Estimating population densities of the Australian sheep blowfly *Lucilia cuprina* (Wiedemann) (Diptera: Calliphoridae) from catches in wind-oriented traps[1]

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Summary
An analysis of 2-hourly catches of the blowfly, Lucilia cuprina, in 10 wind-oriented fly traps on 34 trapping days (06.00 – 18.00h) during the period November 1984 – May 1985 indicated that air temperature was the principal factor regulating the number of insects caught. Small but significant effects were associated with radiation, time of day and relative humidity; effects due to wind were not significant. Temperature (T°C), within days, accounted for 62% of the explained deviance, this value increasing to 71.8% with the inclusion of all significant variables. Using temperature alone, the adjusted hourly catch rate, R, can be derived from the expression: $R_{ij} = exp\ (0.9396T - 0.0156T^2 - 14.148)$*. When radiation (RAD, mWh/cm*^{2}*) is included,* $R_{ij} = exp\ (0.7781T - 0.0127T^2 - 0.0126RAD - 13.488)$*. The age structure of trapped females in wind-oriented traps is shown to differ significantly from that obtained with West Australian traps and probably reflects differences in bait composition. Methods are given to correct wind-oriented trap catches for differences in trappability between males and females and between females of differing physiological age. The transformation of catches of wild flies into estimates of relative and absolute population density is also described.*

Keywords
Lucilia cuprina, trap, population density, weather

Introduction

Field studies on populations of the Australian sheep blowfly *Lucilia cuprina* (Wiedemann) have been based primarily on catches in West Australian (WA) blowfly traps using minced sheep liver/sodium sulfide baits (Gilmour *et al.*, 1946; Vogt and Havenstein, 1974, Williams, 1984). Liver/sodium sulfide baits have also been used effectively in sticky traps to study spatial distributions of *L. cuprina* in relation to resource availability (Wardhaugh *et al.*, 1984) and as a standard for assessing the effectiveness of alternative attractants for *L. cuprina* (Urech *et al., 1*994). More recently, wind-oriented (WO) traps with modified liver/sulfide baits (Vogt *et al.*, 1985; Vogt, 1992) have been used to monitor the abundance of *L. cuprina* (I. Dadour and D.F. Cook *pers. comm*., Dymock *et al.*, 1991, Vogt *et al.*, 1995). Experience indicates that WO traps are easier to use and maintain than WA traps and are more efficient in detecting the presence of flies when populations are low. This paper describes field experiments undertaken to determine the effects of weather, female age-composition and fly density on catch rates of adult *L. cuprina* in WO traps. Relationships derived from these experiments are presented for converting trap catches of wild flies into estimates of population density and their approximate standard errors.

Materials and methods

Trapping procedures
Ten wind-oriented traps of Vogt *et al.* (1985) were employed during the first trapping experiment, from November 1984 to May 1985. The experiment was designed to calibrate the effects of weather variables on catch rates of three fly species, the bush fly *Musca vetustissima* (Vogt, 1986), the hairy maggot fly *Chrysomya rufifacies* (Vogt, 1988) and *L. cuprina*. Traps were arranged at 1 km intervals along roads at Murrumbateman (34.58°S, 145.00°E), New South Wales, at fixed locations for the duration of the trapping program. Flies were trapped over runs of 3 or 4 consecutive days on alternate weeks. On each of

[1] This paper was incomplete at the time Bill Vogt died and has been prepared for publication by Keith Wardhaugh, with helpful advice from colleague Richard Morton. A portion of the paper dealing with a mark and recapture experiment has been omitted because there was insufficient information to verify the results presented. Thanks are due to Pauline Logan for allowing unfettered access to Bill's office.

the 34 trapping days, traps were cleared at 2 h intervals from 08:00 to 18:00 (EST), and at dusk. For calibration purposes, the dusk clearance provided empty traps at dawn of the following day, assumed to occur at 06:00. Traps were each baited with mixtures of 100 ml of fresh cattle dung, minced sheep liver and 1.5% w/v sodium sulfide solution. Newly hatched larvae (2000-3000) of *L. cuprina* were added to each of the freshly prepared baits and these were then held for 2 d at room temperature to enhance their attractiveness. Baits were used for 2 consecutive days of trapping and discarded. Flies were killed by spraying them with absolute ethanol. Catches were sorted, sexed and counted, and female age compositions were determined.

The second trapping experiment, which ran for four consecutive days (23 to 26 January 1989), employed 4 WA traps and 4 WO traps sited 1 km apart, as in the first experiment. Traps were operated from 08:00 to 15:00 (EST) each day and the WA and WO traps were alternated between sites on consecutive days. The purpose of the experiment was to compare the reproductive age-compositions of female catches in the different traps to obtain estimates of female trappability in WO traps relative to those for each of the age classes in WA traps (Vogt and Morton, 1991; Vogt and Woodburn, 1994). Baits were used for 2 consecutive days and then discarded. Catches were handled as in the first experiment, but 50 females from daily catches in both trap types were dissected. Whenever possible 12 to 13 females were selected at random from each trap to make up the 50 to be used for dissection. Females were assigned to 5 age classes on the basis of the length and yolk content of their oocytes (Vogt and Woodburn, 1994).

Weather data

Ambient shade temperature (T°C), relative humidity (%RH), wind speed (m/sec) and total solar radiation (mWh/cm^2) were recorded continuously on site. Temperature and relative humidity were measured inside a standard Stevenson screen; wind speed was measured 2 m above ground; solar radiation was measured at a height of 1.4 m. Rainfall was also monitored, but was recorded on too few occasions to enable a meaningful analysis of its effect.

Results and analysis

Experiment 1 - Effects of weather on catch rates

The procedures used were essentially those described for modelling the effects of the same weather variables on catches of *L. cuprina* in West Australian traps (Vogt *et al.*, 1983) and on catches of *M. vetustissima* (Vogt, 1986) and *C. rufifacies* (Vogt, 1988) in wind-oriented traps. However, only total catches (males + females) were considered here because the earlier analyses showed differences between male and female catch rates to be small compared with those for total catches. Factors affecting trap catches (day, time, weather) were assumed to act proportionally, implying an additive regression relationship between weather variables (temperature, radiation, relative humidity, windspeed) and logarithms of trap catches. Within-day variation was assumed to be unaffected by changes in population size and used to define the regression model. As in the earlier analyses variance of the daily total catch (C), i.e., catches summed over sexes and traps within-days, was not constant, tending to increase with its expectation, $\mu = E(C)$, and in this instance, followed a negative binomial error distribution given by the expression: $var(C) = \mu + \mu b^2$, where b = 0.35 (s.e. = 0.03). The negative binomial model explained 74% of the observed deviance in total daily catches.

Table 1. Analysis of deviance results for effects of weather and time of day on within-day variation in mean 2-h catches of *L. cuprina* using quadratic and threshold temperature models.

Variates in model	Residual deviance	Degrees of freedom	Change in deviance	Percentage deviance
Constant + Day	644	170		
Quadratic Model				
+ TEMP	357	169	287	44.6
+ TEMPSQ	245	168	112	17.4
+ RAD	207	167	38	5.9
+ WIND	204	166	3	0.5
+ RH	197	165	7	1.1
+ TIME	182	160	15	2.3
Threshold Model				
+ TFUN	288	169	356	55.3
+ RAD	233	168	55	8.5
+ WIND	229	167	3	0.5
+ RH	222	166	7	1.1
+ TIME	206	161	16	2.5

The analysis of deviance results comparing effects of weather variables and time of day on catch rates of *L. cuprina* are summarised in Table 1. Generalised linear models were fitted using GLIM software (Crawley, 1993) to compare temperature effects (T) for a simple quadratic model (linear and quadratic regression terms) and the threshold model (TFNCT) fitted by Vogt *et al.* (1983) to catches of *L. cuprina* in West Australian traps. The latter is defined as *min* (temperature, 26), which assigns the value of 26 if the (mean hourly) temperature exceeds 26°C, otherwise it is assigned the value of the mean hourly temperature. The error variance was assumed to follow the negative binomial distribution described above. Effects of windspeed (WIND), solar radiation (RAD), relative humidity (RH) were fitted as linear regression terms based on their 2-hourly means. Time of day (TIME) effects were fitted as a factor with 6 levels.

Percentage deviances shown for the fitted variates in Table 1 are calculated relative to the total residual deviance obtained by fitting the constant (grand mean) and the daily mean catches. Temperature effects clearly dominated the analysis, accounting for more than half the total deviance in both models. Wind effects were not significant in either model. Solar radiation, relative humidity and time of day all significantly influenced catch rates of *L. cuprina* ($0.0001<P<0.05$), but their effects were small in comparison to those of temperature. The quadratic temperature model was adopted for calibrating trap catches because it explained a higher percentage of the total deviance than the threshold model (62.0 vs 55.3, Table 1). Estimated regression coefficients (β) for rate models incorporating temperature alone and in combination with solar radiation are shown in Table 2 along with their standard errors. The effects of relative humidity and time of day on catch rates were considered too small to warrant their inclusion in the rate model.

Table 2. Estimated regression coefficients and standard errors for catch rate models based on the quadratic temperature model alone and in conjunction with solar radiation.

Variable	Estimate	s.e.
TEMP	0.9396	0.081
TEMPSQ	- 0.0156	0.002
TEMP	0.7781	0.080
TEMPSQ	- 0.0127	0.002
RAD	0.0126	0.002

If both temperature and radiation are included, the fitted catch rate model for the j_{th} period of the i_{th} day is

$$\ln(\mu_{ij}) = \alpha_i + \beta_1 T + \beta_2 T^2 + \beta_3 RAD = \alpha_i + \ln(R_{ij}) \quad (1)$$

where μ_{ij} is the expected 2-hourly catch total, α_i is the mean daily catch total and R_{ij} is the estimated mean temperature-dependent catch rate (catch/trap/2 h). If radiation is excluded, the model predicts an optimal temperature of 30.1°C for trapping *L. cuprina*, with respective upper and lower 95% confidence limits of 32.2°C and 29.4°C, which is significantly higher than the estimate of 26°C obtained earlier by Vogt *et al* (1983) using the threshold model. The inclusion of solar radiation does not significantly alter the estimated optimal temperature for trapping (30.5°C vs 30.1°C).

The purpose of the catch rate models is to calibrate trap catches to allow for differences in temperature and solar radiation between trapping days. This was done by adjusting catch rates relative to those expected for 'standard' sets of weather conditions (R_s). For convenience, these have been defined as 30° C for temperature and 125 mWh/cm^2 for solar radiation. The former is effectively the estimated optimal temperature for catches of *L. cuprina* and the latter is the maximum hourly total radiation recorded for the study area. Thus for catch rate models (with and without radiation), the maximum values of adjusted catch rates are approximately 1.0 so that the catch rate models convert the observed catch rates to proportions of the rates expected for the defined 'standard' weather conditions.

For temperature alone, $CR_s = exp(14.148)$, and $CR_s = exp(13.425)$ for temperature and radiation.
Adjusted hourly catch rates are calculated using either relationship

$$R_{ij} = exp(0.9396T - 0.0156T^2 - 14.148) \quad (2)$$

or

$$R_{ij} = exp(0.7781T - 0.0127T^2 - 0.0126RAD - 13.488) \quad (3)$$

Values of R_j were evaluated hourly (Table 3) and then averaged to obtain mean daily catch rates. Table 3 also provides information on female age structure.

Table 3. Estimated catch rates for temperature (T) and temperature + radiation (T+R) models and age-class distributions for female *L. cuprina* Experiments 1 & 2 (see Methods). Age-classes 2 to 5 include both nulliparous and parous females, and reproductive ages of marked females are expressed in day-degrees (dds) above 8°C.

	Day	Rate (R_j) T	Rate (R_j) T + R	Females per age class 1	2	3	4	5	Age (dds)
Experiment 1	1	0.5755	0.3185	11	14	7	10	8	14
	2	0.4058	0.3153	3	9	7	4	2	23
	3	0.4585	0.2789	1	13	13	22	1	31
	4	0.4398	0.2606	2	12	15	17	4	40
	5	0.6054	0.3687	2	9	17	19	3	50
	6	0.4744	0.3339	2	11	22	11	4	59
	7	0.4822	0.3109	6	10	15	15	4	69
Experiment 2	1	0.9343	0.5679	4	12	12	20	2	15
	2	0.9379	0.5570	4	21	10	14	1	29
	3	0.9592	0.5832	2	24	12	12	0	45
	4	0.9627	0.3235†	2	14	14	14	6	59
	5	0.8544	0.4584	5	13	11	19	2	74
	6	0.1767	0.0907	7	15	11	14	3	84
	7	0.4845	0.3322	10	11	8	13	5	90

† this value looks incorrect and perhaps it should be taken as 0.5235 (Keith Wardhaugh)

Experiment 2- Effects of reproductive age on female trappability

Reproductive age compositions of females caught in WO and WA traps during the second experiment are summarised in Table 4. The proportions shown are based on total numbers of females dissected (days x number = 4 x 50 = 200), since contingency tests indicated no significant change in age composition of catches in either WO traps over the 4 consecutive trapping days. Differences between traps, on the other hand, were highly significant ($\chi^2_4 = 98.03$, $P < 0.001$), which indicates that females in some age classes responded differently to the two trap/bait combinations.

Table 4. Proportions of wild female *L. cuprina* caught in wind-oriented (P_{WO}) and West Australian (P_{WA}) blowfly traps over four consecutive trapping days, based on pooled dissections of 50 females/day from each of the daily catches. Absolute trappability of an age class (λ) is the proportion removed from the population/km^2/trap during a 12h trapping period under 'standard' weather conditions. Trappability values denoted by $\lambda^{\#}$ are all expressed relative to an assumed value of unity for age class 1 in WA traps, based on estimates of absolute trappability for WA traps (λ_{WA}) obtained by Vogt and Morton (1991).

Female age class	1	2	3	4	5
P_{WO}	0.0850	0.4200	0.1800	0.2650	0.0500
P_{WA}	0.0650	0.1600	0.1550	0.1850	0.4350
Ratio = P_{WO}/P_{WA}	1.3077	2.6250	1.1613	1.4324	0.1149
$\lambda^{\#}_{WA}$	1.0000	2.5427	2.5427	1.0000	2.5427
$\lambda^{\#}_{WO}$=Ratio x $\lambda^{\#}_{WA}$	1.3077*	6.6746	2.9528	1.4324*	0.2922

* For reasons that were not evident, both these values were given as 1.4012 in the unfinished version of this paper. As such, they did not comply with the defined value of $\lambda^{\#}_{WO}$. They have therefore been revised (Keith Wardhaugh).

Ratios of the proportions of females caught in the different age classes multiplied by the corresponding relative trappabilities established for WA traps (Vogt and Morton, 1991) provide estimates of their relative trappability in WO traps. The main differences indicated in the table relate to age classes 2 and 5; the former (protein-motivated females) responded more strongly (2.6x) and the latter (gravid females) responded more weakly (0.1x) to the WO traps.

Calibration of wild fly catches

For studies dealing with the seasonal phenology of *L. cuprina,* the adjustment of trap catch solely for the effects of weather is usually adequate for monitoring relative population trends. In the case of wind-oriented traps, there appears to be little benefit from including data on time of day, relative humidity or radiation as even their combined effects are rather small. Accordingly, standardised hourly catch rates (R_{ij}) can be evaluated from equation (2) and averaged to provide an estimate of the mean daily catch rate (R_j). The product of R_j and the observed catch/trap/hour provides an estimate the standardised catch, which is a measure of relative population density.

To convert observed catches into estimates of actual population density, catch rates need to be adjusted for differences in absolute trappability of females of differing physiological age, as determined by dissection. The mark-recapture experiment of Vogt and Morton (1991) provided estimates of survival probabilities and the absolute trappabilities (λ_k) of females in stage *k*. If Q_{jk} is the observed proportion of females in stage *k*, then the estimated population E(P) on occasion *j* is given by the expression:

$$E(P_j) = \Sigma_i C_{ij}/n)(\Sigma_k Q_{jk}/\lambda_k)/R_j \qquad (4)$$

where n = the number of traps. It is uncertain if the trappabilities estimated in Vogt and Morton (1991) are applicable to other sites, but it is reasonable to assume that their ratios are the same, in which case the relative trappabilities given in Table 4 can be used. The calibrated trap catches would then be interpreted as an estimate of the population density up to an unknown constant factor. If the population class proportions are assumed to be constant, then $\Sigma_k Q_{jk}/\lambda_k$ is estimating a constant, which can therefore be absorbed in the general constant. If dissection has not been undertaken, we would have to omit this factor anyway. For males, trappability has to be taken as constant, since we cannot identify the stage of development.

Discussion

In wind-oriented fly traps, temperature was the main variable affecting catch rates of *L. cuprina,* its effect explaining 62% of the within-day deviance in trap catches. When significant effects due to time of day, radiation and relative humidity were included, explained deviance increased to 71.8%. The lack of a detectable effect due to wind was somewhat unexpected, as Vogt *et al*. (1983) found wind to be a significant factor determining *Lucilia* catch rates in the widely-used West Australian fly trap. However, the observed effect was small (1.03% of the total deviance) and differences between the two studies may simply reflect the improved efficiency of a trap that orients parallel to the wind.

With wind-oriented traps, the optimum temperature for trapping was estimated to be about 30°C, which is significantly higher than that derived by Vogt *et al*. (1983) (26°C) from their study using West Australian traps. However, it is conceivable that this difference in response to temperature may be concerned more with analytical technique rather than biology. In the current study, the effect of temperature was best described with a convex, quadratic function which, by definition, would be expected to yield a higher optimum temperature for trapping than that obtained with the threshold model used by Vogt *et al*. (1983). This finding should therefore be treated with caution.

Results of more certain biological significance are those derived from a comparison of the age structure of female *L. cuprina* in WO and WA traps (Table 4). The two traps provide quite different profiles of the age structure of the sampled population, WA traps being approximately 10x more attractive to gravid females than WO traps, which are more attractive to protein-motivated insects. Although design factors cannot be excluded, the most likely explanation for this difference is that the two traps use different attractants. The standard liver/sodium sulfide bait is obviously perceived as an oviposition site, whereas the modified bait used in wind-oriented traps is more attractive to feeding flies. This finding means that dissection of flies is essential if catches from WA and WO are to be reliably compared.

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