

SELECTION OF FECUNDITY IN DERMACENTOR VARIABILIS UNDER HARSH ENVIRONMENTAL CONDITIONS

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Abstract. The increase of female size reflects an increase of fecundity under the harsh environmental conditions of newly colonized areas. Restriction of the effective reproductive population selects for increased fecundity. A stepwise extension of the species range is postulated to occur by first the availability of marginal habitats and secondly the increase in fecundity to increase the population in these harsh habitats.

An increase of *Dermacentor variabilis* female, but not male, size was found inland across eastern Massachusetts from the coastal area of Cape Cod (McEnroe 1974a). The Cape included the original area of infestation and the species range has spread inland from 1945 (McEnroe 1974b). This study proposes that the increase of female size was a response to selection for increased fecundity.

The number of eggs of *D. variabilis* laid in a single clutch varies between 700—7000. Oviposition requires a blood meal taken by the female from its host. This engorgement results in ca a 70× increase of female weight. There is a linear relationship between the clutch size and the engorged weight (Nagar 1968, Drummond et al 1971). One factor that allows for the intake of this large volume is the stretching of the cuticle achieved by a flattening of the epicuticular folds (Arthur 1961). That is the size of the female presumably predetermines the volume increase and thus the clutch size.

The female size was related to a scutal index (SI), the length times width of the scutum in mm^2 × 48. This index can be used to compare flat and engorged ticks because the scutum remains at constant size during engorgement (Amin 1969a). Twenty engorged females were collected from dogs when they were easily detached, a sign that the ticks have finished feeding and ready to drop off. Three engorged ticks were from the Rocky Mountain Laboratory culture. The engorged females were held at 25° and saturation and their oviposit converted to clutch size with the factor of average egg weight of 70 μg (Amin 1969b). The linear relationship number of eggs = $-3506 + 47.6 \text{ SI}$; $r = 0.704$ (range SI 88—212) was found by regression analysis with the Texas Instruments 58/59 linear analysis program.

Probit plots of frequency versus SI for populations are in Fig. 1. Hatchville, on Cape Cod, was within the original species range. Infestations progressing inland were noted as follows: Lincoln 1953, Bolton 1967, and Princeton 1976. At probit 50% there is an increase of SI from 141 to 172. This indicates an increase of clutch size from 3206 to 4681. The size distribution appears to reach an upper limit with a decrease of the frequency for the smaller sizes.

Winter survival requires either a distribution of days with means above 2 °C that the tick's water vapor pump can operate and prevent desiccation or a near saturated microenvironment (McEnroe 1975, 1978, 1979). The original range was limited to the immediate coastal area within the average 0°C winter isotherm and here the occurrence of continuous snowcover during the limited periods below an average of 0°C was followed by a doubling of adult seasonal activity over years with winter means below 0°C but with bare ground conditions (McEnroe 1979). In inland Massachusetts, where three winter monthly means are below 0°C, the snow-free winter of 1979—80 with ca normal means was followed by a population crash of these inland populations (McEnroe, in press).

In the coastal area, with its mild winter, the absence of snowcover has only a small effect on tick populations, but in the interior with its harsh winter climate, snowcover appears to be a requirement for the maintenance of the marginal populations found in this area.

The slow continuous inland expansion of the species range over ca 140 km during the past 32 years and 16 generations argues against the random introduction of tick

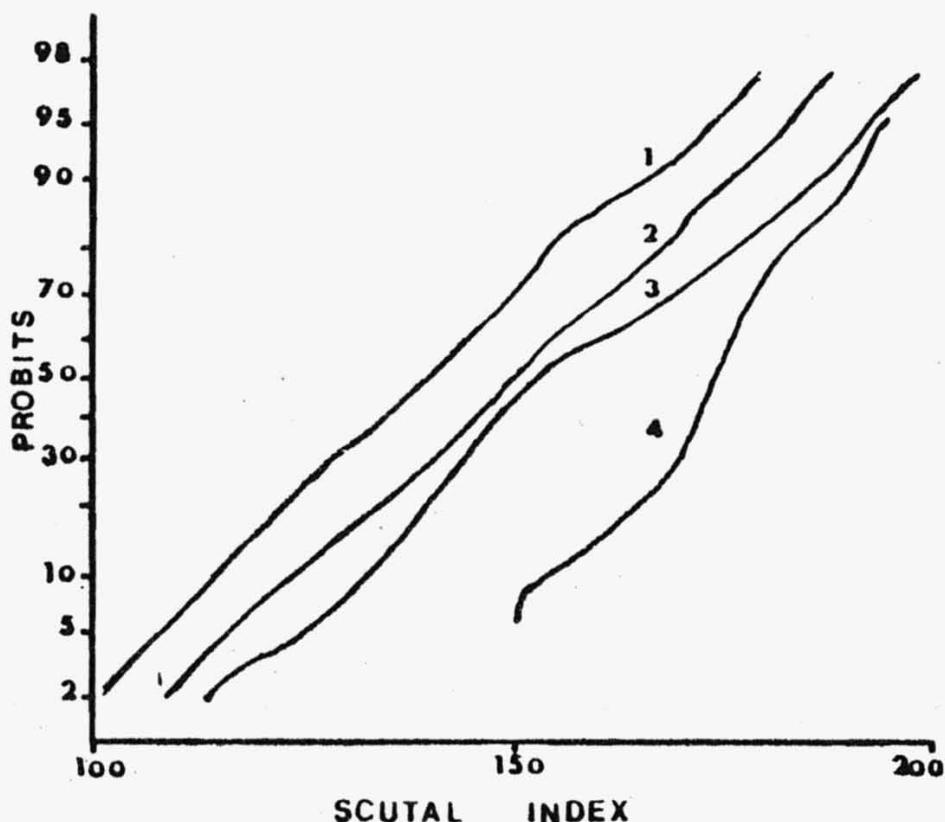


Fig. 1. Probit plot of frequency versus scutal index. 1. Hatchville, Cape Cod, 100 females from 1971 season. 2. Lincoln 100 females from 1971 season. 3. Bolton 100 females from 1971 season. 4. Princeton 49 females from 1978 and 1979 season. No trace of this small infestation was found in 1980 after a snowfree winter. This transect from the coastal area inland includes a decline of average mean winter temperature from 0 °C to -3 °C with an increase of 1 to 4 average monthly means below 0 °C. From the coastal area inland there is a shift in average maximum temperature and 1 PM average relative humidity for May—August, the period of adult activity, from 20.6 °C, 83 RH, to 25.4 °C, 52.5 % RH.

infestations by dogs moved from the cape (the common explanation for new infestations). Ticks planted outside their range were unable to continue their development and establish an infestation (Daniel et al 1977). In inland areas, the number of effective breeding females is not only limited to those females picked up by a host but is also limited to those engorged females dropped in the winter survival area. Pet dogs, with their restricted territories fulfill this host requirement. In this region there are alternate spring and summer adult cohorts. In the Cape Cod area the summer cohort is less restricted in size with the level of summer activity approaching the level of spring activity. Inland the level of summer activity is greatly reduced (McEnroe 1974c, 1979). Under inland conditions the summer cohort acts as a wasp waist on the population size. Selection for fecundity occurs because of the restriction present on the number of reproductive females for these localized infestations.

With increasing suburbanization the presence of pet dogs made available marginal habitats with selection for increased fecundity. The expansion of the species range then

occurred in a stepwise fashion with increasing fecundity allowing the tick to occupy new marginal habitats with harsher winter conditions. That is, the ticks first required the availability of the new marginal habitats to respond to the increased level of selection for increased fecundity.

This increase of female size, outside the original range, fits Roughgarden's postulate for r selection under constant harsh environmental conditions (Roughgarden 1970). The reciprocal response also occurs as Daniel et al. (1977) found decreased fecundity in laboratory ticks reared under natural conditions.

ОТБОР ПО ПЛОДОРОДНОСТИ У *DERMACENTOR VARIABILIS* ПРИ СУРОВЫХ УСЛОВИЯХ ОКРУЖАЮЩЕЙ СРЕДЫ

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Резюме. Увеличение размера самки отражает повышение плодородности при суровых условиях окружающей среды в новозаселенных областях. Ограничение эффективной плодородной популяции влечет за свой отбор по повышению плодородности. Постепенное расширение ареала вида обусловлено во первых наличием маргинальных биотопов и во вторых повышением плодородности для роста популяции в таких суровых условиях.

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