Relationships Among Body Size, Blood Meal Size, Egg Volume, and Egg Production of *Tabanus fuscicostatus* (Diptera: Tabanidae)

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ABSTRACT Number of ovarioles, egg production, and weight of unfed and bloodfed *Tabanus fuscicostatus* Hine females were related linearly to wing length. Wing length did not change whether flies were freshly thawed, preserved in formalin solution, or oven dried. Left and right wings were similar in length. The length from the costa to the anterior cross vein or to the intersection of R4 and R5 veins was associated linearly to wing length. The number of eggs produced by flies bloodfed on one or two bovine hosts was similar when adjusted by wing length. The average number of ovarioles per female was 277 ± 50 (±SD), and eggs developed in only 63% of the ovarioles after a bloodmeal. An estimated 3.1 eggs were produced for each milligram of blood ingested by a fly, and the average bloodmeal size was 110% of the unfed weight of the flies (49.7 mg). Egg volume was unrelated to body size, but was associated inversely with the number of eggs produced per female.

KEY WORDS body size, bloodmeal size, eggs

CORRELATION OF BODY SIZE to egg production is well described for mosquitoes (Hosoi 1954, Colless & Chellapah 1960, Van Den Heuvel 1963), ceratopogonids (Linley et al. 1970), and blow flies (Webber 1955). Although intraspecific, annual and seasonal variations of wing length or ovariole number have been reported in horse flies (Leprince & Lewis 1983, Perich et al. 1985, Leprince & Bigras-Poulin 1988), there is no information on the relationships among body size, bloodmeal size, and egg production of tabanids.

Tabanus fuscicostatus Hine is an anautogenous species (Foil et al. 1989b) and as such females require a bloodmeal before each oviposition. It also is a major pest of livestock in the southeastern United States. This species has been used as a vector in mechanical transmission trials for anaplasmosis (Wilson & Meyer 1966), equine infectious anemia (Hawkins et al. 1976), and bovine leukemia (Foil et al. 1989a), and in studies evaluating the toxicity and sublethal effects of insecticides (Zyzak et al. 1989; Foil et al. 1990, 1991). Information on the reproductive biology of this species could be useful in the interpretation of the sublethal effects of insecticides and age-grading techniques. An objective of this study was to identify a morphological structure that was associated reliably with the body size of flies stored under different conditions, and that was associated with fly weight (unfed and bloodfed), egg production, and the number of ovarioles. Another objective was to determine whether egg production was influenced by the number of hosts (one versus two) when body size of flies was taken into consideration and whether egg volume was affected by body size or the number of eggs produced.

Materials and Methods

Study Site. The study was conducted at the Thistlethwaite Wildlife Management Area in St. Landry Parish, Louisiana (Foil et al. 1989b). Females of *T. fuscicostatus* were collected with canopy traps (Hribar et al. 1991) baited with dry ice.

Estimates of Body Size. A group of 25 *T. fuscicostatus* females were collected from canopy traps, deposited in sealed plastic bags, and stored at −20°C for 2 mo. Total wing length, head width, and thorax width were measured three times: 1 h after thawing at room temperature, after storage in 10% formalin solution for 36 h, and after being pinned and dried for 24 h at 52°C in an oven. An additional 26 flies were processed as above, but were dried unpinned in the oven; thorax width of formalin-preserved and dried unpinned specimens was measured. The left wing was placed upside down between two slides and measured from the base of the costa to the tip of the wing to the nearest 0.08 mm. Head and thorax widths were measured to the nearest 0.04 mm.

Field-collected flies held under laboratory conditions often damaged their wing tips against the walls of the rearing containers. The intact left

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and right wings of 30 flies were measured to determine if wings of the same specimen were of the same length. Total wing length from the base of the costa to the tip of the wing, from the base of the costa to the bifurcation of veins R4 and R5 (R5), and from the base of the costa to the anterior cross vein (ACV) were measured from a group of 25 flies with undamaged wings. Total wing length was regressed on R5 and ACV to determine if they were reliable estimates of total wing length.

Blood Meal Estimates. On 24 July 1987, 147 unfed flies, collected from dry ice–baited canopy traps, were frozen at −20.0°C. Another group of flies collected from canopy traps (n = 130) individually were fed to repletion on Jersey bullocks, inserted in a 33-ml capped plastic cup, immediately deposited on dry ice, to stop metabolic activities and stored at −20°C. Unfed flies from canopy traps and engorged flies were thawed 1 h at room temperature and weighed to the nearest 0.1 mg within 3 d of capture.

Number of Hosts and Egg Production. On 28 and 29 July 1987, 50 flies individually were placed on a Holstein cow and allowed to feed until blood could be seen through the pleural membrane of the abdomen. Then, feeding was interrupted, and flies immediately were transferred to a Jersey bullock and allowed to complete engorgement. Another 108 flies individually were allowed to feed to repletion on the cow. After feeding, flies were transferred to a cardboard container and supplied ad libitum with water and sucrose solution (Zyzak et al. 1989). Gravid *T. fuscicostatus* females rarely lay eggs under these conditions. After 6 d, flies were killed and stored in a 10% formalin solution until the number of eggs were counted, and the wing length measured.

The number of ovarioles of specimens collected from canopy traps from 19 June to 9 July 1987 was determined. One ovary was isolated from other internal structures and placed in a saline solution. Ovarioles were separated gently and counted, and twice that number was considered to be the total. Leprince & Jolicoeur (1986) found no significant differences in the number of ovarioles between right and left ovaries of *Tabanus quinquevittatus* Wiedemann. *T. fuscicostatus* and *T. quinquevittatus* are both in the *Tabanus nigrovittatus* complex (Thompson & Pechuman 1970). Fecundity index and the 99% confidence intervals were calculated in their logarithmic form:

$$Z = \log_{10}(\text{ovariole number or egg number}) - 3\log_{10}(\text{wing length}),$$

which is expected to follow the normal distribution closely (Leprince & Jolicoeur 1986). Logarithmic values then were backtransformed for presentation.

Egg Volume, Body Size, and Egg Production. Between 20 and 25 June 1990, 66 *T. fuscicostatus* flies were allowed to engorge to repletion on Jersey bullocks. After feeding, flies were transferred to containers and held for 6 d; survivors were killed and stored in a 10% formalin solution until dissection. Wing length, number of eggs, and width and length of five eggs were measured.

Tabanid eggs have an ellipsoid shape that is best described as a three-axis ellipsoid where the two equal axes are shorter than the third. The equation for the volume of a sphere was used to calculate egg volume: half the width was used as the radius of both small axes, and half the length was used as the radius of the third axis.

Statistical Analyses. Analyses were performed with SAS software (SAS Institute 1988). Measurements of body structures made in ocular units were converted to millimeters prior to statistical analysis and calculations. Fisher's least significant difference test was used to compare the variations in the measurements among the different preservation techniques (fresh, formalin, and dried). Student's t test for paired samples was used to compare thorax width of formalin-preserved and unpinned-dried specimens. Differences in the length of the right and left wings of 30 flies did not follow a normal distribution, and the nonparametric Wilcoxon signed rank test was used. Differences in the number of eggs in the first and second ovary followed a normal distribution and were analyzed by a paired-difference t test. Simple linear regressions were used to describe the relationships among total wing length and R5, and ACV; wing length and unfed and engorged weight; wing length and number of eggs and number of ovarioles; egg volume and wing length; and egg volume and egg production. A general linear model was used to determine if egg production was influenced by the number of hosts (one or two) when wing length was taken into consideration.

Results

Body Size Estimates. Wing length did not vary significantly among the fresh, formalin-immersed, and pinned-dried specimens, but head and thorax widths were significantly smaller in dried specimens than in other treatments (Table 1). In a second evaluation, the average thorax width and standard deviation of formalin-treated (3.08 ± 0.17 mm) and unpinned-dried specimens (3.10 ± 0.17 mm) were ($\bar{x}$ ± SD) not significantly different ($P > 0.05$). Because of the ease of storage and manipulation of pinned flies, wing length was used to estimate body size for all subsequent flies. The lengths of the right and left wing of *T. fuscicostatus* were similar (Wilcoxon signed rank test, $P > 0.05$). Distances from the base of the costa to the ACV and R5

Table 1. Average and standard deviation of total wing length, head width, and thorax width in mm from fresh (freeze, thawed), formalin (10%)-immersed, and oven-dried specimens (n = 25 females)

Body structure	Size (mm)		
	Fresh	Formalin	Dried[a]
Wing length	8.42 ± 0.41a	8.47 ± 0.41a	8.39 ± 0.41a
Head width	3.64 ± 0.17a	3.62 ± 0.18a	3.43 ± 0.16b
Thorax width	2.99 ± 0.15a	3.00 ± 0.16a	3.14 ± 0.15b

Means in the same row followed by the same letter were not significantly different ($P > 0.05$) by the least significant difference t test.

[a] Dried specimens were pinned before dehydration.

were significantly predictive of total wing length ($P < 0.0001$; Fig. 1) (i.e., either ACV or R5 could be used reliably to estimate total wing length in specimens with damaged wings).

Bloodmeal Estimates. The weight of both unfed and engorged flies increased significantly ($P < 0.001$) as a function of wing length (Fig. 2); engorged weight ($R^2 = 0.47$) was more variable than unfed weight ($R^2 = 0.70$) when associated to wing length. The average body weight and wing length of unfed flies were 49.70 ± 7.32 mg (range, 34.3–67.9) and 8.88 ± 0.46 mm (range, 7.77–10.07), respectively. The average body weight and wing length of engorged flies were 104.57 ± 14.95 mg (range, 69.6–140) and 8.84 ± 0.41 mm (range, 7.95–9.86), respectively. On average, females ingested more than their own unfed weight in blood.

Number of Hosts and Egg Production. The number of hosts (one or two) did not significantly influence egg production when body size was taken into consideration ($P = 0.62$), and therefore flies fed on one or two hosts were pooled for further analysis. The average wing length and number of eggs produced by flies were 8.70 ± 0.44 mm (range, 7.55–9.86) and 168.82 ± 43.53 eggs (range, 61–304), respectively. The average wing length and total number of ovarioles of unfed flies were 8.85 ± 0.52 mm (range, 7.69–10.2) and 276.57 ± 49.88 ovarioles (range, 170–398), respectively.

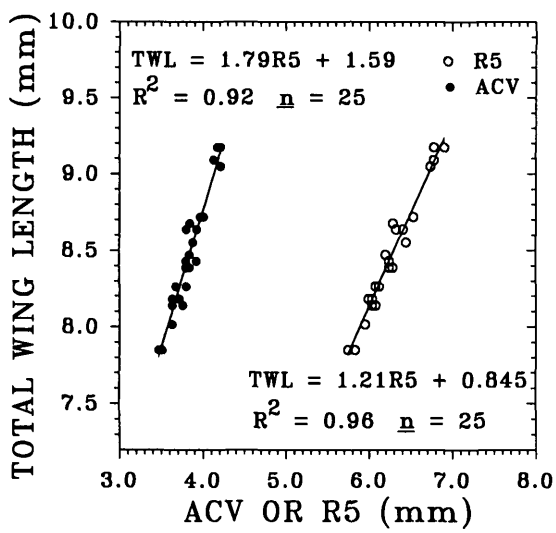

Fig. 1. Total wing length (TWL) of *T. fuscicostatus* females plotted as a linear function of the length from the base of the costa to the anterior cross vein (ACV) and the bifurcation of veins R4 and R5 (R5). Overlapping observations are hidden.

The number of eggs and the number of ovarioles both increased as a linear function of body size ($P < 0.0001$; Fig. 3); egg production was more variable when compared with wing length ($R^2 = 0.28$) than was the number of ovarioles ($R^2 = 0.76$; Fig. 3). The arithmetic values of the fecundity index based on the number of ovarioles or eggs and its 99% confidence interval (CI) were 0.395 (CI = 0.388–0.403) and 0.248 (CI = 0.236–0.261), respectively. Direct comparison of the indices revealed that on average 63% of the ovarioles of *T. fuscicostatus* females were used for egg production.

The ratio of the average number of eggs produced from a blood meal of average size may be derived from the relationships in Figs. 2 and 3. A fly with an average wing length of 8.80 mm took a blood meal of 54.9 mg (103.6–48.66 mg) and produced 174 eggs, for an average of 3.17 eggs per milligram of blood. The number of eggs per milligram of blood for flies with wing length between 8.0 and 10.0 mm (a range of wing length that contains most females of *T. fuscicostatus*) varied from 2.88 to 3.45 eggs per milligram of blood.

Egg Volume, Body Size, and Egg Production. Separation of ovaries was achieved in 58% (n = 66) of the gravid females dissected. No significant difference in the number of eggs produced per ovary was detected among 38 gravid *T. fuscicostatus* flies (paired-differences t test, $P > 0.24$). The average number of eggs produced was 176 ± 55 (range, 53–304), and the average wing length was 8.80 ± 0.02 mm (range, 7.81–9.60). The average egg width was 0.284 ± 0.025 mm (range, 0.228–0.344), and the average egg length was 1.68 ± 0.09 mm (range, 1.44–1.89). The average egg volume was 0.0715 ± 0.0144 mm^3 (range, 0.0408–0.1076). The egg volume of *T. fuscicostatus* was unrelated to body size ($F = 1.4$; df = 1, 64; $P = 0.23$), but was associated inversely with egg production ($F = 7.93$; df = 1, 64; $P < 0.01$; Fig. 4).

Discussion

There are several advantages in using total wing length as an estimate of body size for *T. fuscicostatus*. Total wing length did not vary significantly among different preservation methods and can be measured from either wing or derived from the relationships among ACV and R5 to

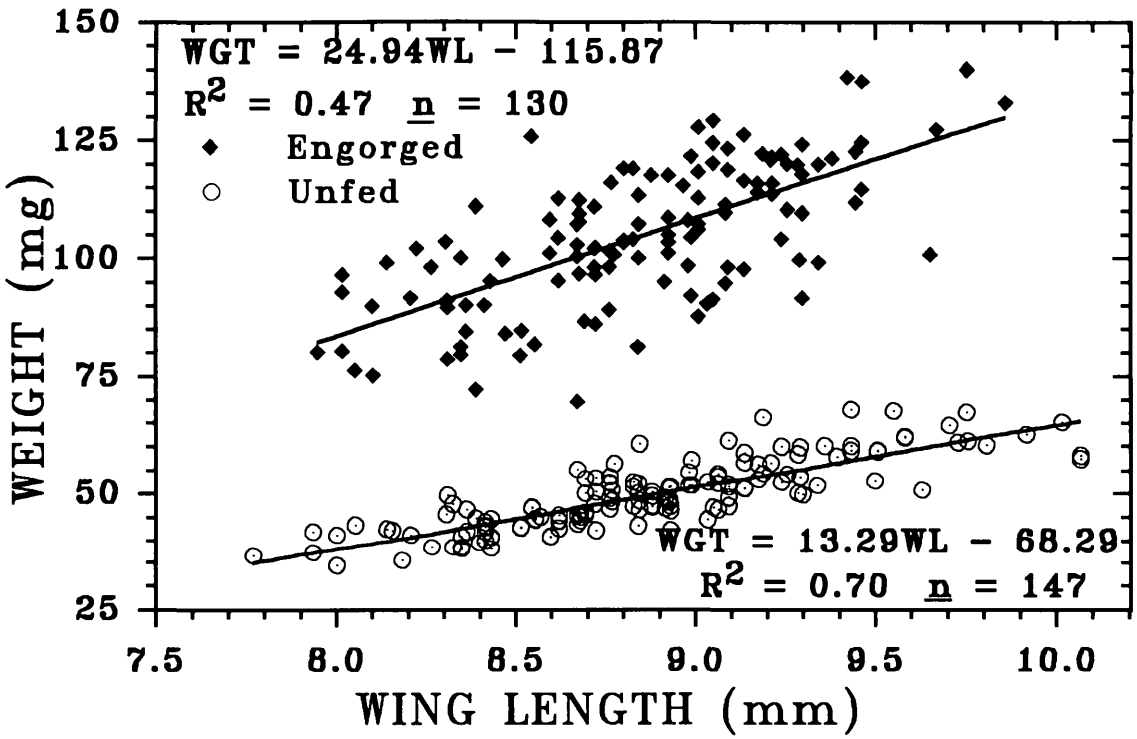

Fig. 2. Weight (WGT) of blood-engorged and host-seeking unfed *T. fuscicostatus* flies plotted as a function of total wing length (WL). Overlapping observations are hidden.

total wing length in specimens with damaged wing tips. Wing length also was linearly associated with number of ovarioles, egg production, and unfed and bloodfed weight.

Egg production was unrelated to the number of hosts when accounting for the body size of *T. fuscicostatus,* indicating that flies ingested a similar amount of blood whether fed to repletion on one or two hosts. Attempts to complete a partial blood meal enhances mechanical transmission of animal disease agents by horse flies (Foil & Issel 1991).

Although the volume of blood ingested and egg production increased as a function of body size (Figs. 2 and 3), the number of eggs produced per milligram of blood was relatively stable over the range of wing lengths recorded (8–10 mm); mean ratio averaged 3.17 eggs per milligram of blood and ranged from 2.88 to 3.45. The relative consistency of the conversion of blood into eggs over the range of wing lengths observed indicated a "viable size" for eggs of *T. fuscicostatus* (i.e., a specific amount of energy invested per egg regardless of body size). In *Lucilia cuprina* (Wiedemann), egg production is associated with body size but not egg size (Webber 1955). Egg volume decreased slightly as an inverse function of egg production in *T. fuscicostatus.*

Based on the ratio of eggs per milligram of blood and assuming that the bloodmeal size ingested was above the threshold regulating egg development (this threshold is unknown for *T. fuscicostatus*), changes in egg production associated with changes in bloodmeal size could be estimated. Foil et al. (1990) reported that *T. fuscicostatus* females feeding on cows sprayed with a 0.05% fenvalerate solution had bloodmeal size reduced by 31%. If the average wing length of *T. fuscicostatus* is 8.80 mm, an average bloodmeal size (54.94 mg) would be reduced by 17 mg (31%), and 54 less eggs would be deposited per female (3.17 eggs per milligram of ingested blood).

The number of ovarioles of *T. fuscicostatus* (277 ± 50 ovarioles per fly) is similar to that of *T. quinquevittatus* (253 ± 37) (Leprince & Jolicoeur 1986), a species belonging to the same *Tabanus* complex (Thompson & Pechuman 1970). The average number of ovarioles of *T. lineola* F. and *T. similis* Macquart, species belonging to the *T. lineola* complex (Fairchild 1983), are both above 520 ovarioles per female (Leprince & Jolicoeur 1986). The arithmetic value of the fecundity index based on the number of ovarioles of *T. fuscicostatus* was 0.395, which was much higher than that for *T. quinquevittatus* (0.295), but was between that of *T. lineola* (0.446) and *T. similis* (0.391) (Leprince & Jolicoeur 1986). *T. fuscicostatus,* a subtropical species, proportionally has more ovarioles per unit of body size than *T. quinquevittatus,* a more temperate life-zone species. If the proportion of

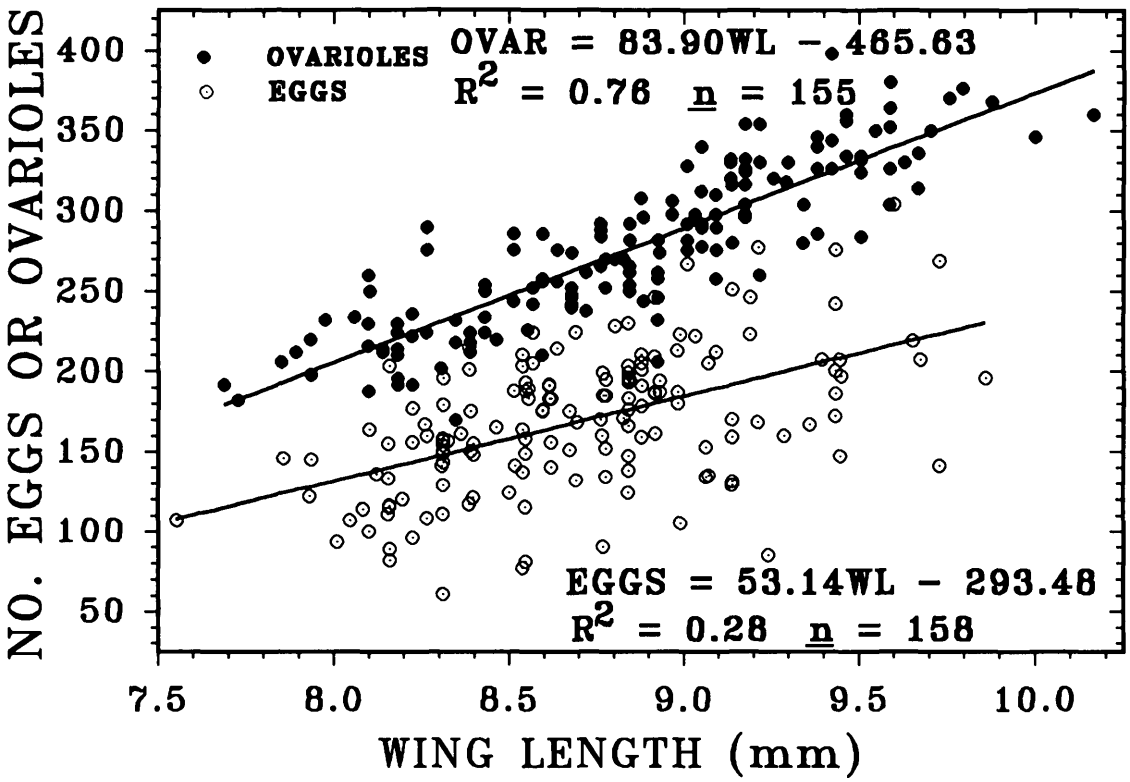

Fig. 3. The number of ovarioles (OVAR) and number of eggs (EGGS) of *T. fuscicostatus* plotted as a function of total wing length (WL). Overlapping observations are hidden.

follicles developing eggs is similar in both species, egg volume of *T. fuscicostatus* would be smaller than that of *T. quinquevittatus*. Therefore, northern tabanid species may invest more energy per egg than southern species.

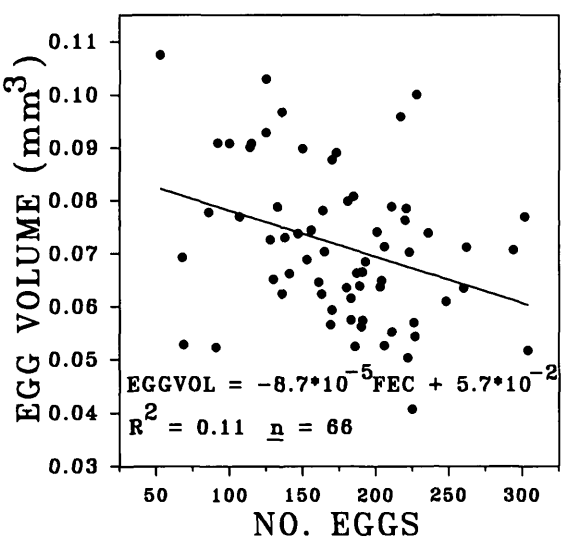

Fig. 4. Egg volume (EGGVOL) of *T. fuscicostatus* plotted as a function of the number of eggs produced (FEC).

In the Australian sheep blowfly, *Lucilia cuprina* (Wiedemann) (Webber 1955), and the autogenous *Chrysops atlanticus* Pechuman (Magnarelli & Anderson 1979), there is equivalence between the number of eggs produced and the number of ovarioles present. However, there is ample evidence in dipterans that some ovarioles fail to produce eggs. In gravid *Chrysops cincticornis* Walker, 15–50 ovarioles had no evidence of prior egg production or development of primary follicles (Magnarelli et al. 1982). In several *Tabanus* species, the number of ovarioles was well above fecundity reported under field conditions (Leprince & Jolicoeur 1986). In ceratopogonids, from 17 to 49% of the ovarioles failed to mature (Linley 1965, 1969). Egg production of *Anopheles maculipennis* Meigen gradually declines during successive gonotrophic cycles (Detinova 1962), indicating a decrease in the number of functional ovarioles through successive gonotrophic cycles. Considering the volume that is occupied by blood in engorged *T. fuscicostatus*, it seems unlikely that 37% more blood could be ingested to permit the development of eggs for the remaining ovarioles. Perhaps the excess number of ovarioles in *T. fuscicostatus* females is used to replace nonfunctional ovarioles in subsequent ovarian cycles, an adaptation to an anautogenous life-style.

Age-grading techniques used for tabanids (Leprince et al. 1992) often rely on dilations (follicular relics) at the base of follicles as an indication of prior oviposition. Because eggs developed in only 63% of the ovarioles possessed by *T. fuscicostatus* females, detection of follicular relics in most, but not all, ovarioles is sufficient evidence of completion of a gonotrophic cycle for this species. Furthermore, detection of multiple dilations in a single ovariole may be hampered by the low number of ovarioles producing eggs during each ovarian cycle. Based on an extreme scenario where a parous female would ingest another full blood meal, all inactive follicles of a previous gonotrophic cycle (37%) could develop an egg along with 26% of the ovarioles previously recruited in the preceding ovarian cycle. In the latter case, evidence of completion of two gonotrophic cycles, as detected by the presence of two dilations, would only be present in 26% of the ovarioles examined.

Frequently, *T. fuscicostatus* has been used in studies on the mechanical transmission of disease agents, insecticide evaluation, and basic biology. This fly is abundant, responds well to carbon dioxide–baited traps, and bovids, and readily feeds on hosts under experimental conditions. Our study describes the relationships among body size, blood meal size, unfed and engorged weight, number of ovarioles, and number of eggs produced, providing baseline data on the reproductive biology of this species. This information will be useful in the interpretation of future studies on the sublethal effects of insecticides and the use of age-grading techniques.

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