

# THE RELATIONSHIP BETWEEN ENGORGED FEMALE WEIGHT AND EGG NUMBER IN IXODID TICKS: A BIOLOGICAL INTERPRETATION OF LINEAR REGRESSION PARAMETERS

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IXODIDAE  
ENGORGED FEMALE WEIGHT  
EGG NUMBER  
LINEAR REGRESSION

**SUMMARY:** : The relationship between the weight of engorged females of ixodid ticks and the number of eggs they produce is considered, using both our own data and numerous literature data. There are three critical weights during female engorgement, which are followed by a change in the relationship of female weight/egg number. When the females acquire an initial weight ( $W_1$ ) after which they are able to lay eggs, they produce a constantly increasing number of eggs per unit weight (partially-engorged females). After the females acquire weight  $W_2$ , they produce a constant number of eggs per unit weight (fully-engorged females), and after reaching the weight  $W_3$ , they produce a diminishing number of eggs per unit weight (over-engorged females). In the linear regression between female weight ( $x$ ) and egg number ( $y$ ) ( $y = a + bx$ ), used in most studies of tick life history, the X-axis not only expresses the whole range of weights (thus mixing together females of all groups, even those which do not produce eggs at all), but also includes non-existing weight values, from 0 to the mean weight of an unfed female. Under these conditions, the parameters  $a$  and  $b$  have no biological meaning, since the linear dependence between female weight and egg number is only valid for fully-engorged females. This means that 0 on the X-axis must correspond to the very beginning of the linear dependence. The regression should only be computed over the part of the X-axis with weights of fully engorged females, where the relationship of female weight/egg number is truly linear ( $Y', X'; W_2, 0'$ ), thus making both parameters informative:  $a$  corresponds to the number of eggs laid by a fully engorged female with a minimal possible weight ( $W_2$ ) and  $b$  is the number of eggs produced per unit of weight increase. Hence, this is a simple way to take into account the real limits of the linear relationship between  $y$  and  $x$  values and to transform the regression, such that its parameters can be interpreted biologically.

IXODIDAE  
POIDS DE FEMELLES GORGÉES  
NOMBRE D'ŒUFS  
RÉGRESSION LINÉAIRE

**RÉSUMÉ :** Le rapport entre le poids de femelles gorgées d'Ixodidae et la production d'œufs est étudié, à partir de nos propres données et de données publiées. Trois poids critiques des femelles sont suivis d'un changement du rapport poids/nombre d'œufs : quand les femelles atteignent le poids initial de ponte ( $W_1$ ), elles produisent un nombre constamment croissant d'œufs ; après avoir

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atteint le poids  $W_2$ , le nombre d'œufs est constant par unité de poids (femelles gorgées) ; au-delà du poids  $W_3$  (femelles surgorgées), le nombre d'œufs produit par unité de poids diminue. Dans la régression linéaire du poids des femelles et du nombre d'œufs ( $x$  et  $y$  respectivement), utilisée couramment dans les études du cycle biologique, l'axe des abscisses exprime tout le registre du poids et toutes les femelles ne sont pas distinguées  $y$  compris celles qui ne pondent pas d'œufs. L'analyse inclut des valeurs sans existence réelle de 0 au poids moyen d'une femelle non nourrie. Les paramètres  $a$  et  $b$  sont donc dépourvus de toute signification biologique. La valeur 0 de cet axe doit correspondre au début de la relation linéaire. La régression ne doit être calculée que sur le segment de l'axe des  $X$  qui contient les femelles pleinement gorgées, et où la relation entre le poids et le nombre d'œufs produit est réellement linéaire. Ce calcul rend informatifs les deux paramètres  $a$  et  $b$  :  $a$  correspond au nombre d'œufs pondus par une femelle gorgée du plus faible poids possible, et  $b$  à celui produit par unité d'accroissement pondéral. Une méthode simple prenant en considération les limites de dépendance linéaires de  $x$  et  $y$  est proposée ainsi que de transformer la régression afin de rendre les paramètres interprétables biologiquement.

## INTRODUCTION

Ixodid ticks are temporary ectoparasites, feeding only once at each active developmental stage. A reduction in the number of gonotrophic cycles in female ticks to just one is compensated for by a considerable increase in the number of eggs produced by a female, which is made possible by the enormous amount of blood engorged during prolonged feeding (BALASHOV, 1967, 1984). The elucidation of features of female engorgement and oviposition is an essential part in the study of tick life-histories. At the same time, these processes are the primary targets of acaricides and the reproductive output is used as a measure of efficacy of acaricidal impact.

The weight of an engorged female, as well as the number of eggs produced by the female, are the most important variables measured. In most studies, the number of eggs increases roughly linearly with increasing weight of an engorged female. This relationship is described as a linear regression

$$y = a + bx$$

which consists of two variables—the engorged female weight  $x$ , and the egg number  $y$ —and two parameters—a constant term  $a$ , and the regression coefficient  $b$ . The possibility of biological interpretation for individual parameters of equations describing relationships between biological variables has

always been considered a strong advantage over formal mathematical descriptions of such relationships (GOULD, 1966; D'ARCY THOMPSON, 1966; MINA, 1975). Such an interpretation should be easier when the regression parameters are calibrated in the linear range, as in the present case. However, in all publications concerning the relationship of female tick weight/egg number, the computed regressions have been given without any comments, as just a formal mathematical description, and no attempt has been made to compare different regressions. The  $a$  values often differed greatly, even having a reversed sign for the same tick species, in studies by the same author. However, as far as we are aware, no attempt has been made to provide an explanation for this phenomenon. In order to clarify this question, data on the engorgement and oviposition of different tick species from our studies, combined with those from obtained by other authors, were considered. In fact, this is an attempt to look at some known facts from an angle different from that routinely used.

## MATERIALS AND METHODS

Numerous data were available to us on the engorgement and oviposition of the taiga tick *Ixodes persulcatus* Schulze from a forest area in the Russian Far East. We also had some data on the engorgement and

oviposition of two other tick species, *Dermacentor silvarum* Olenev and *Haemaphysalis concinna* Koch, from the same area. The techniques of tick collecting, maintenance and feeding in the laboratory, as well as obtaining the necessary data, have been described elsewhere (USPENSKY *et al.*, 1975; IOFFE & USPENSKY, 1985; IOFFE-USPENSKY *et al.*, 1997). Unfed females were fed on the back of rabbits in linen bags, together with an equal number of males. Apart from the data on normally-engorged female *I. persulcatus*, we also had data on oviposition by females that were not completely replete. Females still on the host after 13 days of attachment were forcibly detached, weighed and observed individually

for ability to oviposit. Data on the regressions and the reproduction efficiency indices (REI = the number of eggs per unit weight of the female body [BALASHOV, 1957; DRUMMOND & WHETSTONE, 1970]) from our studies and compiled from the literature were compared. Only the data obtained from at least two different evaluations for the same species were used for the comparison.

## RESULTS AND DISCUSSION

### *Relationship of female weight/egg number: expression by a traditional technique*

| Computed regression                |                   |                               |   |
|------------------------------------|-------------------|-------------------------------|---|
| Species                            | REI               | $y = a + bx$                  | Authors   |
| <i>I. persulcatus</i> <sup>a</sup> | 8.1               | -568.1 + 9.7x                 | USPENSKY & IOFFE-USPENSKY, unpublished  |
|                                    | 8.5               | 677.8 + 6.5x                  |   |
|                                    | 8.0               | -646.8 + 10.1x                |   |
| <i>I. ricinus</i> <sup>b</sup>     | 8.0 <sup>c</sup>  | -447.2 + 9.4x                 | HONZAKOVA <i>et al.</i> , 1975  |
|                                    | ND                | 320.5 + 7.3x                  |   |
|                                    | ND                | 9.0 + 7.4x                    |   |
| <i>D. variabilis</i>               | 8.6 <sup>c</sup>  | 191.5 + 7.7x                  | NAGAR, 1968   |
|                                    | 8.3               | 50.0 + 8.2x <sup>d</sup>      | DRUMMOND <i>et al.</i> , 1971   |
|                                    | 8.1               | -548.0 + 9.5x <sup>e</sup>    |   |
|                                    | ND                | -1,951.3 + 5.1x <sup>f</sup>  | CAMPBELL & HARRIS, 1979   |
| <i>R. sanguineus</i>               | ND                | -2.6 + 7.0x <sup>f</sup>      | SWEATMAN, 1967<br>NAGAR, 1968<br>KOCH, 1982<br>IOFFE-USPENSKY <i>et al.</i> , unpublished<br>DAVEY <i>et al.</i> , 1980 |
|                                    | 10.6              | -255.5 + 11.5x                |   |
|                                    | 13.4 <sup>c</sup> | -77.1 + 13.9x                 |   |
|                                    | 15.2              | -340.0 + 17.3x <sup>d</sup>   |   |
|                                    | 17.1              | -267.0 + 18.3x <sup>e</sup>   |   |
| <i>Boophilus annulatus</i> (Say)   | 17.1              | 1,094.5 + 13.1x               | IOFFE-USPENSKY <i>et al.</i> , unpublished<br>DAVEY <i>et al.</i> , 1980  |
|                                    | ND                | -156.0 + 9.8x <sup>d</sup>    |   |
| <i>A. maculatum</i> Koch           | ND                | 976.0 + 7.7x <sup>e</sup>     | DRUMMOND & WHETSTONE, 1970  |
|                                    | 10.1              | -548.0 + 10.8x <sup>d</sup>   |   |
| <i>A. cajennense</i> (F.)          | 9.7               | -3,621.0 + 13.9x <sup>e</sup> | DRUMMOND & WHETSTONE, 1975  |
|                                    | 9.3               | -684.0 + 10.4x <sup>d</sup>   |   |
|                                    | 9.4               | 100.0 + 9.2x <sup>e</sup>     |   |

TABLE 1: Examples of computed regressions and REI values for female ticks of different species.

Some original values are approximated to 0.1; ND no data;

<sup>a</sup> Data on the same population of ticks in different years;

<sup>b</sup> Data on the different groups of ticks from the same sample kept under different environmental conditions during oviposition;

<sup>c</sup> Computed from data in the original paper;

<sup>d, e</sup> Ticks from a single sample, treated differently; eggs were counted daily (disturbed females) (<sup>d</sup>) or the number of eggs was computed after the end of oviposition from the ratio of weights of the whole batch and of a sample with a known number of eggs (undisturbed females) (<sup>e</sup>);

<sup>f</sup> Ticks from different hosts (rat and porcupine, respectively).

The data on the number of eggs laid by females of different weights are plotted on a graph with the X-axis expressing not only the whole range of possible tick weights, but also including non-existing weight values, from 0 to the mean weight of an unfed female. Thus, 0 is nothing more than a convenient graphical convention. The data obtained in our study of *I. persulcatus* are presented in Fig. 1. In this and many other cases (Table 1), the relationships have been described by linear regressions with significant correlation coefficients. However, the experimental  $a$  values fluctuate greatly and even reverse sign, not only for different species, but even for the same species in different years, or for various groups of ticks from the same sample either differently treated (when counting eggs) or kept under varied experimental conditions (Table 1). The coefficient  $b$  determines the slope of the regression line, i.e., the change in  $y$  per unit increase in  $x$ . Its values are close to the corresponding REI (Table 1), but never coincide, being either more or less than the REI values, depending whether  $a$  in the regression is negative or positive, respectively. Thus, neither  $a$  nor  $b$  can be adequately interpreted from the biological point of view.

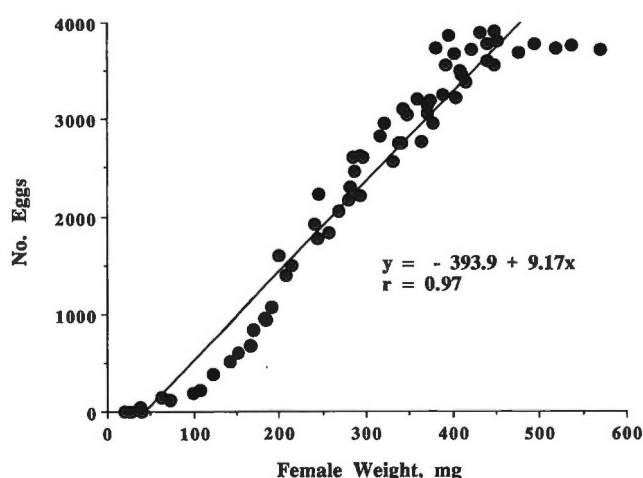


FIG. 1. Relationship between female weight and egg number in *Ixodes persulcatus*, described by linear regressions according to the traditional technique used in previous studies (*I. persulcatus* from the Russian Far East, laboratory feeding:  $n = 67$  females, including 17 partially-engorged, 45 fully-engorged and 5 over-engorged individuals).

As far as we know, the only attempt to clarify the biological meaning of  $a$  and  $b$  was made by NAGAR (1968), who transformed the regression equation to  $y$

$= b(x + a/b)$ . His further speculations were based on the values of the ratio  $a/b$  as a unit weight, though the entire idea of the above transformation looks unconvincing. For *R. sanguineus*, this ratio was found to be negative, while for *D. variabilis* (Say) it was positive. The negative value of the ratio was interpreted by NAGAR as the female body weight when the number of eggs laid becomes zero, whereas the positive value of the ratio, such as in *D. variabilis*, was considered an indication that the number of eggs in this species never becomes zero. The latter conclusion is illogical, since it presupposes oviposition by unfed female ticks, and even oviposition under conditions of non-existing weight values (less than the weight of an unfed female).

This case illustrates the weak point of such an approach. Since  $a$  corresponds to the intercept-point of the regression line with the Y-axis, it should be expressed in terms of egg number. Apparently, consideration of the relationship of female weight/egg number in the routine system of coordinates ( $X, Y; 0, 0$ ) *a priori* deprives the regression of any biological meaning, since it is impossible to expect any egg number ( $a$ ) when  $x = 0$ . In order to find an adequate interpretation for  $a$  and  $b$ , one should choose another X-axis ( $X'$ ) which would be crossed by the  $Y'$ -axis at a point corresponding to a tick weight sufficient for oviposition ( $x > 0$ ). In order to choose a proper  $X'$ , the relationship of female weight/egg number was considered for the whole range of female weights.

#### Critical weights of engorged females

In order to make this relationship more evident, the data on oviposition by engorged female *I. persulcatus* of different weights were expressed by REI (Fig. 2). First of all, the REI values begin to deviate from 0 only when  $x$  is somewhat larger than the weight of an unfed female. In the initial part of positive values, the REI increases gradually, steadily approaching its maximal value. Later, the mean values of REI do not change, the lines being roughly parallel to the X-axis. At the very end, there is a short interval where the REI decreases. Thus, the relationship of female weight/egg number for females in various degrees of engorgement consists of 4 parts: the area where  $REI = 0$ , the area of the gradual

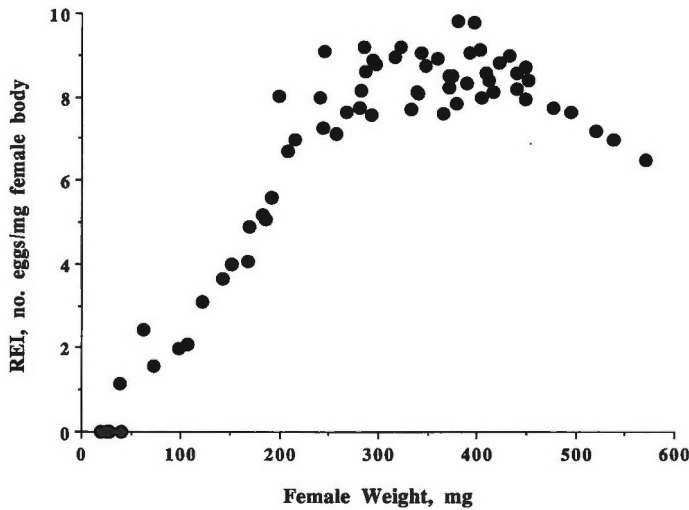


FIG. 2. Relationship between female weight and egg number in *Ixodes persulcatus* (data from Fig. 1) expressed through the relationship of female weight and REI.

increase of REI, the area of the stable REI, and the area of REI decrease. A similar dependence may be also found in the studies by KOCH & DUNN (1980) and by HUELI *et al.* (1988), though they expressed the egg production of *Amblyomma americanum* (L.) and *D. marginatus* Sulzer, respectively, by the conversion efficiency index (CEI = the weight of an egg batch per female weight [DRUMMOND & WHETSTONE, 1970]).

Hence, there are three critical weights of engorged females which are followed by a change in the relationship of female weight/egg number (Fig. 3). Females that have taken too small a blood meal (lighter than  $W_1$  or a critical weight value according to SNOW & ARTHUR, 1966) do not produce eggs at all. Partially-engorged females (heavier than  $W_1$ , but lighter than  $W_2$ ) produce a gradually increasing number of eggs per unit weight. Fully-engorged females (heavier than  $W_2$ , but lighter than  $W_3$ ) produce a constant number of eggs per unit weight. Over-engorged females (heavier than  $W_3$  or a maximum effective engorgement weight, according to DIPEOLU, 1991) produce a constant or even diminishing number of eggs, regardless of their weight, so that the number of eggs per unit weight is decreasing. Moreover, an excessive amount of blood engorged by a female may prevent oviposition entirely, as was shown for over-engorged *A. variegatum* (F.) (DIPEOLU *et al.*, 1991).

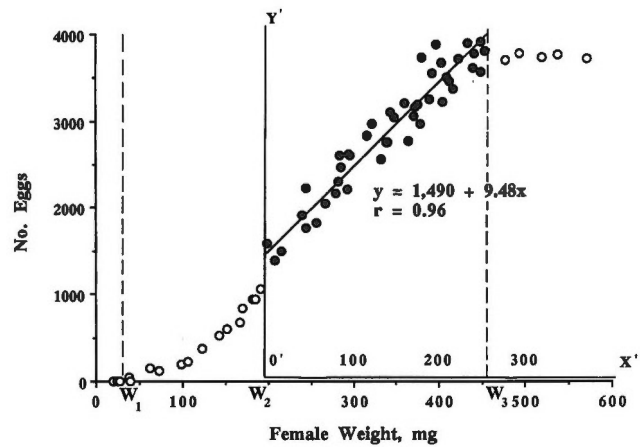


FIG. 3. Relationship between female weight and egg number in *Ixodes persulcatus*. Females of different degrees of engorgement (partly, fully and over-engorged) are divided into separate groups and critical weights, as indicated. The linear regression for fully-engorged females is computed according to the scale reflecting the parameters of this particular group of ticks.

The values of the critical engorgement weights for some species obtained in our studies, as well as those found in the literature, are presented in Table 2. According to BALASHOV (1967) and DIEHL *et al.* (1982), about 10% of the "normal" (presumably "mean",  $W_m$ ) engorgement weight are necessary for the beginning of oviposition ( $W_1$ ). The data in Table 2 coincide well with the above evaluation. The proportion of  $W_2$  of  $W_m$  is more variable, in some cases being as high as 55-60% (*I. persulcatus*) or even 70-75% (*H. concinna*) of  $W_m$  (Table 2). In other cases, the proportion of  $W_2$  is only 35-40% of  $W_m$  (*R. turanicus* and *Hyalomma asiaticum* Schulze & Schlottkie; BALASHOV, 1957). Females heavier than  $W_3$  are found quite often, but the range of their possible weights is not very large. The restriction in the number of eggs produced is explained by the limited number of oocytes in the female ovary (BALASHOV, 1967). For example, female *I. persulcatus* in our study did not produce more than 3,900 eggs regardless of their weight (Fig. 1). The particular values of the critical weights may depend on the conditions of tick feeding, such as host, season and laboratory conditions, and may differ between different populations of the same species or even different experimental samples. It is possible that they are in proportion with each other for one and the same species or population.



| Species                             | Mean weight<br>of fully engorged<br>females, mg <sup>a</sup> | Critical weights of engorged females, mg |         |         | Source of data                      |
|-------------------------------------|--|--|---------|---------|-------------------------------------|
|                                     |  | $W_1$                                    | $W_2$   | $W_3$   |                                     |
| <i>I. persulcatus</i>               | 344.0 ± 71.2   | 30-35                                    | 195-200 | 460-480 | Present study                       |
| <i>D. silvarum</i>                  | 403.5 ± 126.7  |  | <180    | >700    |                                     |
| <i>H. concinna</i>                  | 247.2 ± 37.7   |  | 175-185 | >380    |                                     |
| <i>R. sanguineus</i>                | 282.9 ± 46.0   |  | <215    | 380-470 | IOFFE-USPENSKY <i>et al.</i> , 1997 |
| <i>R. turanicus</i>                 | 174.0  | 15-20                                    | 60-75   | >300    | BALASHOV, 1957                      |
| <i>I. ricinus</i>                   | 257.0  | 25-30                                    | 100-105 | >300    |                                     |
| <i>Hy. asiaticum</i>                | 880.5  | 100-110                                  | 300-350 | >2,000  |                                     |
| <i>B. microplus</i><br>(Canestrini) | 216.5  | 17-20                                    | 100-110 | >370    | BENNETT, 1974                       |
| <i>A. americanum</i>                | 658.5  | <90                                      | 320-340 | >950    | KOCH & DUNN, 1980                   |
| <i>D. variabilis</i>                | 476.6 ± 191.5  |  | 115-125 | >820    | NAGAR, 1968                         |
| <i>D. marginatus</i>                | 500-550  |  | 220-240 |         | HUELI <i>et al.</i> , 1988          |

TABLE 2: Values of critical weights for female ticks of several species.

<sup>a</sup> Mean ± SD in the present study and computed from the data in NAGAR (1968); in other papers only data on mean weights are available.

In fact, a non-linear dependence between the weight of partly engorged females and the egg number, as shown in the present study, was noted by many authors. It can already be seen in the paper by ALLRED & ROSCOE (1956: Fig. 3) on *D. parumapertus* Neumann, which was apparently the first in which the relationship between female weight and egg number was discussed. A similar dependence was later observed by BALASHOV (1957), KITAOKA & YAJIMA (1958), BENNETT (1974), SCOTT & BROWN (1986) and DIPEOLU (1989) for many other species of ticks. In practice, however, these data have never been taken into consideration. The linear extrapolation of the regression to the X-axis intercept and the explanation of the intercept as the minimal weight of a female capable of laying eggs, was made in many studies (beginning with that of SNOW & ARTHUR, 1966). Such an extrapolation presumes the linearity of the relationship of female weight/egg number in the whole range of female weights. Meanwhile, these extrapolations were only made for cases in which  $a$  has a negative value, i.e., when the regression line intercepts the X-axis in the area of positive values, and never when  $a$  is positive, in which case such an extrapolation would lead to an illogical explanation (see NAGAR, 1968).

*Linear regression for fully engorged females with biological interpretation of its parameters*

As shown above, the linear regression is only valid for fully-engorged females (with weights between  $W_2$  and  $W_3$ ). In order to correspond fully to this particular group, the regression should be computed over only that part of the X-axis where the relationship between female weight and egg number is truly linear. In this regression,  $y$  remains the egg number, but  $x$  is now expressed as the weight increase from  $W_2$ , thus assuming that  $W_2 = 0$ . The Y'-axis for this case is moved to point  $0'$  ( $W_2, 0$ ) (Fig. 3). As a result, both parameters of the regression are now informative. Thus,  $a$  corresponds to the number of eggs laid by a female whose weight is  $W_2$  (the very beginning of the linearity), and  $b$  is the number of eggs produced by females per unit of weight increase when all additional blood is utilized for egg production (net growth of productivity). In this case,  $b$  corresponds to REI since, in practice, if we consider this index as species-specific, it should be calculated only for fully-engorged females. Examples of regressions for fully-engorged females of different species from our study, computed under the above conditions, are presented in Table 3.

Thus, the linear approach to the description of the relationship of female weight/egg number is possible only for a limited range of engorged female weights. The relationship for the entire range of female weights is obviously non-linear. An attempt to describe it will be presented elsewhere.

| Species               | $W_2$ , mg | Regression $y = a + bx$   |   |
|-----------------------|------------|---|---|
|                       |            | Computed for females of all weights using traditional technique | Computed only for fully engorged females under conditions $W_2 = 0$ |
| <i>I. persulcatus</i> | 195        | $-393.9 + 9.2x$   | $1,490 + 9.5x$  |
| <i>D. silvarum</i>    | 180        | $16.9 + 11.1x$  | $2,140 + 10.8x$   |
| <i>H. concinna</i>    | 180        | $-758.0 + 12.5x$  | $1,750 + 9.3x$  |

TABLE 3: Regressions describing the relationship between female weight and egg number, computed by different techniques.

### *Universal nature of the relationship between female weight and egg number*

We know only three studies in which the authors found no significant positive correlation between the female weight and egg numbers or egg batch weight. Each of them seems to have its own explanation. The conclusion drawn by SWEATMAN & KOUSSA (1968) is based on a limited number of female *R. sanguineus* studied for other purposes. (In an earlier paper by SWEATMAN [1967] the relationship between female weight and egg number was clearly described by a linear regression.) The lack of a relationship between the female weight and egg number in *A. variegatum* found by YONOW (1995) seems to be a result of a methodologically incorrect combination of data for different populations of the same species, studied under different conditions, over a very wide range of weights. In the original publications used by YONOW, a positive correlation between these variables had been found.

Much more intriguing are the data for *D. variabilis* and *A. americanum* obtained by SONENSHINE & TIGNER (1969), who found no apparent relationship between these variables. For a long time, this fact was mentioned without any explanation. BARNARD (1988) later found that the above relationship for field populations of *A. americanum* is not consistent and fluctuates during the year, completely losing its significance in certain periods. Other possible explanations might be connected with a large proportion of ticks with low oviposition capacity (DIPEOLU, 1991) and/or of over-engorged females in the study of SONENSHINE & TIGNER (1969).

The positive correlation between female weight and egg number is a phenomenon found not only in ixodid ticks, but also in other bloodsucking arthropods, though its manifestation in ixodids with a single

prolonged feeding is characteristic if compared with the arthropods taking several short blood meals. The same relationship was found for argasid ticks (BALASHOV, 1962; MANGO & GALUN, 1977), as well as for some insects, such as mosquitoes (KLOWDEN & CHAMBERS, 1992) and conenose bugs (NORIEGA, 1992). Moreover, the relationship between body size and female fecundity is a widespread phenomenon, demonstrated for animals of various taxonomic groups (PETERS, 1983; REISS, 1989; HONEK, 1993; PREZIOSI *et al.*, 1996).

### CONCLUSION

The linear regression is widely used in biological literature for the description of many different relationships. However, as a rule, its use is not followed by either a biological interpretation of its parameters or a comparison of the equations for different events. This results from the fact that the regressions are mostly used over the standard X-axis without taking into account the real limits of the linear relationship between  $x$  and  $y$ . Only if the value of  $y$  makes sense under  $x = 0$  (when, for example,  $x$  is age), can the regression be interpreted biologically. In this paper, we have shown that there is a simple way to transform the regression so that its parameters can be interpreted biologically in any case.

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