# Host Resistance to the cattle fever tick *Boophilus microplus:* A simulation model

Mary K. Matella
University Undergraduate Fellow, 1995-1996
Texas A&M University
Department of Wildlife and Fisheries Sciences

Approved
Fellows Advisor W. E. Grant
Honors Director [signature]

# HOST RESISTANCE TO THE CATTLE FEVER TICK *BOOPHILUS MICROPLUS*: A SIMULATION MODEL.

Mary K. Matella (William E. Grant), Wildlife and Fisheries Sciences, Texas A&M University.

I describe addition of a submodel representing dynamics of host resistance to the cattle fever tick (*Boophilus microplus*) to the simulation model of host-parasite-landscape interactions developed by Teel et al. (1996). The new submodel represents acquisition and loss of host resistance as a function of breed of cattle and history of exposure to ticks. The entire model is formulated as a deterministic compartment model based on difference equations and runs with a daily time-step. Model evaluation consisted of examining (1) ability of the new submodel to represent basic dynamics of host resistance in a manner consistent with available information and (2) sensitivity of model predictions of host resistance to changes in values of key model parameters. When host resistance rises above the naive level, the number of ticks sustained on the host are reduced and a constant, lower number of ticks are maintained on the animal. The maximum resistance capacity varies according to breed and is the most sensitive component used in calculating the relative resistance mortality factor that increases larval mortality. Thus the new submodel appears to integrate available information on cow resistance to ticks in a manner capable of simulating the basic dynamics of resistance acquisition, maintenance, and loss.

## I. Introduction

Control of the cattle fever tick *Boophilus microplus* is of great economic importance (Sutherst et al. 1979a, Nuñez, et al. 1985, Amoo &

Dipeolu 1992). Effects of the cattle tick on hosts include reduced live weight gain, reduced fertility, and transmission of disease-bearing hemoparasites (Sutherst 1987). In the U.S. costs of managing for tick control amount to millions of dollars annually (Teel 1985). Besides affecting the beef industry, tick damage to animal hides inflicts great monetary losses to the tanning industry (Nuñez et al. 1985). In some areas of the world tick control is often necessary to prevent tick-induced mortality of cattle (Bourne et al. 1988, Sutherst et al. 1988b)

Methods of tick control include pasture spelling, planned dipping, and use of tick-resistant cattle. Due to increased tick resistance to acaricides, the use of natural host resistance to control tick populations and reduce the economic impact of the parasite has received renewed attention (Wharton et al. 1969, Seifert 1971, Sutherst et al. 1979a). Sutherst et al. (1979a) found that the best long-run tick control strategy is the use of tick-resistant cattle with single spelling periods or limited dipping.

The major determinant of tick population size is host resistance (Wharton et al. 1969). Resistance may be measured by assessing larval mortality, number of tick progeny, number of ticks feeding successfully, or size of fed ticks (George et al. 1985, Nuñez et al. 1985). Most studies quantify resistance expression as reduction in the number of ticks maturing on the host. Resistance causes density-independent mortality of larvae (Roberts 1968c, Sutherst et al. 1979a, Sutherst et al. 1979b). Mount et al. (1991) found that *Boophilus* tick population growth is very sensitive to small changes in host resistance levels.

Host resistance levels vary according to breed, season, nutrition, lactation, sex and age (Utech et al. 1978a, Sutherst et al. 1988a, Sutherst et al. 1988b). Sutherst et al. (1988b) found that the proportion of *B. indicus* genes is the strongest factor increasing tick resistance. The amount of resistance gained by a host varies according to breed, with individual variability within a herd being expressed (Roberts 1968a, Roberts 1968c, Hewetson 1971, Seifert 1971).

Resistance is innate and acquired to a threshold level dependent on genetic capacity (Roberts 1968a, Hewetson 1971). About 50% of the larvae complete their parasitic cycle on the majority of naive *Bos taurus* animals, but 8 days after infestation, animals acquire resistance and tend to maintain a constant number of ticks (Roberts 1968c). Previously exposed animals have immediate expressions of resistance (Roberts 1968a). *B. indicus* (Zebu) cattle have a higher level of acquired resistance to ticks than *B. taurus* (Hereford) animals. *B. indicus* X *B. taurus* crosses produce animals of higher resistance than purebred *B. taurus* (Wharton et al. 1969).

Ticks of the genus *Boophilus* express a one-host life cycle. Generally attacking large ungulate hosts, the tick develops from larvae to nymph to adult on the host. Engorged females then drop off into the environment to lay eggs. Hatched larvae later ascend vegetation to await passing hosts. This relatively simple life cycle and the wealth of research on these ticks provide ample information to create a simulation model of the host-parasite system (Teel et al. 1996).

A model simulating host-parasite-landscape interactions integrating temporal and spatial factors regulating tick populations on Mexico-U.S. border rangelands has been developed by Teel et al. (1996). The hosts in this model are represented as moderately resistant to ticks and do not have the ability to acquire and lose resistance as a function of history of exposure to parasites. In this present paper I add a submodel to the model of Teel et al. (1996) that predicts host resistance changes as a function of breed of cattle and previous exposure to ticks. More specifically, the new submodel modifies the representation of tick population dynamics by adding a resistance component to larval mortality.

## II. Model Description

*Overview of Entire Model*

Three submodels representing temporal and spatial interactions between ticks, the environment, and the host compose the model developed by Teel et al. (1996) (Fig. 1). The three submodels include (1) tick development in the environment, representing the off-host phases of the life cycle (pre-oviposition, oviposition, eggs, larvae) within each of three habitat types; (2) tick development on the cow, representing the acquisition of larval ticks, development and mortality of larvae, nymphs, and adults, and the drop of engorged females into the pasture; and (3) cow movement among habitat types.

The new submodel represents the acquisition and loss of host resistance as a function of breed of cattle (represented by maximum and naive capacity for resistance) and history of exposure to ticks, with changes in host resistance subsequently affecting mortality of larval ticks (Fig. 1). Thus the new cow resistance to ticks submodel is linked to the original model via the presence or absence of ticks on the cow, which determines the acquisition or loss of resistance, and a relative resistance mortality factor, which changes larval mortality.

The model is formulated as a deterministic compartment model based on difference equations and runs with a daily time-step using STELLA II (Version 2.2, High Performance Systems, Inc., Hanover, NH) on a MacIntosh II computer.

*Description of New Cow Resistance to Ticks Submodel*

Changes in host resistance to ticks is conceptualized in terms of a RELATIVE RESISTANCE MORTALITY FACTOR that changes via the ACQUISITION and LOSS of units of resistance (Fig. 1). If there are ticks on the cow, ACQUISITION is calculated as a function of the current RELATIVE RESISTANCE MORTALITY FACTOR, RESISTANCE ACQUISITION RATE, RESISTANCE ACQUISITION TIME LAG, and MAXIMUM CAPACITY of the breed to acquire resistance. If there are no ticks on the cow, LOSS is calculated as a function of the current RELATIVE RESISTANCE MORTALITY FACTOR, RESISTANCE DECAY RATE, RESISTANCE DECAY TIME LAG, and NAIVE CAPACITY, which represents the innate resistance of the breed. The RELATIVE RESISTANCE MORTALITY FACTOR adjusts the level of larval mortality (M) between a naive, minimum level and a maximum level, which is determined by breed.

Basic dynamics of the RELATIVE RESISTANCE MORTALITY FACTOR (RRMF) are illustrated in Figure 2. Upon infestation of a naive animal (RRMF = NAIVE CAPACITY), resistance acquisition begins after an ACQUISITION TIME LAG (ATL) and RRMF increases as a sigmoidal function until the animal reaches its MAXIMUM CAPACITY (MC) (Roberts 1968a, Roberts 1968c), which depends on breed (e.g. Utech et al. 1978b).

$$\text{ACQUISITION (units/day)} = RAR*RRMF*(MC-RRMF)/MC$$

where RAR is a constant representing maximum RESISTANCE ACQUISITION RATE. Although there are no quantitative data on acquisition rates, naive animals tend to gain resistance more slowly than previously-exposed animals (Roberts 1968a). With RAR=0.1 for infestation of naive animals and RAR=0.4 for infestation of previously-exposed animals, MC is reached between 20-30 days as suggested by Roberts (1968a). The ATL for naive animals is 8 days, but ATL is zero for previously-exposed hosts (Roberts 1968a). However, if a previously-exposed animal is tick-free for a year or more before being reinfested, the rate of gain is returned to its slower, naive acquisition rate (Teel, pers. comm.), although there is no time lag between infestation and resistance acquisition.

Breed is the most significant factor influencing cow resistance expressions (Seifert 1971, Utech et al. 1978b, George, et al. 1985, Sutherst 1988b). MC values of 1.1, 3.1, and 2.3 are used to simulate *Bos taurus* , *Bos indicus* , and *Bos taurus X Bos indicus* animals, respectively. These MC values produce RRMF values that, when multiplied each day of simulated time by the baseline larval mortality rate in the original model (0.30), result in host resistance levels, represented as the proportion of a cohort of larval ticks that has died by 20 days after infestation, comparable to values in the literature (Utech et al. 1978b) . Although resistance also is expressed at the instar stages of tick development, only larval mortality, which is the primary, most significant stage in which resistance is expressed (Roberts 1968c), is represented in the present model.

If a previously-infested host has been tick-free for a sufficient length of time (RESISTANCE DECAY TIME LAG, RDTL), RRMF declines, but at a different rate (RESISTANCE DECAY RATE, RDR) than it was acquired (Hewetson 1971) (Fig. 2). LOSS is hypothesized to be an exponential decay function.

LOSS (units/day) = RDR*RRMF

Cattle generally begin to lose resistance after ticks are absent for about 15 days (RDTL=15) and after 4 months a cow may lose all of its acquired resistance, that is, RRML will decay to the NAIVE CAPACITY (NC) (Teel, pers. comm). With RDR=0.005, in the absence of ticks RRMF decays from MC to NC during the suggested four months.

## III. Model Evaluation

Model evaluation consisted of examining (1) the ability of the new submodel to represent basic dynamics of RRMF in a manner consistent with available information on the acquisition, maintenance, and loss of host resistance and (2) sensitivity of model predictions of RRMF to changes in representation of key model parameters including MC, RAR, RDR, and RDTL.

### Basic resistance dynamics

To examine basic dynamics of RRMF and its influence on the number of ticks surviving on an initially naive cow, I simulated 4 infestations of 20,000 larval ticks each on days 15, 135, 195, and 380 of simulated time. After the first infestation, the RRMF increased rapidly but failed to reach its MC because ticks were not present on the host long enough for full RRMF expression (Fig. 3). After an appropriate time lag, RRMF began to decline. After the second infestation, the number of ticks on the cow fell and the RRMF reached its maximum capacity. During the third infestation the host's tick burden declined even more as the RRMF remained at maximum capacity because the short 2-month time span between infestations prevented loss of RRMF. After the fourth infestation, the number of ticks sustained on the host increased from the previous number, but remained reduced from the number of ticks sustained by the first infestation because RRMF increased at a quicker rate from a higher RRMF level.

Thus the new submodel appears to integrate available information on cow resistance to ticks in a manner capable of simulating the basic dynamics of resistance acquisition, maintenance, and loss.

Sensitivity Analysis

While many studies of host resistance to ticks have estimated host resistance levels, there are no quantitative data on rates of acquisition or loss of resistance. Thus, sensitivity of model predictions of RRMF dynamics to changes in MC, RAR, RDR, and RDTL was determined by running a series of 1-year simulations, each representing one naive cow infested with a moderate infestation of 20,000 ticks (e.g. Utech et al. 1978a) at days 15, 135, and 195. Simulations examining RAR, RDR, and RDTL were run varying the maximum breed capacity of hosts (MC) from 1.1 to 3.3 in 0.2 increments. Specifically, MC values of 1.1, 2.3, and 3.1 are used to simulate *B. taurus*, *B. taurus* X *B. indicus*, and *B. indicus*, respectively. The analysis consisted of a total of 144 simulations (Appendix 1). Results of the simulations were evaluated in terms of relative resistance mortality factor variations and their effect on the host resistance level (percentage tick mortality) on day 20 following initial infestation.

The distinction between the use of RRMF and the "resistance level" is essential because evaluation based on the literature is only possible in terms of resistance level. RRMF is the resistance measurement used in calculation of a varied larval mortality rate while the resistance level is used in evaluation of the effects of the RRMF. Assuming a 1:1 sex ratio, researchers counted engorged female ticks 18-22 days old on hosts to determine the resistance level measurement as the mean percentage of larval ticks which die before maturation as engorged females (Utech et al. 1978b). The model measures the resistance level as the median percentage of day 18-22 tick mortality, or the day 20 tick mortality. These day 20 mortality values correspond with the classifications of Utech et al. (1978b) who designated animals of certain breeds with high (>98 %), moderate (95-98 %), low (90-95%), and very low (<90 %) resistance. The average Herefords (*B. taurus*) were assigned a resistance of 85.6 % while Brahmans (*B. indicus*) were assigned a level of 99.0 %. The model predicts resistance within these resistance ranges.

The initial Resistance Acquisition Rate for a naive animal was set at 0.1, while Resistance Acquisition Rates for experienced hosts were tested at 0.4 and 0.8 levels (Fig. 4). At the RAR=0.8, animals gain resistance more quickly, reaching a higher resistance level, after the second infestation than do animals with RAR=0.4. The differences between resistance levels attained using each acquisition rate are relatively insignificant. The animals reach similar levels of resistance following the third infestation. Differences in resistance levels as a result of changes of RAR become more evident the higher the MC level is set.

The Resistance Decay Rates that were tested were 0.001, 0.005, and 0.008 (Fig. 5). Variation in resistance level among the three figures grew as MC increased, but resistance following the third infestation was only slightly lower with a RDR of 0.008 than 0.001. Differences in resistance levels as a result of changes of RDR also become more evident the higher the MC level is set. The MC level, or the threshold of the relative resistance mortality factor, is very sensitive to change within the 1.1-3.4 range. The MC is the factor with which animal breeds may be specified to produce expected resistance levels at day 20.

The Resistance Decay Time Lag, the period after all ticks drop off a host before it begins to lose resistance in the absence of ticks, was extensively tested at 15 and 60 days (Fig. 6). RDTL is insensitive to changes ranging from 15, 20, and 25 days. When RDTL was increased to 60 days, host resistance changes between infestations were reduced and resistance decay rates had no effect on the resistance levels achieved by the third infestations.

According to a tick expert (Teel, pers. comm.) the model is reasonable in terms of structure and model relationships. Model behavior corresponds with expected patterns of model behavior. Model predictions and the real data also correspond. The model is sensitive to changes in MC, the maximum limit of resistance set according to breed. Conclusively, this model reasonably addresses its objective of predicting host resistance changes as a function of previous exposure to ticks and breed of cattle.

## IV. Discussion

Although factors such as host age, sex, lactation, nutrition, and season affect resistance levels, only breed is accounted for in this model. The proportion of *B. indicus* genes is the strongest factor influencing resistance (Sutherst et al. 1988b), so it is reasonable to base the model's resistance predictions according to breed. Breed capacity for maximum resistance may be set in the model using the threshold level MC.

Simulations of three infestations begun at day 15, 125, and 195 were run in order to evaluate time lags and effects of loss of resistance on future resistance levels achieved. Resistance levels were determined by day 20 percentage survival of ticks because most studies evaluated resistance between days 18-22 following infestation. Studies were not always clear about how the resistance level was actually determined with data from days 18-22, so the model reading of day 20 is a median figure. Day 20 is an appropriate day to designate relative resistance because some ticks do begin dropping off the host in days 21-22 (Teel 1985).

The resistance acquisition rate for the first infestation of a naive animal was set at 0.1 and is relatively unimportant except in the sense that it is a slower rate than resistance acquisition rates following later infestations of previously-exposed animals. Magnitudes of rates are unknown as only trends have been identified in the literature to date. All animals reach the same resistance level of 85.54% following their first infestations because resistance only increases larval mortality in this model and it takes 8 days for resistance to begin to become expressed (Roberts 1968c). By the time the resistance is gaining expression, the larval ticks have matured to other stages of development and in the present model mortality of nymphs and adults is not affected by increased host resistance.

The base resistance level of 85.54% is a result of innate larval mortality which is set at 30%. This figure was determined in reference to Roberts (1968c) and Utech et al. (1978b). Roberts (1968c) identified innate larval mortality for *B. taurus* animals at 50% although he cited no specific data and included animals of mixed breeds in his study. Utech et al. (1978b) assigned resistance levels to the average animal of various breeds, setting *B. taurus* at a resistance level of 86%. In order to set the innate mortality to yield a resistance level of 86%, innate larval mortality was adjusted to 30%. While innate mortality of larvae may vary according to breed, all breeds are assigned the same innate mortality as they display their variations in resistance at second and third infestations.

The resistance submodel is valuable in that it may be integrated into models used to predict tick population dynamics on particular breeds of cattle. This paper presents analysis of resistance components in reference to the Teel et al. (1996) "tick development on cow" submodel. The resistance modifications would reveal their true value only if implemented and used in evaluation of tick population dynamics in various habitats. Future work examining the effects of resistance in this fashion are necessary.

**Acknowledgments**

I would like to thank my advisor Dr. William Grant, the tick expert Dr. Pete Teel, and the graduate student Michael Corson for their invaluable help in preparing this paper.

References


Amoo, A. O., and O. O. Dipeolu. 1992. Host Resistance to Ixodid ticks: Response of tick naive calves to repeated infestation with larvae of *Boophilus Decoloratus* (Koch, 1844) and *Boophilus gelgyi* (Aeschilman and Morel, 1965). *Insect Sci. Applic.*. 13 (6): 813-818.

Bourne, A. S., R. W. Sutherst, I. D. Sutherland, G. F. Maywald, and D. A. Stegeman. 1988. Ecology of the Cattle Tick (*Boophilus microplus*) in Subtropical Australia. III* Modelling Populations on Different Breeds of Cattle. *Aust. J. Agric. Res.*, 39: 309-18.

George, J. E., R. L. Osburn, and S. K. Wikel. 1985. Acquisition and expression of resistance by *Bos indicus* and *Bos indicus* X *Bos taurus* calves to *Amblyomma americana* infestation. *J. Parasit.*, 71 (2): 174-182.

Hewetson, R. W. 1971. Resistance by cattle to cattle tick, *Boophilus microplus* III. The Development of resistance to experimental infestations by purebred Sahiwal and Austrailian Illawarra Shorthorn Cattle. *Aust. J. Agric. Res.* 22: 331-342.

Mount, G. A., D. G. Haile, R. B. Davey, and L. M. Cooksey. 1991. Computer simulation of *Boophilus* cattle tick (Acari: Ixodidae) population dynamics. *J. Med. Entomol.* 28(2): 223-240.

Nuñez, J. L., M. E. Muñoz-Cobeñas, and H. L. Moltedo. Transl. by Bailie, H. et al. VII. Host resistance to ticks. In: *Boophilus microplus*: The common cattle tick. Springer-Verlag, Germany, 1985, pp. 161-180.

Roberts, J. A. 1968a. Acquisition by the host of resistance to the cattle tick *Boophilus microplus* (Canestrini). *J. Parasit.*, 54 (4): 657-662.

Roberts, J. A. 1968b. Resistance of cattle to the tick *Boophilus microplus* (Canestrini). I. Development of ticks on *Bos taurus*. *J. Parasit.*, 54 (4): 663-666.

Roberts, J. A. 1968c. Resistance of cattle to the tick *Boophilus microplus* (Canestrini). II. Stages of the life cycle of the parasite against which resistance is manifest. *J. Parasit.* 54 (4): 667-673.

Roberts, J. A., and J. D. Kerr. 1976. *Boophilus microplus*: passive transfer of resistance in cattle. *J. Parasit.* 62 (3): 485-489.

Seifert, G. W. 1971. Variations between and within breeds of cattle in resistance to field infestations of the cattle tick (*Boophilus microplus*). *Aust. J. Agric. Res.* 22, 159-168.

Sutherst, R. W. 1987. The role of models in tick control. In: Proceedings of the international conference on Veterinary Preventive Medicine and Animal Production, Medlbourne, Australia. Ed. by K. L. Hughes. Australian Veterinary Association, 32-37.

Sutherst, R. W., G. A. Norton, N. D. Barlow, G. R. Conway, M. Birley, and H. N. Comins. 1979a. An analysis of management strategies for cattle tick (*Boophilus microplus*) control in Australia. *J. App. Ecol.* 16: 359-382.

Sutherst, R. W., K. B. W. Utech, J. D. Kerr, and R. H. Wharton. 1979b. Density dependent mortality of the tick, *Boophilus microplus*, on cattle--further observations. *J. App. Ecol.* 16: 397-403.

Sutherst, R. W., I. D. Sutherland, A. S. Bourne, G. F. Maywald, and D. A. Stegeman. 1988a. Ecology of the Cattle Tick (*Boophilus microplus*) in Subtropical Australia. I. Introduction and Free-Living Stages. *Aust. J. Agric Res.*, 39: 285-297.

Sutherst, R. W., G. F. Maywald, A. S. Bourne, I. D. Sutherland, and D. A. Stegeman. 1988b. Ecology of the Cattle Tick (*Boophilus microplus*) in Subtropical Australia. II. Resistance of Different Breeds of Cattle. *Aust. J. Agric. Res.*, 39: 299-308.

Teel, P. D. 1985. Ticks. In R.E. Williams, R.D. Hall, A.B. Broce, adn P.J. Scholl (Editors). Livestock Entomology. John Wiley & Sons, Inc., Texas A&M University, College Station, Texas, pp. 129-149.

Teel, P. D., S. L. Marin, and W. E. Grant. 1996. Simulation of host-parasite-landscape interactions: influence of season and habitat on cattle fever tick (*Boophilus* sp.) population dynamics. *Ecological Modelling*. 84: 19-30.

Utech, K. B. W., G. W. Seifert, and R. H. Wharton. 1978a. Breeding Australian Illawarra Shorthorn cattle for resistance to *Boophilus microplus*. I. Factors affecting resistance. *Aust. J. Agric. Res.*, 29: 411-422.

Utech, K. B. W., R. H. Wharton, and J. D. Kerr. 1978b. Resistance to *Boophilus microplus* (Canestrini) in different breeds of cattle. *Aust. J. Agric. Res.*, 29: 885-895.

Wharton, R. H., K. L. S. Harley, P. R. Wilinson, K. B. Utech, and B. M. Kelley. 1969. A comparison of cattle tick control by pasture spelling, planned dipping, and tick-resistant cattle. *Aust J. Agric. Res.*, 20: 783-797.

Appendix 1. Resistance level (percentage tick mortality measured on day 20) following each of 3 consecutive tick infestations (on days of 15, 135, and 195) as a function of (1) Maximum Capacity for the Relative Resistance Mortality Factor (ranges from 1.1-3.3), (2) Resistance Acquisition Rate (first infestation=0.1, second infestation=0.4 or 0.8, third infestation=0.4 or 0.8), (3) Resistance Decay Rate (0.001, 0.005, or 0.008); and (6) Resistance Decay Time Lag (15 or 60 days).

| Maximum Capacity | Resistance Acquisition Rate | | | Resistance Decay Rate | Resistance Decay Time Lag |
|---|---|---|---|---|---|
| | First infestation =0.1 | Second infestation =0.4 | Third infestation =0.4 | | |
| 1.1 | 85.54 | 86.04 | 86.16 | 0.001 | 15 |
| 1.3 | 85.54 | 87.25 | 87.40 | 0.001 | 15 |
| 1.5 | 85.54 | 88.46 | 88.64 | 0.001 | 15 |
| 1.7 | 85.54 | 89.66 | 89.87 | 0.001 | 15 |
| 1.9 | 85.54 | 90.86 | 91.11 | 0.001 | 15 |
| 2.1 | 85.54 | 92.06 | 92.35 | 0.001 | 15 |
| 2.3 | 85.54 | 93.26 | 93.58 | 0.001 | 15 |
| 2.5 | 85.54 | 94.45 | 94.82 | 0.001 | 15 |
| 2.7 | 85.54 | 95.64 | 96.05 | 0.001 | 15 |
| 2.9 | 85.54 | 96.82 | 97.28 | 0.001 | 15 |
| 3.1 | 85.54 | 98.01 | 98.51 | 0.001 | 15 |
| 3.3 | 85.54 | 99.19 | 99.73 | 0.001 | 15 |
| 1.1 | 85.54 | 85.98 | 86.15 | 0.005 | 15 |
| 1.3 | 85.54 | 86.79 | 87.39 | 0.005 | 15 |
| 1.5 | 85.54 | 87.82 | 88.63 | 0.005 | 15 |
| 1.7 | 85.54 | 88.94 | 89.86 | 0.005 | 15 |
| 1.9 | 85.54 | 90.06 | 91.08 | 0.005 | 15 |
| 2.1 | 85.54 | 91.17 | 92.32 | 0.005 | 15 |
| 2.3 | 85.54 | 92.28 | 93.54 | 0.005 | 15 |
| 2.5 | 85.54 | 93.38 | 94.77 | 0.005 | 15 |
| 2.7 | 85.54 | 94.49 | 95.98 | 0.005 | 15 |
| 2.9 | 85.54 | 95.59 | 97.19 | 0.005 | 15 |
| 3.1 | 85.54 | 96.69 | 98.39 | 0.005 | 15 |
| 3.3 | 85.54 | 97.78 | 99.60 | 0.005 | 15 |
| 1.1 | 85.54 | 85.97 | 86.14 | 0.008 | 15 |
| 1.3 | 85.54 | 86.80 | 87.38 | 0.008 | 15 |
| 1.5 | 85.54 | 87.55 | 88.62 | 0.008 | 15 |
| 1.7 | 85.54 | 88.38 | 89.85 | 0.008 | 15 |
| 1.9 | 85.54 | 89.43 | 91.06 | 0.008 | 15 |
| 2.1 | 85.54 | 90.48 | 92.30 | 0.008 | 15 |
| 2.3 | 85.54 | 91.52 | 93.53 | 0.008 | 15 |
| 2.5 | 85.54 | 92.56 | 94.73 | 0.008 | 15 |
| 2.7 | 85.54 | 93.60 | 95.96 | 0.008 | 15 |
| 2.9 | 85.54 | 94.64 | 97.16 | 0.008 | 15 |
| 3.1 | 85.54 | 95.67 | 98.34 | 0.008 | 15 |
| 3.3 | 85.54 | 96.70 | 99.52 | 0.008 | 15 |

| Maximum Capacity | Resistance Acquisition Rate | | | Resistance Decay Rate | Resistance Decay Time Lag |
|---|---|---|---|---|---|
| | First infestation =0.1 | Second infestation =0.8 | Third infestation =0.8 | | |
| 1.1 | 85.54 | 86.10 | 86.16 | 0.001 | 15 |
| 1.3 | 85.54 | 87.32 | 87.40 | 0.001 | 15 |
| 1.5 | 85.54 | 88.55 | 88.64 | 0.001 | 15 |
| 1.7 | 85.54 | 89.77 | 89.87 | 0.001 | 15 |
| 1.9 | 85.54 | 90.99 | 91.11 | 0.001 | 15 |
| 2.1 | 85.54 | 92.21 | 92.35 | 0.001 | 15 |
| 2.3 | 85.54 | 93.42 | 93.59 | 0.001 | 15 |
| 2.5 | 85.54 | 94.64 | 94.83 | 0.001 | 15 |
| 2.7 | 85.54 | 95.85 | 96.06 | 0.001 | 15 |
| 2.9 | 85.54 | 97.06 | 97.30 | 0.001 | 15 |
| 3.1 | 85.54 | 98.27 | 98.53 | 0.001 | 15 |
| 3.3 | 85.54 | 99.48 | 99.76 | 0.001 | 15 |
| 1.1 | 85.54 | 86.06 | 86.15 | 0.005 | 15 |
| 1.3 | 85.54 | 87.08 | 87.39 | 0.005 | 15 |
| 1.5 | 85.54 | 88.21 | 88.63 | 0.005 | 15 |
| 1.7 | 85.54 | 89.38 | 89.86 | 0.005 | 15 |
| 1.9 | 85.54 | 90.56 | 91.10 | 0.005 | 15 |
| 2.1 | 85.54 | 91.73 | 92.33 | 0.005 | 15 |
| 2.3 | 85.54 | 92.90 | 93.57 | 0.005 | 15 |
| 2.5 | 85.54 | 94.07 | 94.79 | 0.005 | 15 |
| 2.7 | 85.54 | 95.23 | 96.02 | 0.005 | 15 |
| 2.9 | 85.54 | 96.40 | 97.24 | 0.005 | 15 |
| 3.1 | 85.54 | 97.56 | 98.46 | 0.005 | 15 |
| 3.3 | 85.54 | 98.72 | 99.66 | 0.005 | 15 |
| 1.1 | 85.54 | 86.06 | 86.15 | 0.008 | 15 |
| 1.3 | 85.54 | 87.08 | 87.39 | 0.008 | 15 |
| 1.5 | 85.54 | 88.06 | 88.63 | 0.008 | 15 |
| 1.7 | 85.54 | 89.07 | 89.85 | 0.008 | 15 |
| 1.9 | 85.54 | 90.21 | 91.09 | 0.008 | 15 |
| 2.1 | 85.54 | 91.35 | 92.33 | 0.008 | 15 |
| 2.3 | 85.54 | 92.48 | 93.55 | 0.008 | 15 |
| 2.5 | 85.54 | 93.61 | 94.78 | 0.008 | 15 |
| 2.7 | 85.54 | 94.74 | 96.00 | 0.008 | 15 |
| 2.9 | 85.54 | 95.87 | 97.21 | 0.008 | 15 |
| 3.1 | 85.54 | 97.00 | 98.42 | 0.008 | 15 |
| 3.3 | 85.54 | 98.12 | 99.61 | 0.008 | 15 |

| Maximum Capacity | Resistance Acquisition Rate | | | Resistance Decay Rate | Resistance Decay Tme Lag |
|---|---|---|---|---|---|
| | First infestation =0.1 | Second infestation =0.4 | Third infestation =0.4 | | |
| 1.1 | 85.54 | 86.13 | 86.16 | 0.001 | 60 |
| 1.3 | 85.54 | 87.35 | 87.40 | 0.001 | 60 |
| 1.5 | 85.54 | 88.58 | 88.64 | 0.001 | 60 |
| 1.7 | 85.54 | 89.79 | 89.88 | 0.001 | 60 |
| 1.9 | 85.54 | 91.01 | 91.12 | 0.001 | 60 |
| 2.1 | 85.54 | 92.23 | 92.36 | 0.001 | 60 |
| 2.3 | 85.54 | 93.44 | 93.60 | 0.001 | 60 |
| 2.5 | 85.54 | 94.64 | 94.84 | 0.001 | 60 |
| 2.7 | 85.54 | 95.85 | 96.07 | 0.001 | 60 |
| 2.9 | 85.54 | 97.05 | 97.31 | 0.001 | 60 |
| 3.1 | 85.54 | 98.25 | 98.55 | 0.001 | 60 |
| 3.3 | 85.54 | 99.45 | 99.79 | 0.001 | 60 |
| 1.1 | 85.54 | 86.01 | 86.16 | 0.005 | 60 |
| 1.3 | 85.54 | 87.22 | 87.40 | 0.005 | 60 |
| 1.5 | 85.54 | 88.42 | 88.64 | 0.005 | 60 |
| 1.7 | 85.54 | 89.62 | 89.88 | 0.005 | 60 |
| 1.9 | 85.54 | 90.81 | 91.12 | 0.005 | 60 |
| 2.1 | 85.54 | 92.01 | 92.36 | 0.005 | 60 |
| 2.3 | 85.54 | 93.20 | 93.60 | 0.005 | 60 |
| 2.5 | 85.54 | 94.38 | 94.84 | 0.005 | 60 |
| 2.7 | 85.54 | 95.57 | 96.07 | 0.005 | 60 |
| 2.9 | 85.54 | 96.75 | 97.31 | 0.005 | 60 |
| 3.1 | 85.54 | 97.93 | 98.55 | 0.005 | 60 |
| 3.3 | 85.54 | 99.10 | 99.79 | 0.005 | 60 |
| 1.1 | 85.54 | 85.97 | 86.16 | 0.008 | 60 |
| 1.3 | 85.54 | 87.12 | 87.40 | 0.008 | 60 |
| 1.5 | 85.54 | 88.30 | 88.64 | 0.008 | 60 |
| 1.7 | 85.54 | 89.48 | 89.88 | 0.008 | 60 |
| 1.9 | 85.54 | 90.66 | 91.12 | 0.008 | 60 |
| 2.1 | 85.54 | 91.84 | 92.36 | 0.008 | 60 |
| 2.3 | 85.54 | 93.01 | 93.60 | 0.008 | 60 |
| 2.5 | 85.54 | 94.19 | 94.84 | 0.008 | 60 |
| 2.7 | 85.54 | 95.35 | 96.07 | 0.008 | 60 |
| 2.9 | 85.54 | 96.52 | 97.31 | 0.008 | 60 |
| 3.1 | 85.54 | 97.68 | 98.55 | 0.008 | 60 |
| 3.3 | 85.54 | 98.84 | 99.79 | 0.008 | 60 |

| Maximum Capacity | Resistance Acquisition Rate | | | Resistance Decay Rate | Resistance Decay Time Lag |
|---|---|---|---|---|---|
| | First infestation =0.1 | Second infestation =0.8 | Third infestation =0.8 | | |
| 1.1 | 85.54 | 86.14 | 86.16 | 0.001 | 60 |
| 1.3 | 85.54 | 87.38 | 87.40 | 0.001 | 60 |
| 1.5 | 85.54 | 88.61 | 88.64 | 0.001 | 60 |
| 1.7 | 85.54 | 89.84 | 89.88 | 0.001 | 60 |
| 1.9 | 85.54 | 91.06 | 91.12 | 0.001 | 60 |
| 2.1 | 85.54 | 92.29 | 92.36 | 0.001 | 60 |
| 2.3 | 85.54 | 93.51 | 93.60 | 0.001 | 60 |
| 2.5 | 85.54 | 94.74 | 94.84 | 0.001 | 60 |
| 2.7 | 85.54 | 95.96 | 96.07 | 0.001 | 60 |
| 2.9 | 85.54 | 97.18 | 97.31 | 0.001 | 60 |
| 3.1 | 85.54 | 98.40 | 98.55 | 0.001 | 60 |
| 3.3 | 85.54 | 99.62 | 99.79 | 0.001 | 60 |
| 1.1 | 85.54 | 86.08 | 86.16 | 0.005 | 60 |
| 1.3 | 85.54 | 87.31 | 87.40 | 0.005 | 60 |
| 1.5 | 85.54 | 88.53 | 88.64 | 0.005 | 60 |
| 1.7 | 85.54 | 89.74 | 89.88 | 0.005 | 60 |
| 1.9 | 85.54 | 90.96 | 91.12 | 0.005 | 60 |
| 2.1 | 85.54 | 92.18 | 92.36 | 0.005 | 60 |
| 2.3 | 85.54 | 93.39 | 93.60 | 0.005 | 60 |
| 2.5 | 85.54 | 94.60 | 94.84 | 0.005 | 60 |
| 2.7 | 85.54 | 95.81 | 96.07 | 0.005 | 60 |
| 2.9 | 85.54 | 97.02 | 97.31 | 0.005 | 60 |
| 3.1 | 85.54 | 98.23 | 98.55 | 0.005 | 60 |
| 3.3 | 85.54 | 99.44 | 99.79 | 0.005 | 60 |
| 1.1 | 85.54 | 86.06 | 86.16 | 0.008 | 60 |
| 1.3 | 85.54 | 87.25 | 87.40 | 0.008 | 60 |
| 1.5 | 85.54 | 88.46 | 88.64 | 0.008 | 60 |
| 1.7 | 85.54 | 89.67 | 89.88 | 0.008 | 60 |
| 1.9 | 85.54 | 90.88 | 91.12 | 0.008 | 60 |
| 2.1 | 85.54 | 92.09 | 92.36 | 0.008 | 60 |
| 2.3 | 85.54 | 93.29 | 93.60 | 0.008 | 60 |
| 2.5 | 85.54 | 94.50 | 94.84 | 0.008 | 60 |
| 2.7 | 85.54 | 95.70 | 96.07 | 0.008 | 60 |
| 2.9 | 85.54 | 96.90 | 97.31 | 0.008 | 60 |
| 3.1 | 85.54 | 98.10 | 98.55 | 0.008 | 60 |
| 3.3 | 85.54 | 99.30 | 99.79 | 0.008 | 60 |

Fig.1. Conceptualization of the new host resistance sumodel and its integration into the host-parasite-landscape interaction model of Teel et al. (1996). The original model consisted of three submodels representing (1) tick development in the environment, (2) tick development on the cow, and (3) movement of cattle among habitat types. The new cow resistance to ticks submodel represents the acquisition and loss of resistance as a function of breed of cattle and presence or absence of ticks on the cow, which subsequently affects larval mortality (M).

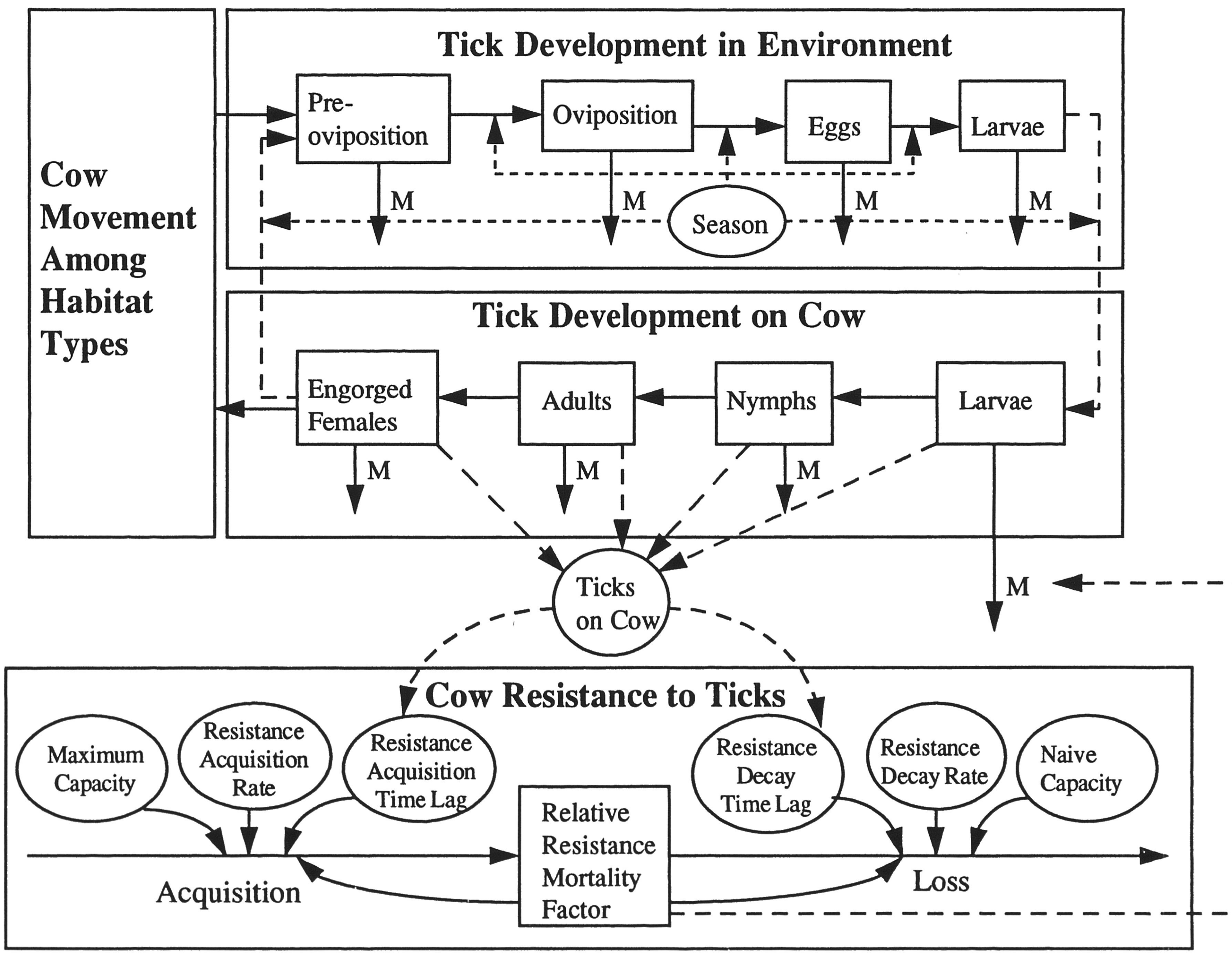

Cow Movement Among Habitat Types
Tick Development in Environment
Pre-oviposition
Oviposition
Eggs
Larvae
M
M
M
M
Season
Tick Development on Cow
Engorged Females
Adults
Nymphs
Larvae
M
M
M
M
Ticks on Cow
Cow Resistance to Ticks
Maximum Capacity
Resistance Acquisition Rate
Resistance Acquisition Time Lag
Relative Resistance Mortality Factor
Resistance Decay Time Lag
Resistance Decay Rate
Naive Capacity
Acquisition
Loss

Fig. 2. Diagrammatic representation of changes in host resistance following a single infestation of larval ticks as represented by dynamics of the Relative Resistance Mortality Factor in the new Cow Resistance to Ticks submodel. (RAR and RDR represent resistance acquisition and decay rates, respectively.)

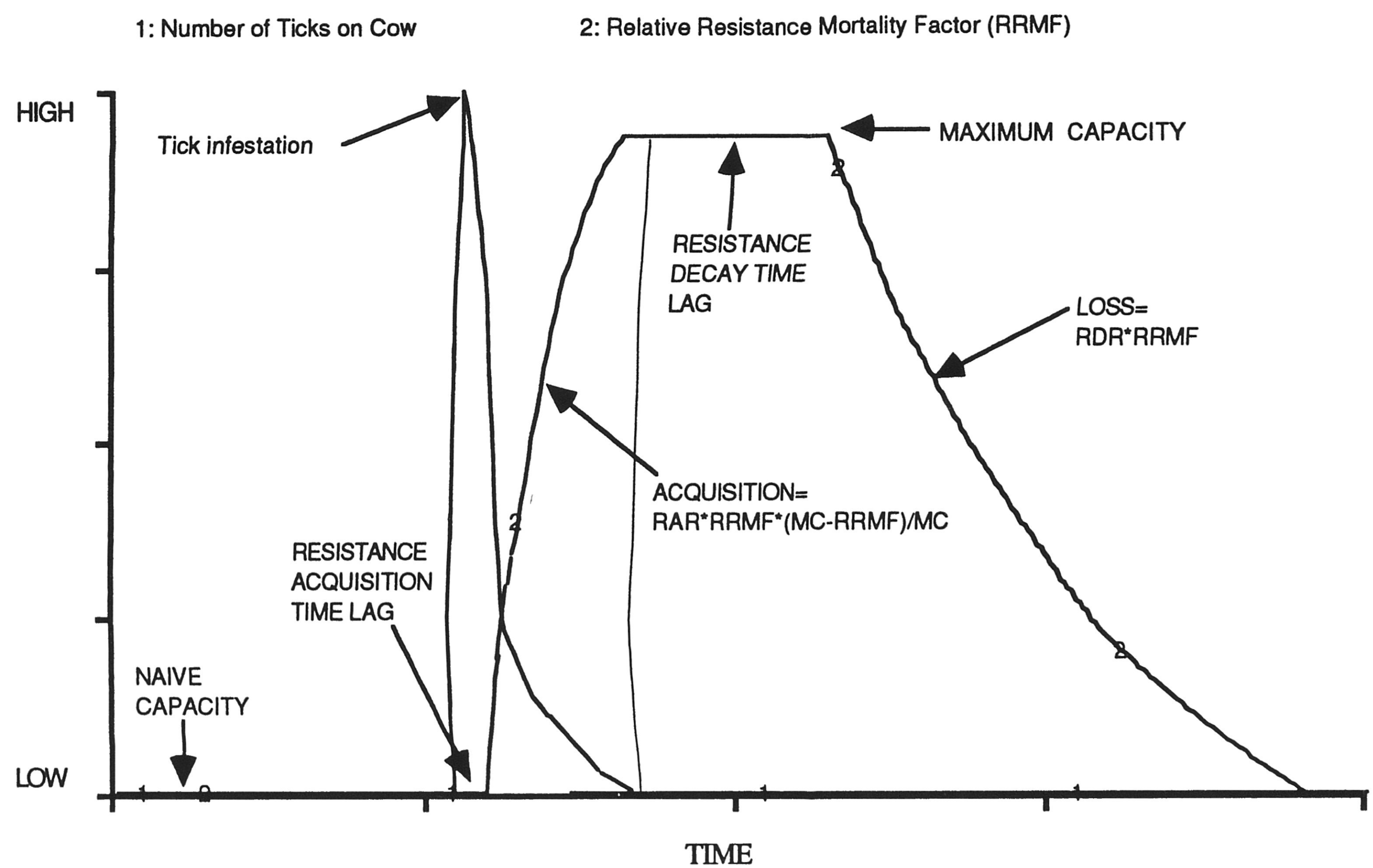
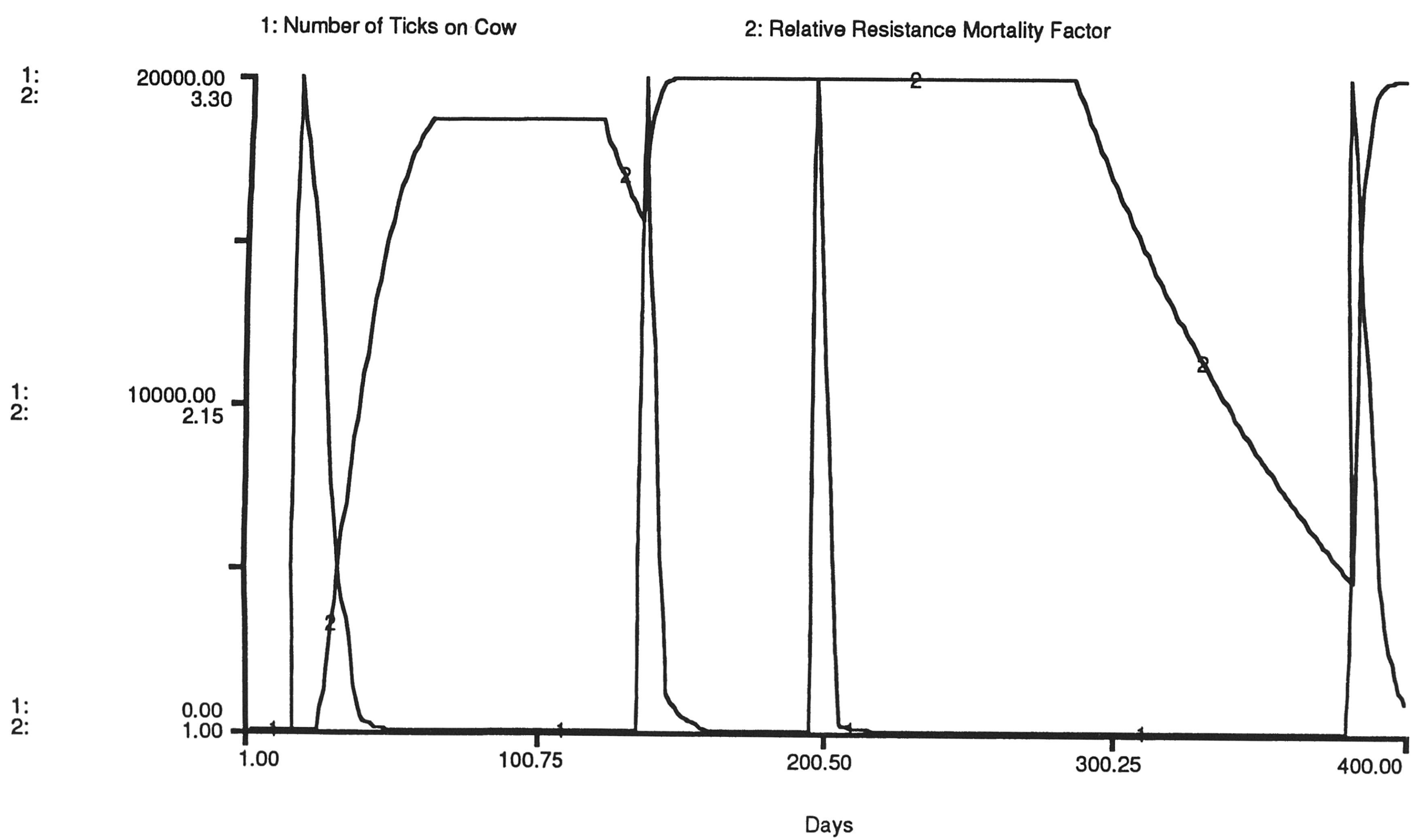
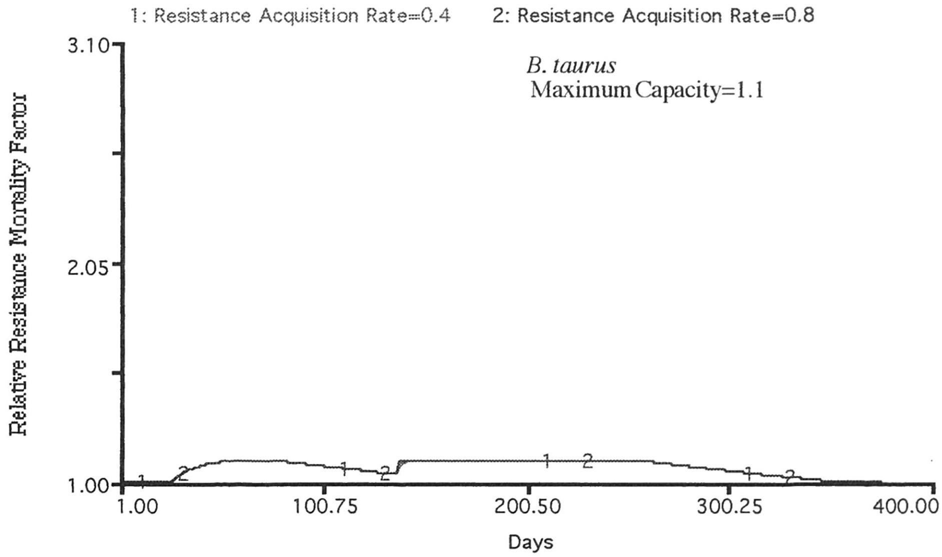

1: Number of Ticks on Cow
2: Relative Resistance Mortality Factor (RRMF)
HIGH
LOW
Tick infestation
MAXIMUM CAPACITY
RESISTANCE DECAY TIME LAG
LOSS= RDR*RRMF
ACQUISITION= RAR*RRMF*(MC-RRMF)/MC
RESISTANCE ACQUISITION TIME LAG
NAIVE CAPACITY
TIME

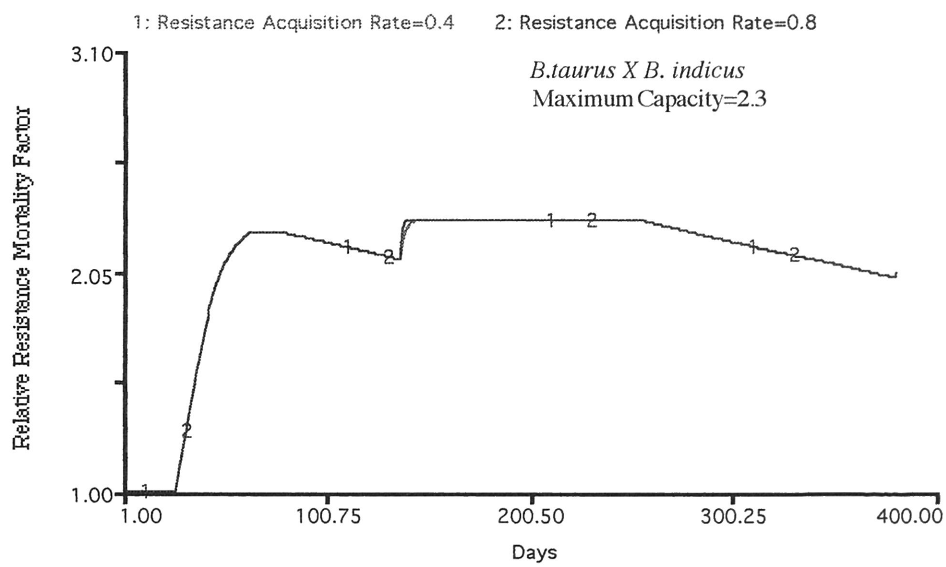
Fig. 3. Dynamics of the Relative Resistance Mortality Factor and total number of Ticks on the Cow in response to four infestations of 20,000 larval ticks each on days 15, 135, 195, and 380 of simulated time.



1: Number of Ticks on Cow
2: Relative Resistance Mortality Factor
1: 20000.00
2: 3.30
1: 10000.00
2: 2.15
1: 0.00
2: 1.00
1.00
100.75
200.50
300.25
400.00
Days

Fig. 4. Sensitivity of the Relative Resistance Mortality Factor to changes in Resistance Acquisition Rates (0.4 and 0.8) for *B. taurus* (Maximum Capacity=1.1), *B. taurus* X *B. indicus* (Maximum Capacity=2.3) and *B. indicus* (Maximum Capacity=3.1). Resistance Decay Rate was set at 0.001 and Resistance Decay Time Lag was set at 15 days.


1: Resistance Acquisition Rate=0.4
2: Resistance Acquisition Rate=0.8
B. taurus
Maximum Capacity=1.1
Relative Resistance Mortality Factor
3.10
2.05
1.00
1.00
100.75
200.50
300.25
400.00
Days


1: Resistance Acquisition Rate=0.4
2: Resistance Acquisition Rate=0.8
B.taurus X B. indicus
Maximum Capacity=2.3
Relative Resistance Mortality Factor
3.10
2.05
1.00
1.00
100.75
200.50
300.25
400.00
Days

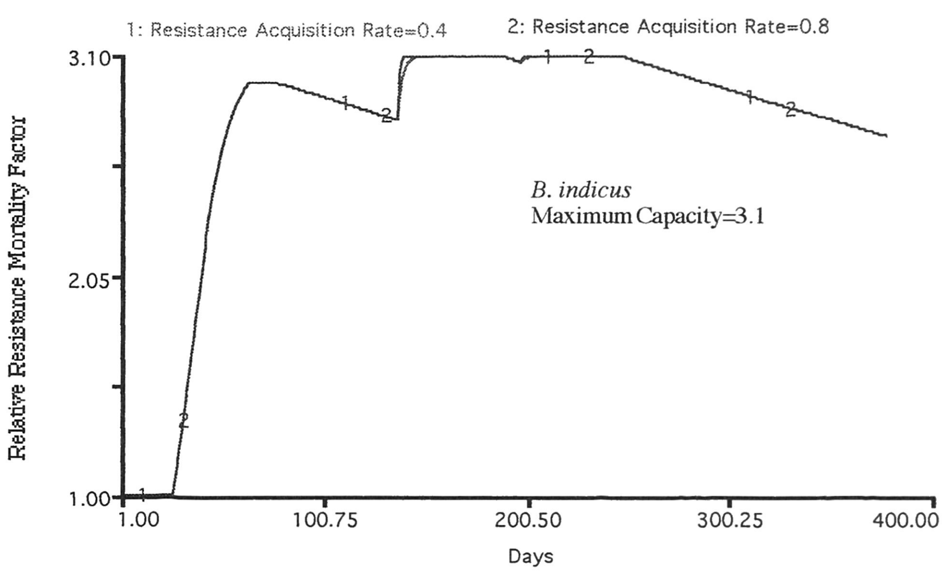
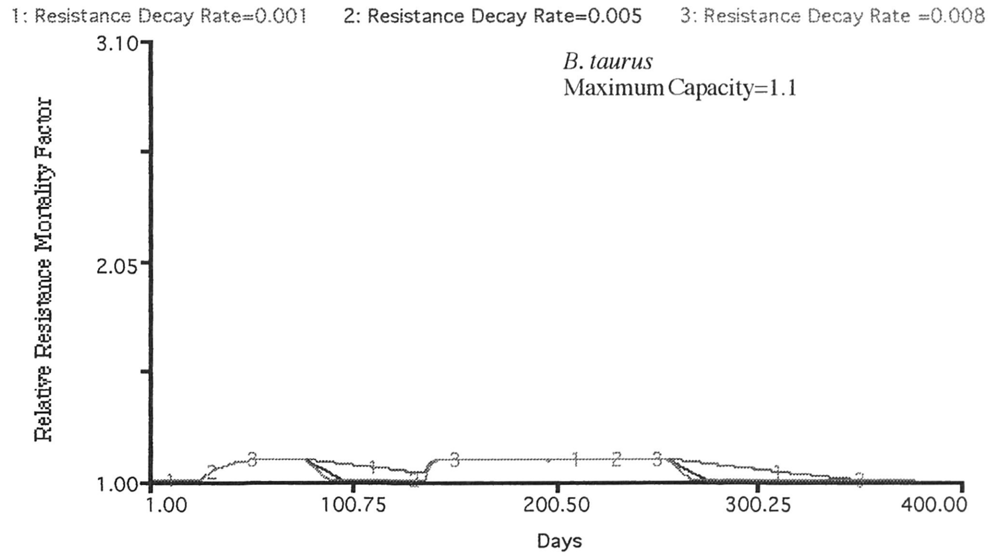
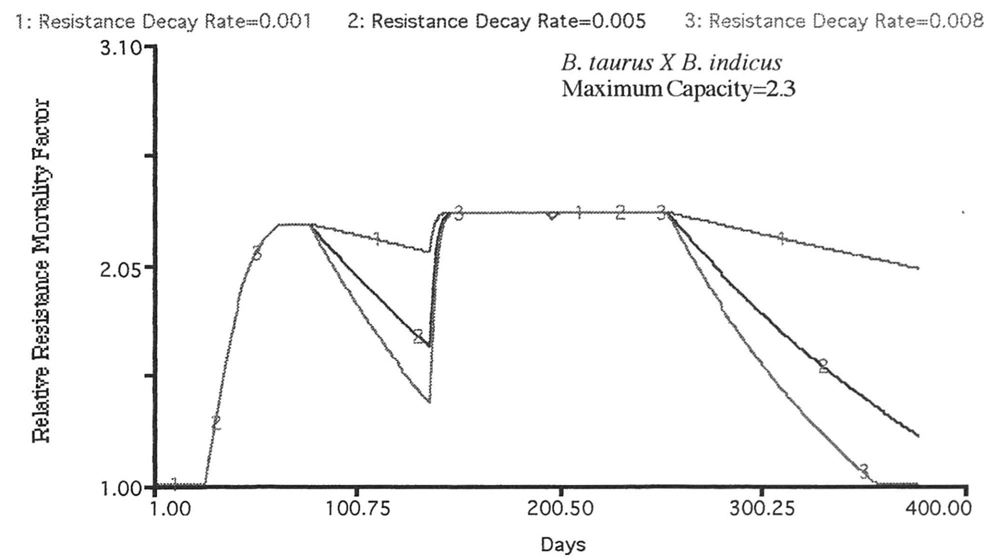

1: Resistance Acquisition Rate=0.4
2: Resistance Acquisition Rate=0.8
B. indicus
Maximum Capacity=3.1
Relative Resistance Mortality Factor
3.10
2.05
1.00
1.00
100.75
200.50
300.25
400.00
Days

Fig. 5. Sensitivity of the Relative Resistance Mortality Factor to changes in Resistance Decay Rates (0.001, 0.005, and 0.008) for *B. taurus* (Maximum Capacity=1.1), *B. taurus* X *B. indicus* (Maximum Capacity=2.3) and *B. indicus* (Maximum Capacity=3.1). Resistance Acquisition Rate was set at 0.4 and Resistance Decay Time Lag was set at 15 days.


1: Resistance Decay Rate=0.001
2: Resistance Decay Rate=0.005
3: Resistance Decay Rate =0.008
B. taurus
Maximum Capacity=1.1
Relative Resistance Mortality Factor
3.10
2.05
1.00
1.00
100.75
200.50
300.25
400.00
Days


1: Resistance Decay Rate=0.001
2: Resistance Decay Rate=0.005
3: Resistance Decay Rate=0.008
B. taurus X B. indicus
Maximum Capacity=2.3
Relative Resistance Mortality Factor
3.10
2.05
1.00
1.00
100.75
200.50
300.25
400.00
Days

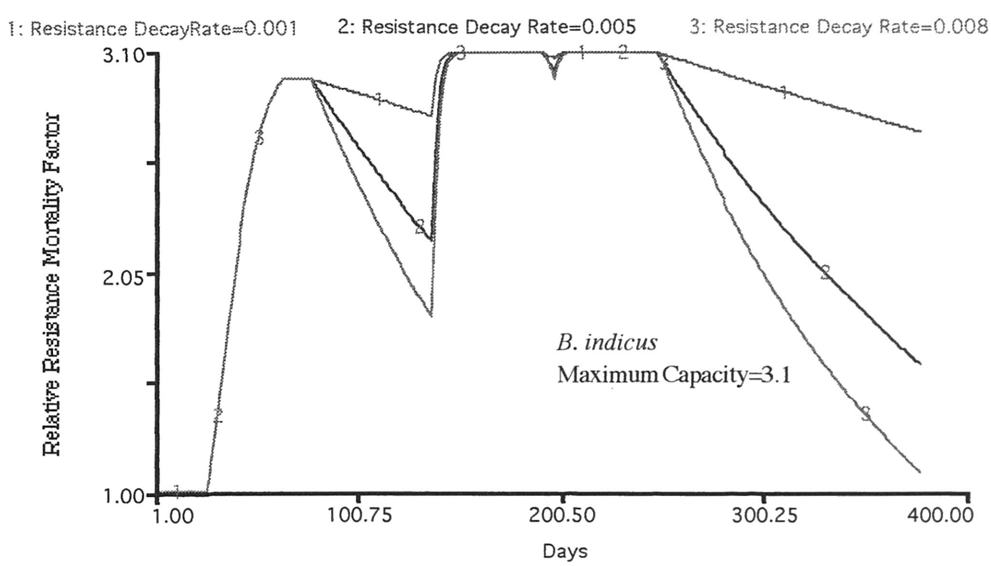
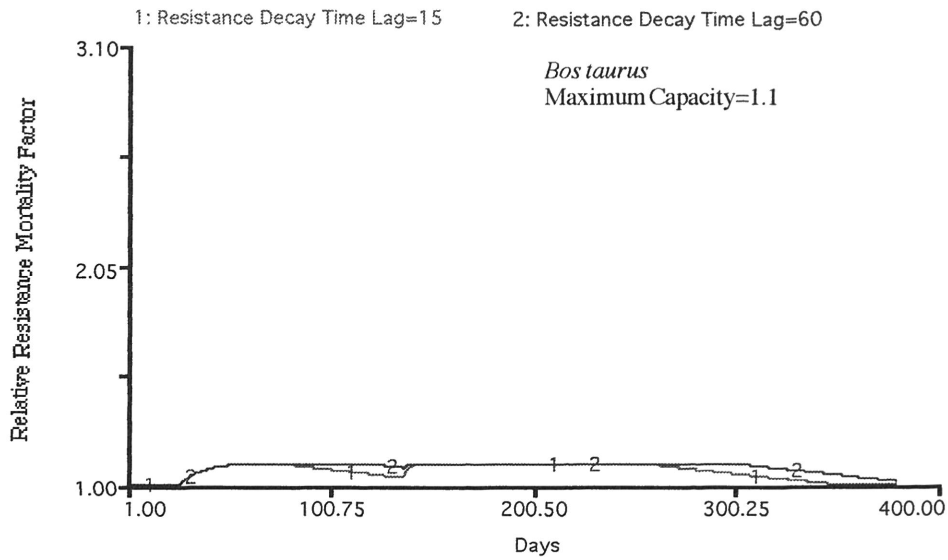
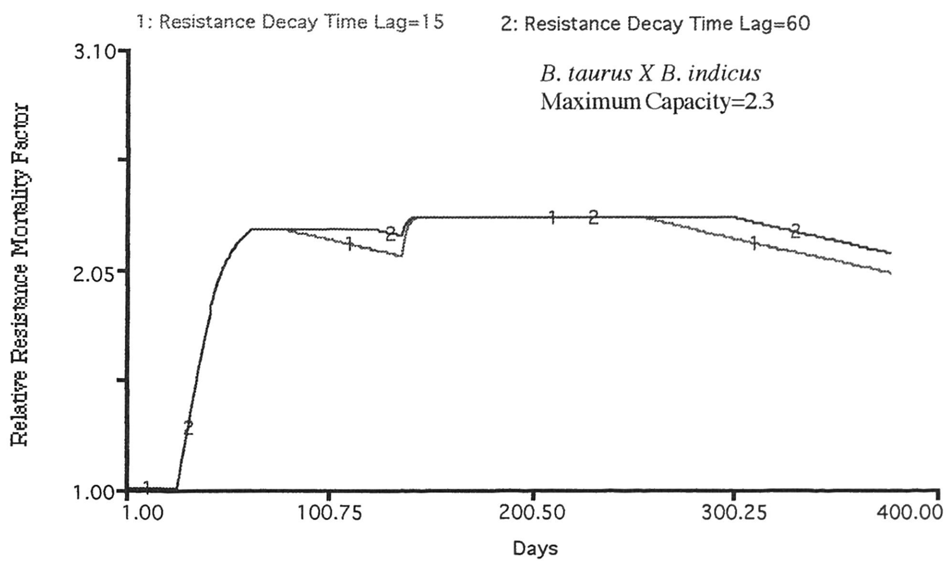
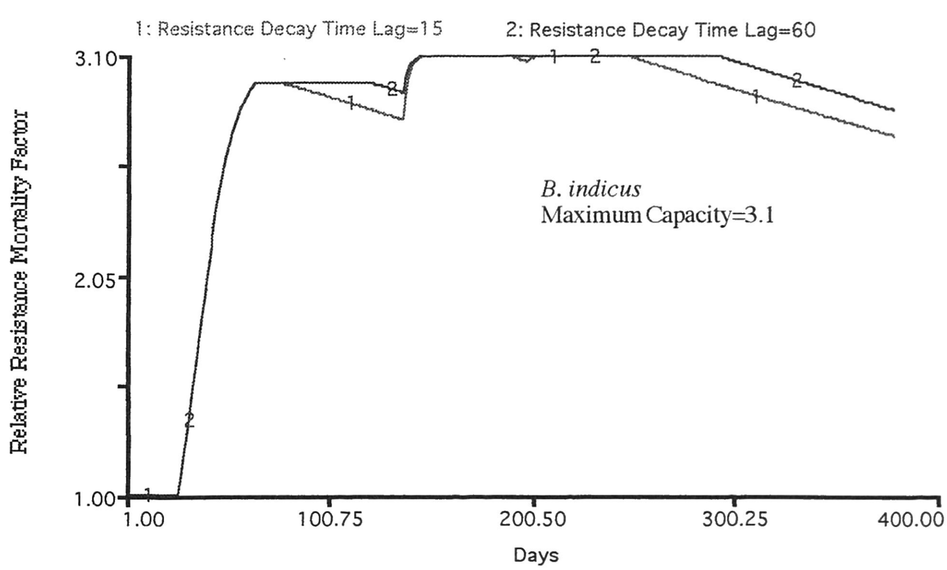

1: Resistance DecayRate=0.001
2: Resistance Decay Rate=0.005
3: Resistance Decay Rate=0.008
B. indicus
Maximum Capacity=3.1
Relative Resistance Mortality Factor
3.10
2.05
1.00
1.00
100.75
200.50
300.25
400.00
Days

Fig. 6. Sensitivity of the Relative Resistance Mortality Factor to changes in Resistance Decay Time Lag (15 and 60 days) for *B. taurus* (Maximum Capacity=1.1), *B. taurus* X *B. indicus* (Maximum Capacity=2.3) and *B. indicus* (Maximum Capacity=3.1). Resistance Acquisition Rate was set at 0.4 and Resistance Decay Rate was set at 0.001.


1: Resistance Decay Time Lag=15
2: Resistance Decay Time Lag=60
Bos taurus
Maximum Capacity=1.1
Relative Resistance Mortality Factor
3.10
2.05
1.00
1.00
100.75
200.50
300.25
400.00
Days


1: Resistance Decay Time Lag=15
2: Resistance Decay Time Lag=60
B. taurus X B. indicus
Maximum Capacity=2.3
Relative Resistance Mortality Factor
3.10
2.05
1.00
1.00
100.75
200.50
300.25
400.00
Days


1: Resistance Decay Time Lag=15
2: Resistance Decay Time Lag=60
B. indicus
Maximum Capacity=3.1
Relative Resistance Mortality Factor
3.10
2.05
1.00
1.00
100.75
200.50
300.25
400.00
Days