of a simple linear regression was not different from zero (Table 3, model 1b; $t = 0.1$, $P = 0.92$), so we forced a line through the origin, yielding a simple linear yield-loss function, $\Delta ADM = 0.22 \times LC$ (Table 3, model 1c).

This result indicates that for dairy herds with LCs in the range of 0–15 flies per leg, each additional fly caused an additional loss of 0.22 kg milk per cow day. Losses expressed as percentages of mean daily production (model 1d, Table 3) were 2.26% per fly (Fig. 1). While we believe that a yield-loss function for lactating cattle should be curvilinear over a wider range of LCs, the asymptotic model (equation 1) could not be fit to Bruce and Decker's (1958) data.

Bruce and Decker (1947, 1958) worked mainly with commercial Jersey herds producing ≈10 kg of whole milk per day at seasonal peak in June. Since then, advances in breeding, nutrition, and management have increased milk production in dairy cows nearly three-fold to 25.6 kg in 2009 (USDA-NASS 2010a). Two approaches for applying loss functions to the higher productivity of modern dairies are to consider loss to be 1) an absolute amount of milk per fly, or (2) a relative percent of production potential per fly. If absolute (Table 3, model 1c), then current losses would be similar to those observed by Bruce and Decker (1958), $\Delta ADM = 0.22$ kg hd^{-1} d^{-1} per fly. This approach assumes that stable flies deprive their host of a fixed amount of metabolic energy directly equivalent to milk production and independent of production potential. However, if losses are relative (Table 3, model 1d), then losses for modern animals would be

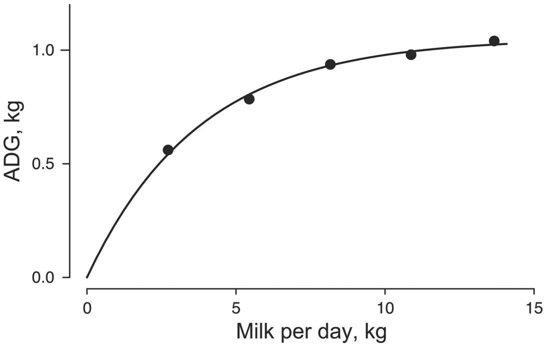

Fig. 2. Basis of yield-loss function for calves in cow-calf herds (adapted from Abdelsamei et al. 2005). Points are mean average daily gains (ADG, kg) of penned preweanling calves provided with different amounts of milk replacer (ADM, kg hd^{-1} d^{-1}) and ad libitum chopped alfalfa hay. Curve is model 2b (Table 3).

2.26% of 25.6 kg or %ADM = 0.58 kg hd^{-1} d^{-1}. Because empirical data are not available to justify either approach, we estimate losses both ways.

Calves in Cow-Calf Herds. We could find no published reports of effects of stable flies on growth rates or weaning weights of calves in cow-calf herds. Anecdotes from calf producers at a 1998 meeting in North Platte, NE, indicated stable flies were reducing calf weaning weights by 9–13.5 kg (20–30 lbs). Earlier, Campbell (1976) found that horn flies reduced calf weaning weights, and he presumed those losses were a result of decreased milk production of cows. Assuming effects of stable flies on lactating beef cows are similar to those on dairy cows, we combined a relationship between milk supply and calf ADG with the dairy yield-loss function (Table 3, model 1c) to estimate effects of stable flies on ADG of preweanling beef calves.

Abdelsamei et al. (2005) raised Holstein replacement heifers with diets containing ad libitum amounts of forage but different amounts of milk replacer (Fig. 2). Linear and quadratic effects of milk supply on ADG were significant (Table 3, model 2a), so we fit the asymptotic model (Table 3, model 2b) to the ADG-supply data. To model calf milk supply, we set average daily milk production of fly-free beef cows at 5.6 kg hd^{-1} d^{-1} (George 1984, as cited in Fox et al. 1988), substituted 5.6 – (0.22 × LC) for ADM in model 2b, and then derived model 2c by defining calf ΔADG as a difference between solutions of model 2b with LC set to zero and an arbitrary LC. The difference, expressed as a percentage of the solution with LC set to zero, led to model 2d. These models are valid for LC within 0–15.

To illustrate, milk production of a brood cow with five stable flies per front leg would be ADM = 5.6 – (0.22 × 5) = 4.5 kg hd^{-1} d^{-1}, and corresponding calf ΔADG would be a 0.08 kg hd^{-1} d^{-1} loss; 10 flies would cause 0.19 kg hd^{-1} d^{-1} loss. Over a 90 d stable fly season, these losses would amount to 7.3 or 17.0 kg reductions in calf weaning weights, respectively. Using the relative loss function (model 2d), LCs of 5 and 10 flies would reduce ADG by 7.7 and 17.9%, respectively. Assuming ADG were 1.05 kg for uninfested calves (the maximum ADG observed by Abdelsamei et al. 2005), LCs of 5 and 10 flies on cows would reduce calf weaning weights by 7.3 and 17.0 kg. These estimates are similar to the Nebraska cattlemen's anecdotal estimates of 9–13.5 kg per calf. Both yield-loss functions (Table 3, models 2c and 2d) give conservative estimates of the impact of stable flies on nursing calves. The expected ADG for uninfested calves used, 1.05 kg h^{-1} d^{-1}, was derived from the Abdelsamei et al. (2005) study with Holstein calves. Increasing this value to the 1.2–1.5 kg h^{-1} d^{-1} expected of beef calves increases estimated losses significantly. In addition, unlike horn flies, stable flies feed on calves and may be causing direct damage in addition to reducing the cows' milk production.

Stocker Cattle. Three studies examined the effects of stable fly control on ADG of grazing yearling calves. Control of biting flies increased ADG by 0.3 kg in Pennsylvania (Cheng 1958) and 0.1 kg in Minnesota (Cutkomp and Harvey 1958). However, horn flies were abundant on the animals in both studies, so benefits of control could not be attributed solely to reductions in stable fly. Campbell et al. (2001) studied split herds of grazing yearlings over 3 yr in central Nebraska. Pastures were described as Nebraska canyon, mixed grass, and sandsage. Both subherds were treated with insecticidal ear tags to control horn flies (but not stable flies). One subherd was treated three times per week with permethrin body sprays to control stable flies. Nonsprayed herds had an average LC = 3.6 stable flies, while sprayed ones had 0.9, for a difference of 2.7. Partial control of stable flies increased average ADG 21%, from 1.14 to 1.38 kg hd^{-1} d^{-1}.

To derive a yield-loss function for stocker cattle, we fit a quadratic regression to average ADGs and matching mean LCs for the two subherds from the 3 yr combined. The y-intercept (1.29 ± 0.06 kg hd^{-1}) was interpreted as an estimate of what ADG would have been if treatments had created fly-free subherds. We then calculated ΔADG for each of the six infested subherds, and fit equation 1 to obtain model 3b (Fig. 3; Table 3). Results indicated an asymptotic loss of 0.52 ± 0.08 kg hd^{-1}. Division through by 1.29 and multiplication by 100 led to the %ADG loss function (Table 3, model 3c). Although more data are needed from stocker herds with LC >4, extrapolation of the absolute loss function model (3b) suggests herds with LC of 5 or 10 could experience losses as great as 0.45 or 0.51 kg hd^{-1} per day, respectively. Over a 90-d grazing period, total losses would be 41 and 46 kg hd^{-1} for LCs of 5 and 10. The relative loss function (model 3c) indicates 35 and 40% reductions in ADG with LCs of 5 and 10, or 47 and 53 kg over a 90 d fly season, respectively.

Feeder Cattle. Five studies, all at North Platte, NE (1974–1991), examined the effects of stable flies on confined feeder cattle (Campbell et al. 1977, 1987, 1993; Catangui 1992; Wieman et al. 1992). In the first

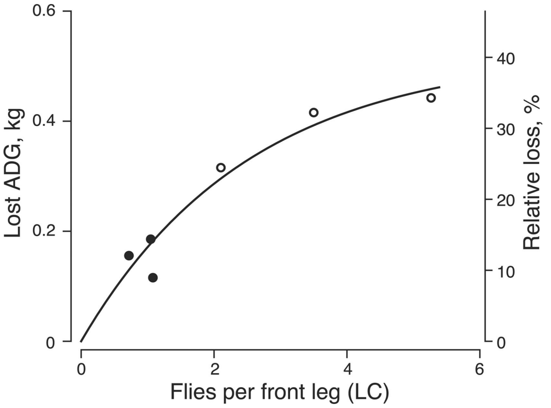

Fig. 3. Yield-loss function for stocker cattle, adapted from Campbell et al. (2001). Points reflect leg counts and reductions from estimated fly-free ADGs (see text); filled circles, treated subherds, open circles not treated. Curve is model 3b (Table 3).

2 yr, groups of 13-mo old heifers were subdivided into four screened pens, two pens excluded stable flies, and laboratory reared flies were released into the two remaining pens to achieve desired levels of fly abundance (reported as mean WBCs). In later years, levels of fly abundance (reported as mean LCs), and additional factors including heat stress, cattle breed, and exposure duration were evaluated, resulting in a total of 20 comparisons between time-matched infested and fly-free feeder cattle. Two reports (Catangui et al. 1993, 1995) summarized seven of the 20 cases described earlier, and a third (Catangui et al. 1997) used data from nine of the 20 cases to illustrate a procedure for calculating economic thresholds for different fly control tactics.

Effects of stable flies in all 20 cases were measured as differences between daily rates of feed intake, body growth and feed conversion (kilogram feed per kilogram growth) by replicate groups of 5–10 animals with and without flies. For the present analysis, we calculated mean daily feed intake, ADG, and feed conversion rates for replicate pens receiving the same experimental treatment, and then calculated absolute and relative differences between infested and matching fly-free control groups. Stable fly-infested animals ate 0.12 kg hd^{-1} d^{-1} (SE = 0.10) less feed than did uninfested ones, 12.13 versus 12.25 kg hd^{-1} d^{-1}. Regression analysis indicated feed consumption rates were independent of LC ($b_1 = 0.002 \pm 0.011$, $P = 0.79$). Similar conclusions were obtained with relative feed intake rates ($b_1 = 0.07 \pm 0.09$, $P = 0.47$). Pens with high numbers of flies consumed as much feed, on average, as pens with few or no flies.

In contrast, mean ADGs of infested animals were lower than those of matching fly-free animals in all studies, and both ΔADGs and %ADGs were proportional to LCs (Fig. 4). Quadratic regression revealed no evidence for curvature in ΔADGs ($P > 0.9$), the intercept was significant ($P = 0.045$), but not substantially different from zero. Forcing through the origin yielded $\Delta ADG = 0.006 \times LC$ (Table 3, models 4a–c). However, analysis of the residuals suggested the response was curvilinear, so we fit equation 1 and obtained model 4d for absolute differences (Table 3; Fig. 4A) and corresponding model 4h for relative differences (Table 3; Fig. 4B). The latter function is similar to one obtained by Catangui et al. (1997), although the subset of nine cases they analyzed was substantially less variable than the full 20 cases analyzed here.

Based upon the absolute yield-loss function, LCs of 5 and 10 reduce ADGs of feeder cattle by 0.08 and 0.12 kg, respectively, and result in losses of 7.1 and 10.5 kg per head over a 90 d fly season. Corresponding losses estimated with the relative loss function are 4.4 and

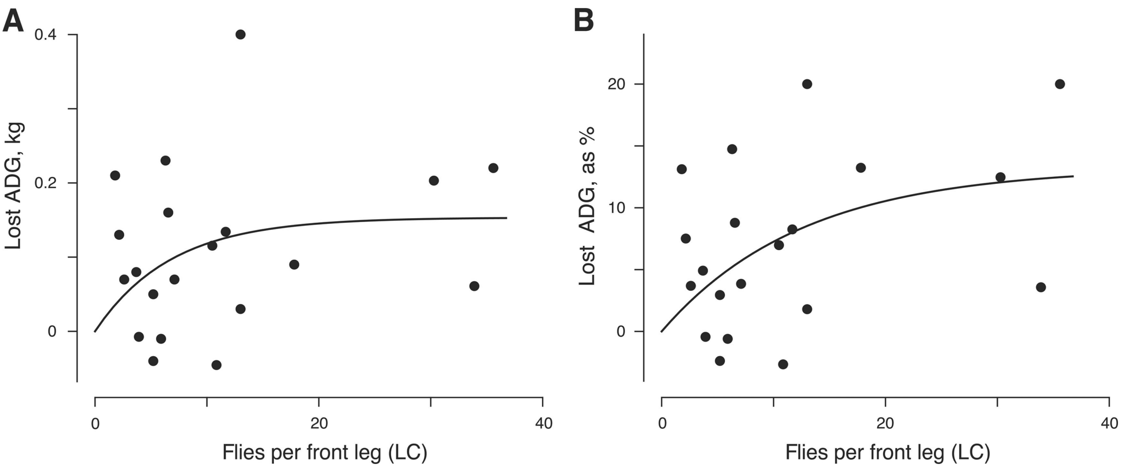

Fig. 4. Yield-loss functions for feeder cattle (adapted from multiple sources, see text). Each point shows difference between ADGs of matched growing heifers in fly-free and experimentally infested pens in relation to numbers of flies on animals in the infested pens. (A) Absolute losses, ΔADG; (B) relative losses, as % of matching controls. Curves are models 4d and 4h (Table 3), respectively.

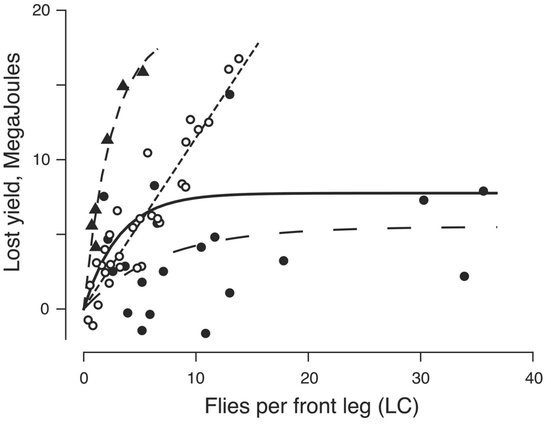

Fig. 5. Absolute yield-loss data expressed as megajoules (MJ) of metabolizable energy required to produce 1 kg of 4% fat-corrected milk or body mass (see text). Data and fitted functions are for dairy cattle (open circles, finely dashed line), stocker cattle (triangles, intermediate dashed curve), and feeder cattle (filled circles, coarse dashed curve) separately, or all combined (solid curve).

7.3%, and amount to 7.1 and 11.9 kg per head over a 90 d fly season.

Metabolic Equivalence. The relationships between losses in productivity expressed in megajoules of metabolic energy (MJ of ME) and corresponding LCs differed among dairy, stocker, and feeder cattle (Fig. 5, one curve vs. three separate curves; $F = 2.08$; df = 4, 50; $P < 0.01$). Losses reached 12–17 MJ d^{-1} for dairy cows and stocker cattle, but remained below 10 MJ d^{-1} for feeder cattle, even though higher LCs were observed in the feeder cattle studies. Differences among sector-specific yield-loss functions indicate effects of stable flies differ among animals in different production systems. Therefore, we rejected the metabolic equivalence model and used separate yield-loss functions for dairy cows, stockers, and feeder cattle to derive loss estimates.

Estimated Losses. *Individual Herds.* We found 12 studies that characterized seasonal stable fly infestation levels on dairy and beef herds in North America (Table 4). Four published and unpublished reports described dairy herds in pastures and drylots, three were cow-calf herds in pastures, one was yearling stockers in pastures, and four were feeder cattle in feedlots. Lengths of the stable fly season varied from three to 12 mo, depending on geographic location. Peak levels ranged from a monthly mean of fewer than two flies per leg in a New York dairy (D. A. Rutz, unpublished data) to 23.9 flies per leg in a study at Nebraska feedlots (Thomas et al. 1990). Median monthly stable fly infestation levels were not strikingly different between herds on pastures or those in drylots.

Using monthly mean LCs (Table 4) and absolute yield-loss functions for corresponding animal types (Table 3), we estimate that annual production losses per animal for the dairy herds ranged from 42 to 299 kg of milk with a median of 139 kg. Those losses (in 2009 dollars) were worth \$13 to \$85 with a median of \$40. Corresponding losses estimated with the relative yield-loss function (Table 3, model 1d) and potential productivity of 25.6 kg of milk per day ranged from \$33 to \$224 per year. For beef cattle, annual losses using the absolute method (Table 3, models 2c, 3b, or 4d) were 6, 26, and 9 kg for calves, stocker, and feeder cattle, respectively (Table 4). Estimates with the relative method (models 2d, 3c, and 4h) were within 10% of those with the absolute method for all cases except Thomas et al. (1990). In that study, mean monthly LCs exceeded 15, the level at which the two yield-loss functions diverge (Fig. 4A vs. B).

Losses From Hay Feeding Sites. Areas (A) of winter hay feeding site residues in eastern Kansas ranged from 13 to 262 m^2 with a mean of $A = 77$ m^2 (Broce et al. 2005). Mean monthly densities ($\overline{D}$) of emerging adult stable flies from six sites in eastern Nebraska were 6.7, 28.4, 45.8, 2.1, and 0.5 adults m^{-2} d^{-1} for May through September, respectively (Taylor and Berkebile 2011). The numbers of cattle associated with feeding sites were not reported; however, managers of the Nebraska herd indicated a target of 50 animals per feeding site. Life expectancy (e_0) of adults was based on field estimates of daily mortality rates (m) of 0.17 (Berry 1986) and 0.09 (Scholl 1986) per day in eastern Nebraska feedlots, and 0.08 in Iowa and Minnesota pastures (Krafsur et al. 1994). Corresponding life spans ($e_0 = \ln[0.5]/\ln[1 - m]$) were 3.2, 7.3, and 8.3 d, for a mean life expectancy of 6.3 d. Assuming survivors fed daily on $N_s = 50$ animals, equation 3 predicts monthly mean LCs of 0.2, 0.9, 1.5, and 0.1 for May through August, respectively. Using these LCs in equation 2, production losses for the 50 dairy cows, would be 890 kg milk, or for 50 cow-calf pairs, stockers, or feeders 60, 561, or 77 kg body weight. With 2009 commodity prices (Table 5), the value of these losses was \$253, \$136, \$1,057, or \$142, respectively. Site specific loss estimates can be derived by substituting specific values for area (A), emergence density ($\overline{D}$), and number of animals affected (N_s). Such estimates could be used to determine if predicted production losses exceed costs of site remediation.

National Losses. Studies reporting seasonal abundance of stable flies on cattle (Table 4) are limited with respect to regional coverage and production sector. Within regions, population levels can vary among premises and years depending upon weather and availability of developmental habitats. Among regions, population levels and seasonality vary depending upon climatic conditions. Consequently, we chose to use a model seasonal abundance pattern derived from medians of ranked monthly mean leg counts (Table 4) to represent an average infestation level for cattle herds in the United States. The resulting abundance pattern indicated a typical stable fly season of 5 mo with median monthly LCs of 6.6, 5.4, 2.9, 0.8, and 0.6. From this pattern, the estimated annual production loss for an average dairy cow in the United States would be 109 kg of milk, and live weight losses for a

Table 5. Animal inventories and commodity values (in 2009 dollars) used to estimate annual losses caused by stable flies for 2005–2009 in four sectors of the U.S. cattle industry

Year	All cattle	Dairy			Cow-calf			Stocker			Feeder		
	No. × 10^6	No. × 10^6	Milk		No. × 10^6	Weaned calves		No. × 10^6	Feeders		No. × 10^6	Fat cattle	
			\$ cwt^{-1}	\$ kg^{-1}		\$ cwt^{-1}	\$ kg^{-1}		\$ cwt^{-1}	\$ kg^{-1}		\$ cwt^{-1}	\$ kg^{-1}
2005	97.1	9.1	16.72	0.37	16.6	148.50	3.27	12.6	103.73	2.29	14.1	96.35	2.12
2006	97.0	9.1	13.75	0.30	16.4	140.98	3.11	12.9	97.84	2.16	14.3	91.05	2.01
2007	96.7	9.2	19.79	0.44	16.3	122.57	2.70	12.9	98.26	2.17	14.3	95.71	2.11
2008	94.5	9.3	18.45	0.41	15.8	110.00	2.43	12.6	94.5	2.08	13.9	93.12	2.05
2009	93.7	9.1	12.93	0.29	15.7	103.00	2.27	12.5	85.4	1.88	13.6	83.33	1.84
Avg:	95.8	9.1	16.33	0.36	16.2	125.01	2.76	12.7	95.95	2.12	14.0	91.91	2.03
CV:	0.01	0.01	0.18	—	0.02	0.16	—	0.01	0.07	—	0.02	0.06	—

Assembled from United States Department of Agriculture, National Agricultural Statistics Service reports (USDA-NASS 2005–2009d).

calf, stocker or feeder animal would be 8, 47, and 8 kg, respectively.

Based on adjusted national inventories and prices (Table 5), absolute yield-loss functions for the four sectors (Table 3), and the model seasonal abundance pattern, we estimate that stable flies reduced productivity of United States cattle industries by an average of \$2.21 billion per yr in 2005–2009 (Table 6). Estimates calculated with the relative loss functions were \$0.57 billion higher, totaling \$2.78 billion. The discrepancy was mainly in the dairy sector, where losses estimated with the relative loss function and a modern productivity of 25.6 kg hd^{-1} d^{-1} were ≈2.6× those estimated with the absolute loss function. Losses for cow-calf, stocker, and feeder sectors over 2005–2009 using absolute and relative functions were similar. In 2009, the total value of milk and beef production in the United States was about \$56.2 billion (USDA-NASS. 2010a, 2010c), so the \$2.2 billion production loss because of stable flies was ≈4% of production value.

Breeding stock, which make up about one-third of the total cattle inventory (Table 5), were excluded from this analysis because data are lacking to quantify the effects of stable fly on cattle reproduction. Possible effects include reduced weight gain of heifers resulting in delayed puberty and failure to calve as 2 yr olds, a critical parameter in beef and dairy herd management (Engelken 2008). In addition, the breeding season for production of spring and early summer calves (Wheat and Riggs 1952) coincides with the seasonal peak in stable fly population levels (Table 4). Producers report reduced insemination rates when fly populations are high, presumably because of reduced libido in heavily infested animals. Economic losses from reduced reproductive success remain to be modeled.

Possible carry-over and secondary effects of stable flies also have not been considered. Bruce and Decker (1958) indicated that reductions in milk production persisted for several months after fly exposure ceased, but such latent effects were not observed in feeder cattle (Catangui et al. 1993). Secondary effects may include reductions in feed intake and feed conversion efficiency (see Campbell et al. 1987), qualities of milk, beef and hides (Stosic et al. 2000), and effects of defensive behaviors of cattle on pasture and water quality (Campbell and Hermanussen 1971, Lenehan et al. 2004). Lastly, expenditures for fly control have not been estimated.

Our national loss estimate more than doubles the most recent estimate (Table 1), mainly because we have included effects of stable flies on pastured cow-calf and stocker herds. Before the 1980s, populations of stable flies on pastured cattle were considered to be insignificant (Hall et al. 1982). The increasing problem of stable flies in pastures coincides with use of large round hay bales in stationary feeders for winter feeding (Broce et al. 2005). Waste hay and manure that accumulates around winter feeding sites become substrate for the development of immature stable flies the following spring (Broce et al. 2005, Talley et al. 2009). In eastern Kansas and Nebraska, winter hay feeding sites are primary sources of early summer stable fly

Table 6. Estimated annual losses (millions of 2009 dollars) in four U.S. cattle industry sectors caused by stable flies in 2005–2009, using equation 2, calculated with absolute (Abs.) or relative (Rel.) yield-loss functions (see Table 3)

Year	Dairy		Cow-calf		Stocker		Feeder		Combined	
	Abs.	Rel.	Abs.	Rel.	Abs.	Rel.	Abs.	Rel.	Abs.	Rel.
2005	364	910	436	436	1,360	1,371	238	235	2,398	2,951
2006	302	769	409	409	1,310	1,321	227	224	2,248	2,722
2007	439	1,132	352	352	1,317	1,328	239	236	2,347	3,048
2008	414	1,078	307	307	1,238	1,248	225	222	2,185	2,856
2009	282	742	285	285	1,113	1,122	198	196	1,879	2,345
Avg:	360	926	358	358	1,268	1,278	226	223	2,211	2,785
CV:	0.19	—	0.18	—	0.08	—	0.07	—	0.09	—

Losses based on animal inventories and commodity values in Table 5, and a 5 mo stable fly season with monthly leg counts (LCs) of 6.6, 5.4, 2.9, 0.8, and 0.6. To calculate losses with relative loss functions, mean daily productivity levels were set at 25.6 kg hd^{-1} for dairy cows, 1.05 kg hd^{-1} for nursing calves, 1.29 kg hd^{-1} for stocker cattle, and 1.82 kg hd^{-1} for feeder cattle.

populations (Broce et al. 2005, Taylor and Berkebile 2011).

Our analysis highlights two needs for additional research. The yield-loss functions for dairy cattle (Table 3, models 1c and 1d) are based on Bruce and Decker's (1958) studies of cows with a lactation potential of <8 kg of milk per day, roughly a third of current national herd average. More recently, Mullens et al. (2006) used regression to analyze measures of milk production by individual cows in relation to variation in stable fly leg counts and concurrent defensive behaviors of drylot cows in southern California, but concluded infestation levels were too low to detect effects. More studies are needed to determine how stable flies affect lactation of modern dairy cows under current management practices. A second need is for direct study of effects of stable flies on calf growth in cow-calf herds. The present cow-calf yield-loss functions (Table 3, models 2c and 2d) were derived by assuming that response to stable flies by grazing beef cows is the same as Bruce and Decker's (1958) dairy cows, and ΔADG for nursing calves in cow-calf herds is the same as Abdelsamei et al.'s (2005) penned dairy steers. Experimental data on beef calf ADG relative to stable fly infestation levels are needed.

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