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Environmental Factors Affecting Early Carcass Attendance by Four Species of Blow Flies (Diptera: Calliphoridae) in Texas

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ABSTRACT As the most common primary colonizer of carrion, adult blow flies (Diptera: Calliphoridae) play an important role in initiating arthropod-mediated breakdown of soft tissue; however, their timing is highly variable. This variability complicates the estimation of precolonization intervals or periods of insect activity by forensic entomologists. In this study, the size of the adult blow fly on swine carcasses was compared with various environmental conditions including time of day, temperature, wind speed, and light levels. Four trials were conducted: two in August and September 2008, one in January 2009, and one in February–March 2010. Of the measured variables, time of day was the only consistent factor explaining the population size of blow fly on a carcass, although precipitation and high winds affected winter-active *Calliphora vicina* Robineau-Desvoidy. Male flies were also collected, suggesting that carcasses may play additional roles in adult blow fly ecology beyond that of a simple oviposition site. For both sexes of flies, a strong diel pattern of behavior emerged, which could be useful in estimating precolonization intervals by considering the environmental conditions at a scene, and thus forensic entomologists may be better able to estimate the likelihood of adult activity at a carcass.

KEY WORDS forensic entomology, precolonization interval, *Cochliomyia macellaria*, *Chrysomya rufifacies*, *Calliphora vicina*

Under normal circumstances, after an animal dies, it becomes one of a "patchy" distribution of remote resources for various necrophilous organisms (Hanski 1987). As the resource ages, it passes through a continuum of decay from fresh to dried bony remains (Haglund and Sorg 1996). This process of carcass change is exploited and facilitated by a succession of different arthropod taxa (Carter et al. 2007). This faunal succession, and its relationship to the state of decomposition, has been studied in depth in a variety of systems, including humans (Motter 1898, Rodriguez and Bass 1983), dogs (Reed 1958), and swine (Payne 1965). The successional waves of insects that arrive at each corpse are typically described based on the decompositional phase they arrive and their overall order. In these studies, blow flies (Diptera: Calliphoridae) are most commonly cited as the first insects to arrive at fresh carrion. These early-arriving flies effectively "start the clock" for arthropod-facilitated decomposition of a carcass, a major concern for forensic entomologists whose major service is to estimate the postmortem interval (PMI) of the carcass or cadaver in question.

The traditional entomological means of estimating the PMI is based on determining the age of insects, particularly blow fly larvae, collected from a corpse of interest. The age of these immatures is then calculated using the accumulated degree–day and accumulated degree–hour concepts of insect growth (Higley and Haskell 2010, Wells and LaMotte 2010). The exact mathematical methods for making such estimates can be quite complex, ranging from simple summation to nonlinear general additive models encompassing length, weight, developmental stage, and the strain or population membership (Tarone and Foran 2008). None of these models explicitly considers the role of the adult flies, although Amendt et al. (2007) recommend the term "minimum PMI" to account for the fact that arthropods (particularly immatures) are not generally present instantaneously following death.

In contrast to the larvae-focused method, the Tomberlin PMI model is a comprehensive interpretation for PMI that divides the relationship between the corpse and the associated arthropods in a precolonization (pre-CI) and postcolonization (post-CI) intervals (Tomberlin et al. 2011b). Beginning with neurosensory detection and behavioral activation, followed by searching and location of the carcass, the pre-CI accommodates all of the necessary neurosensory and behavioral activities that must occur before blow fly oviposition. In a complementary fashion, the post-CI then accounts for the rest of the period of insect use of the carcass, commonly the development of immatures. In this respect, the post-CI is functionally equivalent to the minimum PMI. Unlike the post-

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CI, factors affecting the pre-CI have been little studied. Blow fly arrival times are not a constant. Although arrival times as low as 30 s have been reported (Gruner et al. 2007), location and colonization of a corpse can be delayed by days owing to factors such as corpse wrapping or low temperature episode (Goff 1992, Watson and Carlton 2005). Furthermore, blow flies do not typically seek out carrion at night, although there have been at least two reports of nocturnal oviposition under artificial illumination (Greenberg 1990, Baldridge et al. 2006).

Understanding the wide variation in adult arrival times serves two purposes. From an ecological perspective, it is useful to understand how adult blow flies make use of a specific carrion patch. As a highly mobile group of insects, their choices about which patches to colonize affect diversity and species coexistence (Hanski 1987). Variation in adult fly attendance at carcasses could also radically alter the critical ecosystem service of carrion decomposition. Because many flies involved in the carrion breakdown process are also human nuisance flies, understanding the role that a carrion patch plays in mate-finding and adult nutrition could also play a role in developing control strategies. However, the more direct value of understanding adult blow fly behavior is its critical importance in creating accurate estimations of pre-CI lengths (Tomberlin et al. 2011a). Fundamental information necessary to understand the pre-CI is documenting when, and under what conditions, adult blow flies appear at a carcass. Such factors play a role in the critical switch between the pre-CI and the post-CI: acceptance of the carrion by the adult female flies and oviposition upon it. The purpose of this study, therefore, was to examine the role of season, species, and selected environmental and physiological factors on the initiation and variation in population size at a carcass for locally dominant species of Calliphoridae. Environmental effects, such as temperature, time of day, and wind level, affect blow fly activity levels to the point that activity can be mathematically modeled with some degree of success (Nicholson 1934, Digby 1958, Crystal 1964, Vogt et al. 1983, Vogt 1988, Wall et al. 1993b). Within this context, the intent of this study was to characterize the species, sex, size, time of first arrival, and population size with respect to parameters such as PMI, temperature, time of day, and season.

Methods and Materials

Field Site. For each trial, three white commercial swine (*Sus scrofa domesticus* L.) were obtained from a commercial abattoir. The swine were mixed-sex, with individuals weighing 60–80 kg (Catts and Goff 1992). Each pig was killed by cranial trauma to avoid any tranquilizer effects (Patrican and Vaidyanathan 1995) and to better mimic traumatic human death (Schoenly et al. 2007).

Within 1 h of death, the swine were placed in a fallow pasture near Snook, TX (30° 26′14″ N/96° 25′12″ W). Each pig was placed in full sun along a north–south line ≈40 m apart at sites labeled A, B, and C. There were no obvious microenvironmental differences between the sites, although Site A was ≈20 m from a fence line, ditch, and low-traffic county road and Site B was ≈15 m from the solitary large tree in the pasture. For consistency, pigs were placed on their left side with abdomens facing west. At the experimental site, vegetation was typical for the upland Post Oak Savannah ecoregion of Texas (Correll and Johnston 1970), with this particular area dominated by oak (*Quercus* spp. L) and pecan (*Carya illinoinensis* (Wangenheim) K. Koch) trees, yaupon (*Ilex vomitoria* (Solander ex Aiton)) and American beautyberry (*Callicarpa americana* L.) shrubs, and mixed grasses and forbs, predominantly bluestem (*Andropogon* spp. L) and buffalograss (*Bouteloua dactyloides* (Nutt)). For the summer trials (7–9 August 2008 and 5–7 September 2008), pigs were killed at 0745 hours and placed in the field at 0845 hours. In winter Trial 1 (7–13 January 2009), pigs were killed at 0945 hours and placed in the field at 1045 hours; for winter Trial 2 (24 February−7 March 2010) pigs were killed at 0830 hours and placed in the field at 1045 and 0945 hours, respectively. Each trial period was selected for seasonally typical temperatures and predicted clear weather. To prevent nocturnal vertebrate scavenging, each carcass was placed beneath a wire cage each evening. The cage was removed each morning.

Each carcass was observed at hourly intervals following placement in the field, between sunrise and sunset as defined by the US Naval Observatory–Astronomical Applications Department ([USNO–AAD] 2011). An observation consisted of a standardized collection of 10 directed sweeps of a 21-cm aerial net made over each carcass within 30 s. The flies so collected were preserved immediately in ≈80% ethanol. Ambient air temperature was recorded to 0.1°C, and wind speed was assessed on a 5-point scale using a plastic portable anemometer (Dwyer Instruments, Michigan City, IN): 0 was calm, 1 was $<$2.25 m/s, 2 was 2.25–4.5 m/s, 3 was 4.5–9 m/s, and 4 was $>$9 m/s. Ambient light intensity was qualitatively assessed on a 3-point scale with 0 equating to deep twilight, 1 for 50–70% cloud cover, and 2 for normal daylight. Observations were made until third-instar dipteran larvae were observed on the carcass.

Statistical Analysis. Only species with a total collection of more than two individuals were used for statistical analysis using SPSS 15.0 (SPSS Inc, Chicago, IL). As there was a large difference in the total number of flies captured between trials, capture numbers were transformed to proportionate catch per observation. One-way analysis of variance (ANOVA) was used to compare temperatures, wind speed, and light intensity between trials for each season. Full factorial ANOVA was run to compare number of flies collected and time of first arrival by trial, species, and position for each season of collection.

Crepuscular time, the amount of time elapsed since sunrise or time remaining until sunset was calculated for each observation (Mohr et al. 2011). Species-appropriate accumulated degree hour values were also calculated for each observation, using a lower biolog-

Table 1.Numeric capture of all collected Calliphoridae adults for each species, sex, trial, and season at each position during each of four trials (7–9 August 2008, 5–7 September 2008,7–13 January 2009, and 24 February−7 March 2010) in a rural pasture near Snook, TX

Trial	Species	Sex	Position			Total
			A	B	C	
Trial 1	*Co. macellaria*	F	118	104	92	314
	Co. macellaria	M	18	10	11	39
	Ch. rufifacies	F	121	208	105	434
	Ch. rufifacies	M	2	4	5	11
Trial 2	*Co. macellaria*	F	209	381	324	914
	Co. macellaria	M	28	44	31	103
	Ch. rufifacies	F	247	325	267	839
	Ch. rufifacies	M	15	18	35	68
	Chrysomya megacephala (F.)	F	0	2	0	2
	Summer total		758	1096	870	2724
Trial 3	*Co. macellaria*	F	1	0	0	1
	C. vicina	F	5	8	10	23
	P. regina	F	39	28	59	126
	P. regina	M	2	5	3	10
Trial 4	*C. vicina*	F	12	7	7	26
	P. regina	F	1	3	2	6
	P. regina	M	4	1	3	8
	L. sericata	F	0	1	0	1
	Winter total		64	53	84	201

ical threshold of 10°C for *Cochliomyia macellaria* (F.) (Byrd and Butler 1996) and *Chyrsomya rufifacies* (Macquart) (Byrd and Butler 1997), 8°C for *Phormia regina* Meigen (Nabity et al. 2006), and 1°C for *Calliphora vicina* Robineau-Desvoidy (Donovan et al. 2006). Analysis of covariance (ANCOVA) was used to regress proportionate capture data for each season, trial, species, and sex against objective time of day, wind speed, and light intensity. Accumulated degree hour, PMI, temperature, and crepuscular time were tested as covariates. Lowest mean square error was used to refine the regression equation. As part of this ANCOVA, Tukey's honest significant difference post hoc test was used to compare capture between factor levels, generally time of day. Because the observations generally did not meet the assumptions of normality or of equality of variances, the Kruskall–Wallis (KW) test was used with Dunn's posttest to compare on-carcass population size across times of day, for species and sexes using GraphPad Instat 3.0 (GraphPad Software, LA Jolla, CA). Size zero collections from early morning hours before the first capture of a fly type were omitted to avoid artificially inflating the test statistic.

Results

Over the course of this study, 2,925 calliphorid flies were collected (Table 1). Although ≈10 species of blow fly occur in central Texas (Tenorio et al. 2003), only four species were collected in great number: *Co. macellaria* and *Ch. rufifacies* in the summer and *C. vicina* and *P. regina* in the winter. In terms of total collections, for summer trials, significantly more flies were captured in Trial 2 (September) than in Trial 1 (August; $F = 35.451$; df = 1; $P = 0.027$). There were no differences in overall capture between species ($F = 0.009$; df = 1; $P = 0.993$) or position ($F = 2.455$; df = 2; $P = 0.289$); nor were there significant interactions between species, trial, or position ($F < 1.152$; df = 4; $P > 0.05$). For winter trials, significantly more flies were caught in Trial 3 (January) than in Trial 4 (February–March; $F = 27.712$; df = 1; $P = 0.034$). There were no significant differences in capture between positions ($F = 1.552$; df = 2; $P = 0.392$), but there was a significant interaction between trial and species ($F = 21.62$; df = 1; $P = 0.002$) such that significantly more *P. regina* were captured than *C. vicina* in Trial 3; however, there was no significant difference in capture in Trial 4.

Environmental Conditions. The summer trials were characterized by high heat, up to 38.2°C. Trial 1 was an average of 4.2°C warmer than Trial 2, though temperatures for both trials were consistent with the normal temperature for the area for the time of year (National Environmental Satellite, Data, and Information Service [NESDIS] 2011). Winds were generally light, and there was little cloud cover. In the first 3 d of the winter trials, Trial 3 averaged 10.2°C warmer than Trial 4 and was very close to the area's record high of 27.8°C. On ensuing days, Trial 3 was ≈3.3°C cooler than Trial 4, slightly cooler than the normal low of 5.0°C for mid-January. Trial 4's temperatures were generally consistent with the local area normal of 9–20°C for late February to early March (NESDIS 2011). Wind speed was variable in the winter trials, although Trial 4 often had the strongest wind during mid-afternoon. Both of the winter trials also exhibited at least 1 d each with heavy cloud cover. Trial 4 had two rain events: a short shower at 0830 hours on 26 February and a sustained light rain from 0830 to 1130 hours on 1 March 2010. No flies were collected during rain.

For both male and female *Co. macellaria*, time of day was the only significant explanatory variable for population size, with an adjusted R^2 of 0.146 for the males and 0.179 for the females ($F > 2.038$; df = 1; $P < 0.031$). For females, the relationship between time of day and population size was borne out by the nonparametric test, with population sizes between 1845 and –1945 hours significantly higher than the 0645–0845 (KW = 31.502, df = 13, $P = 0.0028$; Fig. 1). For males, no

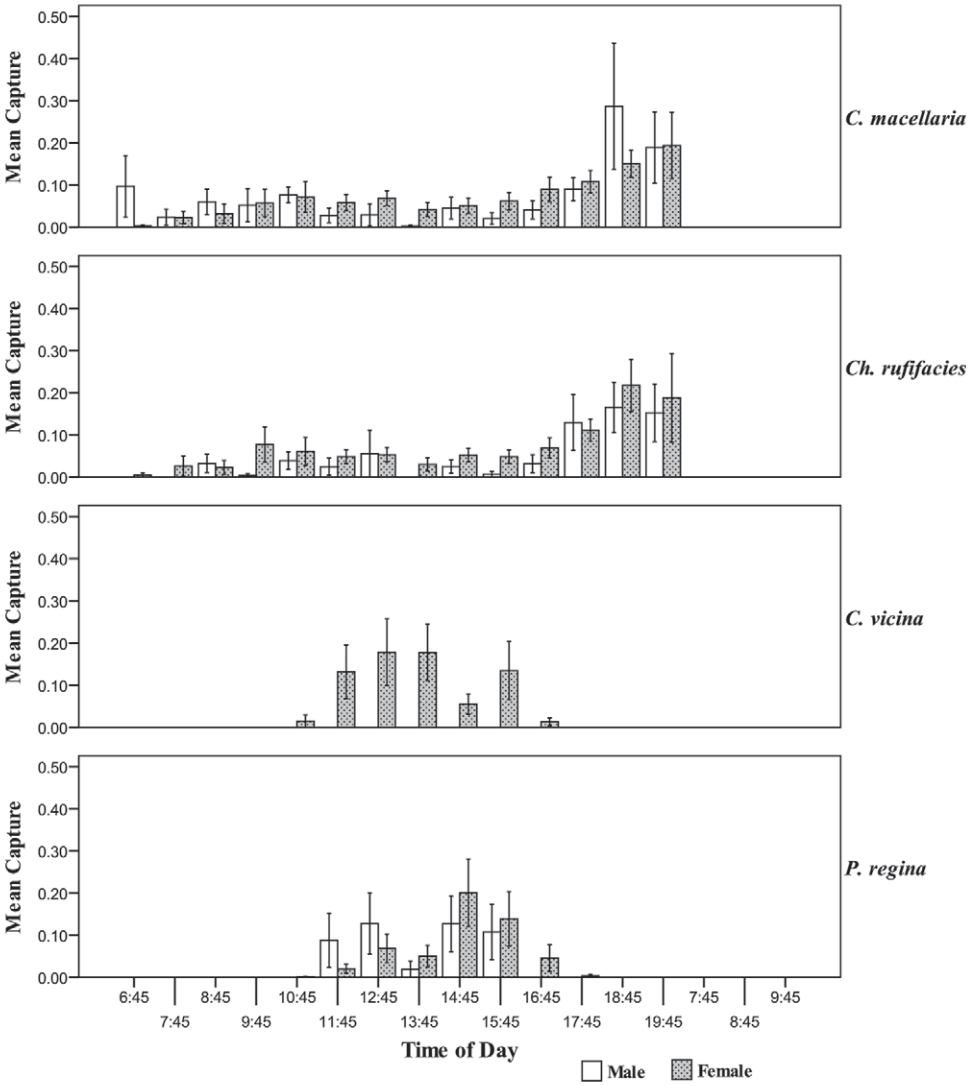

Fig. 1. Mean ± 1 SEM of the percentage capture of each sex and species of fly collected from the carcasses for each time of day. Summer Trials 1 and 2 are pooled, as are winter Trials 3 and 4. For the summer trials, $n = 6$ for each time of day between 0645 and 1945 hours. For the winter trials, $n = 51$ for each time of day.

significant variation in the medians was found (KW = 20.315, df = 13, $P = 0.0876$; Fig. 1). Similarly, time of day was the only significant explanatory variable for female *Ch. rufifacies,* with an adjusted R^2 of 0.173 ($F = 2.269$; df = 13; $P = 0.3098$). They also had a significantly higher population size at 1845 versus 0645 hours (KW = 27.198, df = 13, $P = 0.0117$; Fig. 1).

Male *Ch. rufifacies* had a slightly more complex ANCOVA result, with PMI being the most important explanatory variable, but including a significant interaction between PMI and time of day, with an adjusted R^2 of 0.300 ($F > 2.516$; df = 13; $P < 0.007$). This interaction may help explain the high standard error of the mean for *Ch. rufifacies* males (Fig. 1).

Populations of *C. vicina* were explained by a complex interaction of time of day, light level, and wind level, with an adjusted R^2 of 0.178 ($F = 1.565$; df = 14; $P = 0.015$). The presence of high wind or heavy cloud cover significantly reduced capture during their active time of day ($F = 4.232$; df = 2; $P < 0.001$). For *P. regina,* PMI strongly interacted with time of day ($F = 2.907$; df = 10; $P = 0.002$), with later PMI seeing higher population. Males of this species, however, were explained by the interaction of ambient temperature and time of day ($F = 2.319$; df = 10; $P = 0.011$). For winter flies of both sexes, the KW test statistics showed a strong likelihood of median differences between times of day (KW > 18.275; df = 10; $P < 0.032$). Despite this low P-value, the Dunnett's post hoc test found no significant differences in capture, probably because of the large number of zero-value collections and ties.

Discussion

Environmental Factors on Population Size. In this study, summer flies population size was unaffected by wind. We expected a positive response because wind spreads odor cues and allows anemotaxis, which are important in resource location (Ashworth and Wall 1994). However, wind speeds as low as 2.5 m/s inhibit flight in *Lucilia cuprina* (Wiedemann) (Diptera: Calliphoridae) (Vogt et al. 1983). Although wind speeds up to 4.5 m/s were observed in the summer, no such inhibitory effect was seen, consistent with two studies of *Ch. rufifacies* (Vogt and Starick 1985, Vogt et al. 1985). These conflicting results suggest that the fly body size may play an important role. This idea is borne out by the results of the winter flies. *C. vicina*, a relatively large blow fly compared with *Co. macellaria* or *Ch. rufifacies* (Mohr 2012) is reportedly capable of coordinated flight between 4.5–8.0 m/s (Digby 1958). In the winter trials, wind speeds above 9.0 m/s were frequently observed. These high speeds may explain why wind speed was a significant component of the regression equation for female *C. vicina.*

Temperature is a significant predictor of activity level for a variety of species, explaining 97.7% of variation in tabanid (Diptera: Tabanidae) host-seeking (Cilek and Schreiber 1996) and up to 67% of variation in *Lucilia sericata* (Meigen) trap counts (Wall et al. 1993a). For *L. cuprina,* temperature explained 74.3% of within-day variation in catch rates (Vogt 1988), although that study did not attempt to separate the effect of time of day from temperature. In this experiment, temperature was never an explanatory variable for population size, but time of day was a predictor for all four species and both sexes. The significant relationship between time of day and population size at the carcass seems to indicate that carcass attendance may have a strong circadian rhythm component. Solar-activated circadian control might also explain the diel behavioral patterns (Saunders 2009). Adult *Co. macellaria* and *Ch. rufifacies* assemble at the carcass after dawn and stay at a relatively constant level until significantly increasing in the 2 h or so before sunset (Fig. 1).

Nocturnal–crepuscular activity is not uncommon in Diptera, typically in hematophagous species (Barrozo et al. 2004). However, there is an abrupt drop-off of blow fly activity after sunset (Payne 1965) and lack of nocturnal oviposition (Baldridge et al. 2006, Amendt et al. 2008). Only in cases of artificial illumination have there been documented findings of nocturnal activity of blow flies (Greenberg 1990), probably because light is an exogenous activity stimulant, particularly in the presence of an odor cue (Wooldridge et al. 2007). Curiously, the overnight resting places of the summer-active flies could not be readily located, although the surrounding vegetation and trees and the experimental carcasses themselves were searched thoroughly.

There was a marked difference in diel behavior pattern in the winter species. Adult *C. vicina* were only active on the carcass at midday, regardless of morning temperatures (Fig. 1), consistent with the findings of Deonier (1940). Heavy cloud cover was a deterrent to activity, as also documented by Payne (1965) and Deonier (1940). Heliotaxis cannot be assumed in this species; however, Isiche et al. (1992) found them to strongly prefer shady to sunlit conditions. This complex interaction may indicate an overall greater sensitivity to environmental conditions for this species. For *P. regina,* activity during the middle of the day is unsurprising, as this species is less cold tolerant than *C. vicina*–it is considered a summer active species in South Carolina, not far north of the study site (Tomberlin and Adler 1998).

Male Flies. The collection of male blow flies (Table 1) was unexpected, as they neither oviposit nor do they require a protein meal to produce sperm (Mackerras 1933). They do, however, need to locate females, so they are probably attracted to carcasses for mating opportunities (Archer and Elgar 2003). Therefore, it is not surprising that in males the on-carcass populations generally tracked with the relative size of female populations across the day. Synchronizing their activity to females increases males' likelihood of mating (Zeil 1986) and avoids substantial wasted energy (Hocking 1953). Female flies typically arrive at a carcass either fully gravid or nulliparous (Mohr 2012). In laboratory colonies of *Co. macellaria* cogener *Cochliomyia hominivorax* (Coquerel), peak mating occurs preoogenty at 3–4 d old (Crystal 1964). Likewise, *Ch. rufifacies* mate early in life, before oogeny is complete (Baumgartner 1993). Even if mating occurs at preoogeny, it may be successful for males, as females of *L. cuprina* have been found to be refractory to further mating attempts for up to 7 d following a first mating (Smith et al. 1990), likely a sufficient period to complete oogeny and oviposition. Female blow flies require a protein meal before oogenesis, one which can be readily obtained from decomposing animal tissue (Rasso and Fraenkel 1954). As both mates and protein meal can be found together, this suggests that carcasses may play an important role in adult blow fly biology well before the carcasses are used as an oviposition site. Using carcasses as an aggregation point avoids extensive energy use during mate searching, and may also serve to increase the chances of successful reproduction in otherwise widely distributed species.

In this experiment, during both winter and summer, the size of the fly population on the carcass was governed by time of day and extreme weather conditions. The species collected in each season had notably similar diel patterns of behavior. These two observations seem to indicate that carcass attendance for these four species of necrophilous flies is governed by an endogenous circadian mechanism (Saunders 2009). Understanding the circadian rhythm of blow flies to a carcass may make it possible to predict how likely adult blow flies are to react to and locate a carcass at a given time of day. When paired with basic ecological information, such as relative species abundance, understating the diel pattern of activity would make the estimation of the pre-CI and the PIA much more accurate and reliable, something that has long been a challenge for forensic scientists (Tomberlin et al. 2011b). These findings also represent an important increase in the usefulness of the adult flies themselves in forensic investigations. Although these results were unable to successfully model adult carcass attendance in terms of environmental factors, some inferences can be made. The strong diel pattern of fly behavior allows, in a qualitative sense, an assessment of the likelihood that adults will respond to a carcass, and may explain some of the variation in arrival times documented throughout the forensic entomological literature, an important goal in meeting the legal challenges to forensic evidence (National Academy of Science–National Research Council [NAS–NRC] 2009).

Obviously, further research is necessary to elucidate the complex relationship between adult blow fly behavior and decaying carrion, which might allow the development of mathematical models similar to those already applied to blow fly larvae. Although the R^2 values in this study were too low to merit serious calculation, the emergence of some environmental factors as significant begins to explain why adult flies show such extreme variability in their response to a carcass.

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References Cited

Amendt, J., C. P. Campobasso, E. Gaudry, C. Reiter, H. N. LeBlanc, and M.J.R. Hall. 2007. Best practice in forensic entomology - standards and guidelines. Int. J. Legal Med. 121: 90–104.

Amendt, J., R. Zehner, and F. Reckel. 2008. The nocturnal oviposition behaviour of blowflies (Diptera: Calliphoridae) in Central Europe and its forensic implications. Forensic Sci. Int. 175: 61–64.

Archer, M. S., and A. A. Elgar. 2003. Effects of decomposition on carcass attendance in a guild of carrion-breeding flies. Med. Vet. Entomol. 17: 263–271.

Ashworth, J. R., and R. Wall. 1994. Responses of the sheep blowflies *Lucilia sericata* and *L. cuprina* to odor and the development of semiochemical baits. Med. Vet. Entomol. 8: 303–309.

Baldridge, R. S., S. G. Wallace, and R. Kirkpatrick. 2006. Investigation of nocturnal oviposition by necrophilous flies in Central Texas. J. Forensic Sci. 51: 125–126.

Barrozo, R. B., P. E. Schilman, S. A. Minoli, and C. R. Lazzari. 2004. Daily rhythms in disease-vector insects. Biol. Rhythm. Res. 35: 79–92.

Baumgartner, D. L. 1993. Review of *Chrysomya rufifacies* (Diptera, Calliphoridae). J. Med. Entomol. 30: 338–352.

Byrd, J. H., and J. F. Butler. 1996. Effects of temperature on *Cochliomyia macellaria* (Diptera: Calliphoridae) development. J. Med. Entomol. 33: 901–905.

Byrd, J. H., and J. F. Butler. 1997. Effects of temperature on *Chrysomya rufifacies* (Diptera: Calliphoridae) development. J. Med. Entomol. 34: 353–358.

Carter, D. O., D. Yellowlees, and M. Tibbett. 2007. Cadaver decomposition in terrestrial ecosystems. Naturwissenschaften 94: 12–24.

Catts, E. P., and M. L. Goff. 1992. Forensic entomology in criminal investigations. Annu. Rev. Entomol. 37: 253–272.

Cilek, J. E., and E. T. Schreiber. 1996. Diel host-seeking activity of *Chrysops celatus* (Diptera: Tabanidae) in northwest Florida. Fla. Entomol. 79: 520–525.

Correll, D. S., and M. C. Johnston. 1970. Manual of the vascular plants of Texas. Texas Research Foundation, Richardson, TX.

Crystal, M. M. 1964. Observations on role of light temperature age and sex in response of screw-worm flies to attractants. J. Econ. Entomol. 57: 324–325.

Deonier, C. C. 1940. Carcass temperatures and their relation to winter blowfly populations and activity in the Southwest. J. Econ. Entomol. 33: 166–170.

Digby, P.S.B. 1958. Flight activity in the blowfly, *Calliphora erythrocephala*, in relation to wind speed, with special reference to adaptation. J. Exp. Biol. 35: 776–795.

Donovan, S. E., M.J.R. Hall, B. D. Turner, and C. B. Moncrieff. 2006. Larval growth rates of the blowfly, *Calliphora vicina*, over a range of temperatures. Med. Vet. Entomol. 20: 106–114.

Goff, M. L. 1992. Problems in estimation of postmortem interval resulting from wrapping of the corpse - a case study from Hawaii. J. Agric. Entomol. 9: 237–243.

Greenberg, B. 1990. Nocturnal oviposition behavior of blow flies (Diptera: Calliphoridae). J. Med. Entomol. 27: 807–810.

Gruner, S. V., D. H. Slone, and J. L. Capinera. 2007. Forensically important Calliphoridae (Diptera) associated with Pig Carrion in Rural North-Central Florida. J. Med. Entomol. 44: 509–515.

Haglund, W. D., and M. H. Sorg. 1996. Forensic taphonomy: The postmortem fate of human remains, CRC, Boca Raton, FL.

Hanski, I. 1987. Carrion fly comunity dynamics - patchiness, seasonality, and coexistence. Ecol. Entomol. 12: 257–266.

Higley, L. G., and N. H. Haskell. 2010. Insect dvelopment and forensic entomology. *In* J. H. Byrd and J. L. Castner (eds.), Forensic entomology: The utility of arthropods in legal investigations, 2nd ed. CRC Press, Boca Raton, FL.

Hocking, B. 1953. The intrinsic range and speed of flight of insects. Trans. R. Entomol. Soc. Lond. 104.

Isiche, J., J. E. Hillerton, and F. Nowell. 1992. Colonization of the mouse cadaver by flies in southern England. Med. Vet. Entomol. 6: 168–170.

Mackerras, M. J. 1933. Observations on the life-histories, nutritional requirements and fecundity of blowflies. Bull. Entomol. Res. 24: 353–362.

Mohr, R. M. 2012. Female blow fly (Diptera: Calliphoridae) arrival patterns and consequences for larval development on ephemeral resources. Ph.D, Texas A&M University, College Station, TX.

Mohr, R. M., B. A. Mullens, and A. C. Gerry. 2011. Diel patterns of female host seeking, male swarming, and sugar feeding in *Fannia conspicua* (Diptera: Muscidae) in Southern California. J. Med. Entomol. 48: 188–195.

Motter, M. G. 1898. A contribution to the study of the fauna of the grave. A study of on hundred and fifty disinterments, with some additional experimental observations. J.N.Y. Entomol. Soc. 6: 201–231.

Nabity, P. D., L. G. Higley, and T. M. Heng-Moss. 2006. Effects of temperature on development of *Phormia regina*

(Diptera: Calliphoridae) and use of developmental data in determining time intervals in forensic entomology. J. Med. Entomol. 43: 1276–1286.

(NAS–NRC) National Academy of Science–National Research Council. 2009. Strengthening forensic science in the United States: a path forward. National Academy of Science, National Research Council, Washington, DC.

(NESDIS) National Environmental Satellite, Data, and Information Service. 2011. Climatography of the United States No. 84, 1971–2000: Station #411889. National Environmental Satellite, Data, and Information Service. National Oceanic and Atmospheric Administration, Asheville, NC.

Nicholson, A. J. 1934. The influence of temperature on the activity of sheep blowflies. Bull. Entomol. Res. 25: 85–99.

Patrican, L. A., and R. Vaidyanathan. 1995. Arthropod succession in rats euthanized with carbon dioxide and sodium pentobarbital. J.N.Y. Entomol. Soc. 103: 197–207.

Payne, J. A. 1965. A summer carrion study of the baby pig *Sus scrofa* Linnaeus. Ecology 46: 592–602.

Rasso, S., and G. Fraenkel. 1954. The food requirements of the adult female blow-fly, *Phormia regina* (Meigen), in relation to ovarian development. Ann. Entomol. Soc. Am. 47: 636–645.

Reed, H. B., Jr. 1958. A study of dog carcass communities in Tennessee, with special reference to the insects. Am. Midl. Nat. 59: 213–245.

Rodriguez, W. C., and W. M. Bass. 1983. Insect activity and its relationship to decay rates of human cadavers in East Tennessee. J. Forensic Sci. 28: 423–432.

Saunders, D. S. 2009. Circadian rhythms and the evolution of photoperiodic timing in insects. Physiol. Entomol. 34: 301–308.

Schoenly, K. G., N. H. Haskell, R. D. Hall, and J. R. Gbur. 2007. Comparative performance and complementarity of four sampling methods and arthropod preference tests from human and porcine remains at the forensic Anthropology Center in Knoxville, Tennessee. J. Med. Entomol. 44: 881–894.

Smith, P. H., C. Gillott, L. B. Browne, and A.C.M. Vangerwen. 1990. The mating-induced refractoriness of *Lucilia cuprina* females - manipulating the male contribution. Physiol. Entomol. 15: 469–481.

Tarone, A. M., and D. R. Foran. 2008. Generalized additive models and *Lucilia sericata* growth: Assessing confidence intervals and error rates in forensic entomology. J. Forensic Sci. 53: 942–948.

Tenorio, F. M., J. K. Olson, and C. J. Coates. 2003. Decomposition studies, with a catalog and descriptions of forensically important blow flies (Diptera: Calliphoridae) in Central Texas. Southwest. Entomol. 28: 37–45.

Tomberlin, J. K., and P. H. Adler. 1998. Seasonal colonization and decomposition of rat carrion in water and on land in an open field in South Carolina. J. Med. Entomol. 35: 704–709.

Tomberlin, J. K., M. E. Benbow, A. M. Tarone, and R. M. Mohr. 2011a. Basic research in evolution and ecology enhances forensics. Trends Ecol. Evol. 26: 53–55.

Tomberlin, J. K., R. Mohr, M. E. Benbow, A. M. Tarone, and S. L. VanLaerhoven. 2011b. A roadmap for bridging basic and applied research in forensic entomology. Annu. Rev. Entomol. 56: 401.

(USNO–AAD) U.S. Naval Observatory–Astronomical Applications Department. 2011. Complete sun and moon data for one day. U.S. Naval Observatory Astronomical Applications Department, Washington, DC.

Vogt, W. G. 1988. Influence of weather on trap catches of *Chrysomya rufifacies* (Macquart) (Diptera: Calliphoridae). J. Aust. Entomol. Soc. 27: 99–103.

Vogt, W. G., and N. T. Starick. 1985. A wind-oriented fly trap for quantitative sampling of adult *Musca vetustissima* Walker. J. Aust. Entomol. Soc. 24: 223–227.

Vogt, W. G., T. L. Woodburn, R. Morton, and B. A. Ellem. 1983. The analysis and standardization of trap catches of *Lucilia cuprina* (Wiedemann) (Diptera: Calliphoridae). Bull. Entomol. Res. 73: 609–617.

Vogt, W. G., T. L. Woodburn, R. Morton, and B. A. Ellem. 1985. The influence of weather and time of day on trap catches of males and females of *Lucilia cuprina* (Wiedemann) (Diptera: Calliphoridae). Bull. Entomol. Res. 75: 315–319.

Wall, R., N. P. French, and K. L. Morgan. 1993a. Predicting the abundance of the blowfly *Lucilia sericata* (Diptera: Calliphoridae). Bull. Entomol. Res. 83: 431–436.

Wall, R., N. P. French, and K. L. Morgan. 1993b. Sheep blowfly population control - development of a simulation model and analysis of management strategies. J. Appl. Ecol. 30: 743–751.

Watson, E. J., and C. E. Carlton. 2005. Insect succession and decomposition of wildlife carcasses during fall and winter in Louisiana. J. Med. Entomol. 42: 193–203.

Wells, J. D., and L. R. LaMotte. 2010. Estimating the postmortem interval. *In* J. H. Byrd and J. L. Castner (eds.), Forensic entomology: the utility of arthropods in legal investigations, 2nd ed. CRC, Boca Raton, FL.

Wooldridge, J., L. Scrase, and R. Wall. 2007. Flight activity of the blowflies, Calliphora vomitoria and *Lucilia sericata*, in the dark. Forensic Sci. Int. 172: 94–97.

Zeil, J. 1986. The territorial flight of male houseflies (*Fannia canicularis* L). Behav. Ecol. Sociobiol. 19: 213–219.

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