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Hypotrachy in the Phytoseiidae: adaptation or phylogenetic constraint?

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INTRODUCTION

In a recent paper (Sabelis and Bakker, 1992) we calculated the optimal number of dorsal setae required to minimize somal contact with sticky structures, such as silken threads forming the chaotically structured web spun by two-spotted spider mites. This calculation was based on two vital assumptions: (1) full avoidance of somal contact is achieved when the imaginary central axis is fully covered by the projections of the dorsal setae on this axis; and (2) investment per seta is proportional to setal length to the power 3 (which holds only when the seta is cone-shaped and the setal diameter-length ratio is constant). While the first assumption is a gross oversimplification, the second assumption lacks support by hard data. In this paper we will (1) extend the optimality model to include a more general class of diameter-length relations with respect to dorsal setae, (2) present measurements of diameter-length relations in various genera of the Phytoseiidae and (3) predict the optimal number of setae for comparison with the actual number of dorsal setae. This test of the model will then be used to determine whether the number of dorsal setae in phytoseiid mites can be considered as an adaptation or a phylogenetic constraint.

OPTIMAL INVESTMENT IN SETAE

Suppose that (1) the central axis has length L , (2) each seta has length l and a hooked shape with e being the length of the part perpendicular to the soma and $l - e$ being the length of the remaining part parallel to the soma, (3) the setae are standing in a longitudinal row, are equal in length and their projections on the central axis (l') do not overlap. Finally, suppose that (4) the per seta investment in terms of resources (r) is proportional to the volume of a cone with length l and diameter d and that (5) because d and l should pass through the origin, the functional relationship is of the

form $l^a = \alpha d$, where α and a are specific constants for the setae of the mites under study. Based on the last two assumptions total resource investment in setae (R) obeys the following relationship:

$$R = n \quad r = n \beta l^b, \text{ where } b = 2a + 1 \text{ and } \beta = \frac{\gamma \pi}{12\alpha^2}$$

Here, γ is a constant of resource-volume proportionality.

To obtain 100% protection over the full length of the central axis (L) without overlap of setae the number of setae should be equal to L divided by the projection length per seta: $n = \frac{L}{(l-e)}$ or $l = e + \frac{L}{n}$. The optimal number of setae is now found by minimizing total resource investment R with respect to L :

$$R_{min} = \min \left[n \beta \left(e + \frac{L}{n} \right)^b \right]$$

The first derivative of R with respect to n yields:

$$\frac{dR}{dn} = \beta \left[\left(e + \frac{L}{n} \right)^b - nb \left(e + \frac{L}{n} \right)^{b-1} \left(\frac{L}{n^2} \right) \right]$$

Setting the first derivative equal to zero some algebraic manipulation leads to the following unique solution for n :

$$n = (b-1) \frac{L}{e} = 2a \frac{L}{e}$$

This solution represents the number of setae that minimizes R (the second derivative with respect to n is always positive!). Note that this solution differs by a factor 2 from the one presented in Sabelis and Bakker (1992); this was caused by an incorrect change of sign ($n - A$ in equation 4 of the Appendix should have been $n + A$).

This result shows that optimal investment in setae depends on (1) the difference ($= e$) between setal length and its projection on the central axis, and on (2) the type of non-linearity (a and thus also b), but not on the details of proportionality (α and thus also β) in the functional relationship between setal diameter and length. Hence, it is important to estimate the power for assessment of the type of non-linearity.

DIAMETER-LENGTH RELATIONS IN DORSAL SETAE

Using a light microscope with an ocular provided with a metric scale (0.25 μ) the diameter and length of dorsal setae (j1, j3, j4, j5, j6, J2, z2, z4, s4, s6, Z1, Z4, Z5,

S2, S4, S5) were measured in slide-mounted specimens of the following species and genera of the Phytoseiidae: 2 *Phytoseius* spp. (*Phytoseius hawaiiensis* and *macropilis*), 11 *Amblyseius* spp. (*Amblyseius andersoni*, *barkeri*, *bibens*, *cucumeris*, *andersoni deleoni*, *finlandicus*, *graminis*, *idaeus*, *massei*, *reductus* and *teke*), 5 *Typhlodromus* spp. (*Typhlodromus aberrans*, *annectens*, *okanagensis*, *porresi* and *pyri*), and 6 specimens of *Phytoseiulus persimilis*.

The exponent a in the expression $l^a = \alpha d$ was estimated by means of linear regression after taking logarithms at both sides and rewriting the expression as:

$$\ln(l) = \frac{1}{a} \ln(\alpha) + \frac{1}{a} \ln(d) = \text{constant} + \text{slope} \ln(d)$$

From the slope of the regression the exponent a can be calculated, whereas α can be obtained from the constant. The results are presented in Table 1. Most remarkably, the slopes of three regression lines for *Amblyseius*, *Typhlodromus* and a single species in the genus *Phytoseiulus* are quite similar! This suggests that the structure of the setae in these three genera have much in common. That the data on *Phytoseius* do not conform to this pattern does not come as a surprise as the structure of their dorsal setae is strikingly different; they are very thick and strongly serrated. If we ignore *Phytoseius* spp., it can be concluded that the most simple and best fitting model to describe the relation between diameter and length for the other three genera is $l^a = \alpha d$ with $\alpha = 5.7$ and $a = 0.64$.

A FUNCTIONAL VIEW ON HYPOTRICHY IN THE PHYTOSEIIDAE

Under the assumptions in Sabelis and Bakker (1992) model correction leads to a twofold increase in n^* . However, the estimate of a appears to be lower than the value $a=1$ taken in Sabelis and Bakker (1992) and therefore leads to a reduction in

TABLE 1

Estimates of the exponent a from linear regression of $\ln(l)$ on $\ln(d)$ (i.e. the natural logarithms of the length and the basal diameter of dorsal setae). SE = standard error; R^2 = squared correlation coefficient; N = number of data pairs.

Genus	Constant (SE)	Slope (SE)	R^2	N	a
<i>Phytoseius</i>	2.300 (0.092)	1.067 (0.068)	0.936	19	0.937
<i>Typhlodromus</i>	2.725 (0.046)	1.424 (0.068)	0.875	65	0.702
<i>Amblyseius</i>	2.634 (0.034)	1.632 (0.056)	0.833	172	0.613
<i>Phytoseiulus</i>	2.791 (0.064)	1.639 (0.064)	0.907	69	0.610

n^* . Thus, the two modifications have opposite effects on the optimal number of setae and the following formula for n^* results:

$$n^* = 1.28 L/e.$$

This formula is instrumental in inferring whether phytoseiid mites are hypotrichous from a functional point of view. For central axes varying in length (L) from 250 to 350 μm and for e being maximally 10 μm , the optimal number of setae for 100% protection of either the margino-dorsal or the mid-dorsal region varies from 32 to 45 (for a definition of the two categories of dorsal setae see Sabelis and Bakker, 1992). Clearly, Phytoseiidae with maximally 10 margino-dorsal and 12 mid-dorsal setae do not fall within this range. For this number of setae to be optimal the exponent a should be in the range of 0.13 to 0.24, which is definitely much lower and far outside the range of the values estimated from the diameter-length measurements. Note in addition that for *Phytoseius* with an exponent a larger than 0.64 the difference between predicted n^* and the actual number of setae is even more pronounced!

From a phylogenetic point of view evolution of idiosomal setation in the Phytoseiidae has proceeded largely through irreversible setal suppression from a holotrichous ancestor (Chant, 1993). Because of this reduced number of setal positions Phytoseiidae are referred to as being hypotrichous. From a functional viewpoint hypotrichy can be expected to evolve when the need for idiosomal protection is small. Foraging on glabrous leaves represents a case where the risk to get stuck is very low and a reduction in the number of setal positions might actually lead to increased fitness. Hence, if the ancestral phytoseiid mites foraged on glabrous leaves, hypotrichy is likely to have evolved. However, due to the irreversible nature of the setal suppression a reduced number of setal positions may become a constraint when the foraging environment changes such that there is a need for increased protection of the idiosoma; for example, when phytoseiid mites may find profitable prey/food on pubescent leaves or in chaotically structured webs. Thus, the Phytoseiidae may have been trapped in an evolutionary path to hypotrichy and had no option but to lengthen the setae still present.

While the optimal allocation model is elegant due to its simplicity, it is not yet clear whether its predictions can stand up to scrutiny. Soil-inhabiting mesostigmatic mites, for example, basically have a larger number of setal positions (e.g. *Lasioseius alii* Chant has 20 mid-dorsal and 16 margino-dorsal setae; see Lindquist and Evans, 1965) and their soil environment presumably requires full protection, but the larger number of setal positions is still lower than the optimum n^* , predicted by our model. Thus, there is much room for a more elaborate model that takes into account that setae have a bended rather than hooked shape, that they are positioned on a hemisphere, not in perfectly straight rows and not equidistantly, that setal structure and protection effect may depend on the type of environment (i.e. the exponent a is not a fixed constraint!) etc. However, if we succeeded in outlining a quantitative approach

to understand evolutionary trends in setal arrangement, we have reached our main goal.

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