

Extinction dynamics in the  
American marten (*Martes americana*)

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Abstract: Because of recent interest in the use of the marten as an indicator species for old-growth forests, and management initiatives for specific endangered and extirpated populations, there is a need for an understanding of the dynamics of small populations and the process of local extinction in the marten. To address these concerns we have constructed a model of marten population dynamics and used it to investigate the extinction process over a broad region of parameter space. The model was based on rules governing the behavior and physiology of individual martens, focusing on energy balance. Spatial dynamics and both demographic and environmental stochasticity were incorporated. The outcome of interest was the probability of extinction and quasi-extinction (20 females remaining) over 500 years.

Three qualitative forms of extinction were delineated. The first was deterministic extinction, associated with those parameter combinations leading to a negative population growth rate. The second was probabilistic extinction in systems with a strong positive growth rate but restricted population size due to habitat constraint. The transition from 100% persistence to 100% quasi-extinction as the habitat size was decreased was abrupt and generally corresponded to a population of between 75 and 125 females. The final dynamic form leading to extinction was in systems near the deterministic threshold. Their dynamic behavior was similar to a random walk, and even relatively large populations had non-trivial probabilities of extinction. The empirical research required for site-specific application of these findings are discussed.

## Introduction

The marten has long been of interest to wildlife managers as a consequence of its status as a valued furbearer. In recent years there has been additional interest in this species as a potential indicator of the health of boreal forest ecosystems (Thompson, 1991; Buskirk, 1992). Furthermore, the reestablishment of extirpated populations is being undertaken in several locations (Boss et al., 1987; Slough, 1989) and recovery plans are being implemented for certain endangered populations, such as the subspecies found in Newfoundland, Canada (RENEW, 1990).

A fundamental understanding of the dynamics of small populations and the factors influencing the extinction process are central to the implementation of these new management initiatives. Factors that are amenable to management control and those involved in historical population declines and in site to site variation are of particular interest. These include mortality rate (influenced by harvesting), habitat quality and habitat size (influenced by forestry practices).

The objective of this study was to provide a fundamental understanding of the extinction process in the marten through the development of a model of marten population dynamics. In particular, we sought to define the relationship between the key system parameters described above and the probability of population extinction over a 500 year time frame. It was intended that this research should provide the basis for future site-specific analyses

and help guide field research efforts, therefore the investigation of parameter space was constrained only to biologically plausible limits.

A substantial body of empirical data was available for the construction of the model, largely as a consequence of the marten's status as a furbearer. A number of studies have followed specific populations over time, providing information on demographic parameters (e.g., Weckwerth and Hawley, 1962; Archibald and Jessup, 1984; Thompson and Colgan, 1987; Bissonette et al., 1988), and other studies have focused on territory size, food habits and habitat preferences (e.g., Soutiere, 1979; Steventon and Major, 1982; Bateman, 1986; Buskirk and McDonald, 1989). Furthermore, data (including age and ovulation rate) have been compiled on over 2,000 martens that were harvested over 12 years in central Ontario, Canada (Strickland and Douglas, 1987). Some data on ranch-reared marten were also available (Markley and Bassett, 1942; Ritchie, 1953).

## Materials and Methods

### *Model Construction*

A review of the literature was conducted and a set of rules describing the essential features of marten demography at the individual-animal level was compiled (Appendix A). Based on these

rules, a family of individual-based models running in discrete time steps of one year were constructed. The base model was deterministic and analytical in nature (Appendix B). The other models were computer simulations which included demographic stochasticity, either alone or in combination with environmental stochasticity. Only the dynamic behavior of females was followed, based on the assumption that the population would always contain enough males to breed all females and that males and females did not compete for resources (Strickland and Douglas, 1987). The density of the total population was calculated as twice the density of females, based on a spring census.

It was assumed that the entire population was confined to a contiguous patch of homogeneous habitat of definable dimension, and that immigration and emigration did not occur. Spatial dynamics (detailed below) were incorporated into the computer simulations by dividing the available habitat into discrete 25 hectare cells.

A central concept in the model was that of an optimum territory size (OTS); the amount of territory required to ensure access to sufficient prey to meet all energetic requirements, including reproduction. The OTS was used as a proxy measure for prey availability, integrating the influence of habitat type (territories are larger in poor quality habitat; Soutiere, 1979) and annual variations in prey density (territory size is inversely proportional to prey density; Thompson and Colgan, 1987). It was assumed that all marten strive to reach the OTS but do not exceed it because of the energetic costs involved (Thompson, in press).

It was assumed that fluctuations in the prey base constitute the major source of environmental stochasticity for marten. This was simulated in the models by a linear mapping of annual changes in prey density to annual changes in regional OTS, both expressed as the percentage deviation from a long-term mean. The pattern of prey fluctuations was based on 32 years of standardized trapping of *Peromyscus* spp. in Algonquin Park, Ontario (Falls, 1986; Falls, pers. comm.) and sequences of random numbers within specified ranges. For model runs using the field data, the 32 year pattern was sequentially repeated. In all cases the prey density was assumed to be uniform across the habitat grid within a given year.

The computer models consisted of sequential modules for spatial dynamics, reproduction and mortality. The module for spatial dynamics simulated an annual competition for space among females for the establishment of territories. Each female would attempt to acquire 100% of the OTS specified by the local habitat type and current prey density. Resident females, as the best competitors, were given first opportunity to establish territories, followed by transient adults and then juveniles. Within each group, territory acquisition was incremental and simultaneous among females.

Each female would begin the competition with one 25 hectare cell, representing her core area from the previous year. If she was unable to establish a minimum territory locally, due to the presence of conspecifics, she was given the opportunity to disperse to a patch of unoccupied habitat. Dispersal was to the nearest

patch available, but otherwise was unrestricted. Once the habitat was fully occupied, the remaining females without territories (primarily juveniles) entered the transient class.

In the module for reproduction the mean ovulation rate was calculated for each female as a linear function of the percentage of OTS achieved (Fig. 1). The minimum percentage of OTS required for ovulation to occur was a definable parameter in the model (Table 1). The maximum ovulation rate, in females achieving 100% of the OTS, was a function of territory size, to account for the energetic costs of territoriality. The exact form of this function was not known, therefore two extremes were modeled: a constant maximum, and a linear decrease in the maximum resulting in a mean ovulation rate of zero at the largest territory size. To incorporate stochastic processes, the actual number of eggs ovulated for each female was determined by Monte Carlo sampling a Gaussian distribution based on the individual mean ovulation rate calculated above.

In the final module, a probabilistic determination of mortality was made for each individual. For resident and transient adults the probability of death was constant (Table 1). The probability of juvenile mortality incorporated the combined impact of intrauterine, perinatal and postweaning losses up to one year of age and was modeled as a linear function of the mother's percentage of OTS. The maximum probability of mortality (100%) was associated with the smallest territory size for ovulation to occur and the minimum (Table 1) with territories equal to 100% of the OTS.

## *Model Experimentation*

As the initial step, the behavior of the model at carrying capacity was compared with data from existing populations in central Ontario (Francis and Stephenson, 1972; Strickland and Douglas, 1987; Thompson and Colgan, 1987). A computer model using the maximum habitat size (1,600 Km<sup>2</sup>) and incorporating both demographic and environmental stochasticity was used for this purpose. An estimate of 2.0 Km<sup>2</sup> was used for the OTS, based on observed territory sizes in this region (Thompson and Colgan, 1987), and the other parameters were set at their base levels (Table 1).

Subsequent investigation centered on extinction dynamics, focusing on mortality rate, mean OTS (reflecting habitat quality) and habitat size. Sensitivity testing of the other parameters in the model was conducted to determine the effect of error in their estimation on these primary results.

Extinction dynamics were investigated in two phases, beginning with deterministic extinction. For this the model was run for 500 years starting with a population at carrying capacity on the largest habitat grid, with model parameters at their base levels. Juvenile mortality rate, adult resident mortality rate and mean OTS were varied across their potential ranges in sequential runs, with the outcomes of interest being the mean equilibrium density and the threshold at which deterministic extinction was first observed (reflecting a transition to negative population growth rate). This

investigation was repeated using different forms of stochasticity in the model, and an analytical solution was derived using the deterministic model.

For the investigation of stochastic extinction the outcome of interest was the probability of extinction over 500 years. Extinction was defined as death of the last marten, but a quasi-extinction threshold of 20 adult females was also used. As above, juvenile mortality, adult resident mortality and mean OTS were sequentially varied across their potential ranges, but in this case six habitat sizes from 25 to 900 Km<sup>2</sup> were examined at each parameter level. Each parameter combination was run 200 times, always starting as a subpopulation from a population at carrying capacity on the largest habitat patch. The number of repetitions was chosen so that the observed extinction probabilities would be within 7% of the mean, 95% of the time, based on the assumption of random sampling from a binomial distribution (Snedecor and Cochran, 1980). The sensitivity of these results to other parameters in the model was tested by repeating the entire process using extreme values for the secondary parameters (Table 1). In addition, model runs were conducted using random number sequences of defined range as an alternative to the field data patterns for prey fluctuation.

For most parameter combination runs (200 repetitions of 500 years each) the mean size of those populations that did not go extinct was calculated and graphically compared to the overall probability of extinction for that run. Also, with the model parameters at their base levels, the coefficient of variation and

minimum population size over 500 years was determined over a range of habitat (and hence population) sizes.

## Results

The initial investigation was of the model's behavior at carrying capacity, with model parameters at their base levels (Table 1) and the OTS at 2.0 Km<sup>2</sup>. The density ranged from 0.8 to 1.9 martens/Km<sup>2</sup> and the ratio of resident to transient marten ranged from 0.9:1 to 100% residents, over a 500 year run. The average age structure of the population, in comparison with 12 years of aggregated data from adult female marten harvested in central Ontario (n=829; Strickland and Douglas, 1987), is shown in Figure 2. Harvest data for 1960 to 1992 from traplines adjacent to Algonquin Park (OMNR, 1992) and the corresponding density fluctuations over 32 years in the model, are shown in Figure 3. The model output in this figure was averaged over 10 runs to minimize stochastic distortion of the deterministic pattern.

A comparison of the density at carrying capacity for various models over a range of OTS values was made (Fig. 4). An asymptotic increase in population density with decreasing OTS was apparent in all models. When the energetic cost of territoriality was proportional to territory size, deterministic extinction was observed at an OTS of between 2.7 and 3.4 (Fig. 4; lines C and E).

The relationship between equilibrium density and mortality

rate for juveniles and adult residents was linear (average slope = -3.1 and -3.0, respectively) until reaching a threshold for deterministic extinction. This threshold was a linear function of OTS in models where the energetic cost of territoriality was proportional to territory size (Fig. 5). The mortality rate of transient marten had little impact on the model's function, and deterministic extinction was not observed within the range investigated (Table 1).

The probability of extinction with respect to habitat size and habitat quality (OTS), with model parameters at their base levels, is shown in Figure 6 (a-d). In general, as the habitat size was decreased the transition from 100% persistence to 100% extinction was abrupt. There was no difference between models using field data as prey input and models using random number sequences, as long as the amplitude of variation was similar (minimum = 37% and maximum = 180%, relative to the long-term mean = 100%). There was an appreciable response when the amplitude was increased, however (minimum = 15% and maximum = 190%; Fig. 6c). The energetic cost of territoriality in these runs was constant, therefore deterministic extinction was not observed (in agreement with Figure 5). Deterministic extinction did occur when the energetic cost was proportional to territory size, but the pattern of Figure 6 was unchanged for values of OTS below the deterministic extinction threshold.

The probability of extinction with respect to juvenile mortality rate and habitat size, with OTS equal to 2.0 Km<sup>2</sup> and other

parameters at their base level, is shown in Figure 7. The pattern for adult resident mortality was similar (data not shown).

Populations of between 75 and 125 females consistently remained above the quasi-extinction threshold for all 500 year runs for the majority of parameter combinations (e.g. juvenile mortality rate  $<0.7$ ; Fig. 8). Within this range, populations that persisted were generally 26% larger for models incorporating environmental stochasticity as compared to models with demographic stochasticity alone. The incorporation of an energetic cost proportional to territory size did not affect these results. A major qualitative difference was observed for models with parameter combinations approaching the deterministic extinction threshold (e.g. juvenile mortality rate  $=0.7$ ; Fig. 8). For these systems the decrease in probability of quasi-extinction associated with increased population size was gradual, and did not reach zero even for very large populations.

The coefficient of variation (CV) for the population density of the base model over 500 years was almost four times as great when environmental stochasticity was incorporated into the model, as compared to models with demographic stochasticity alone (Fig. 9). In both types of model, the CV increased rapidly once populations fell below 100 females. The minimum population size (over 500 years) was a linear function of the mean population size (Fig. 9).

Sequential variation of the other parameters in the model, across their plausible ranges (Table 1), resulted in no appreciable

change in the results presented here.

## Discussion

The results presented here are, in essence, logical inferences drawn from a set of basic premises concerning marten biology. These premises -- the "rules" of the model -- therefore merit close scrutiny, particularly in light of the fact that experimental verification of the predictions concerning extinction are not feasible.

An attempt was made to restrict the assumptions used in the model to basic observations concerning marten physiological processes and individual behavior. The central concept was that demographic processes are a function of energy balance subject to stochastic variation. The stochasticity in the model was used to take into account the many processes operating at the individual-animal level for which functional relationships are unknown, as well as true chance events. Constructed in this way, the model was not dependent on large population sizes or specific habitat features to function properly.

For marten, energy intake is directly related to the amount of prey consumed, which is in turn a function of prey availability. This has been clearly demonstrated in a number of studies in which marten demographic and physiological parameters were followed through one or more cycles of prey fluctuation (Weckwerth and

Hawley, 1962; Falls, 1986; Thompson and Colgan, 1987; Bissonette et al., 1988). Estimating prey availability for modeling purposes is problematical, however. For example, prey density estimates are influenced by when, where and how often the samples are taken, as well as by which species are included and specific trapping methodologies. Furthermore, hunting success at a given prey density varies among habitats, and this must be incorporated if the model is to have general applicability.

Our response was to abandon the direct estimation of prey availability and instead use the integrated proxy measure of OTS. The use of this measure is supported by the empirically demonstrated temporal link between mean territory size and prey density (Weckwerth and Hawley, 1962; Thompson and Colgan, 1987) and by the changes in territory size that have been observed after habitat modification (Soutiere, 1979; Thompson and Colgan, 1987). Historical data on territory size are readily available (reviewed by Buskirk and McDonald, 1989); however, the OTS for a region will generally be greater than the observed mean territory size because of the effects of intraspecific competition on the latter. For this study it was simply assumed that the true range of the OTS for marten in different habitats was contained within the broad range of optimum territory sizes that were investigated.

The final factor influencing prey availability is individual hunting efficiency. This was implicitly incorporated into the model as one of the individual-level stochastic processes discussed earlier.

Prey density was modeled as an external input as it was not feasible to construct a realistic linked predator-prey model for all of the species involved, given the data that were available. We feel this simplification was reasonable, given that 1) it does not appear that predation is the major factor influencing small mammal dynamics (Krebs and Myers, 1974) 2) the marten is only one of many predators which utilize the small mammal species in question and 3) the focus of the model was on marten populations that are in danger of extinction and therefore are particularly unlikely to have a significant impact on their prey.

Previous population viability models have been criticized for failing to incorporate environmental stochasticity, or for using a form of stochasticity which is unrealistic, such as the "white noise" terms added to many analytical models (Boyce, 1992). Our approach was to equate environmental stochasticity with fluctuations in prey density based on field data, under the assumption that prey availability is the most important external factor influencing marten dynamics. The 32 years of data that were used should have been sufficient to capture the essential features of the temporal pattern and magnitude of the variation typically encountered (Thomas, 1990). It was assumed, with empirical support, that the densities of the principal marten prey species fluctuate synchronously (Thompson and Colgan, 1987). Prey density was uniform across the model grid within a given year in accordance with the regional nature of prey fluctuations observed in the field (Saitoh, 1987; Bissonette et al., 1988).

The substitution of random number sequences in place of the field data for fluctuations in prey density had no effect on the model's output, as long as the amplitude of the fluctuations was similar. Changes in the amplitude of the fluctuations did have an effect (Fig. 6c). Given that marten can switch among prey species, and assuming that the combined minimum density of prey is unlikely to go below 15% of its long-term mean, the system in Figure 6c likely represents an extreme. These are encouraging findings for the site-specific application of models of this sort, since long-term data on the prey base at the site where they are needed are generally lacking. It appears that an assumption of random environmental fluctuations will suffice, accompanied by an estimate of the anticipated long-term maximum range in the fluctuations.

In modeling recruitment the emphasis was placed on juvenile mortality, with the maximum ovulation rate treated as a physiological constant for the species. This was because accurate estimates of ovulation rate have been made by sectioning the ovaries of harvested marten (Strickland and Douglas, 1987), but estimates of juvenile mortality, including in-utero losses, are almost completely lacking. In an effort to contain this uncertainty, it was all combined into the one variable labelled juvenile mortality which was then investigated in detail.

The results of the model's function at carrying capacity provide support for the various assumptions listed above. The range of mean densities observed at carrying capacity (0.8 to 1.9

martens/Km<sup>2</sup>) using an OTS appropriate for central Ontario were in the same range as those reported by Thompson and Colgan (0.4 to 1.9/Km<sup>2</sup> over 5 years; 1987) and Francis and Stephenson (1.2 to 1.9/Km<sup>2</sup>; 1972) for this region. The age structure, temporal pattern of density fluctuations and magnitude of density variations were all qualitatively similar to field data collected on natural populations (Strickland and Douglas, 1987; OMNR, 1992). The comparison between the model's output and harvest data from traplines adjacent to Algonquin Park (Fig. 2) was particularly illustrative as both populations were subject to the same pattern of prey fluctuations. Given the myriad of external factors which could have influenced the harvest results, we feel that the qualitative similarity between the two patterns is a clear indication of the strength of the prey signal which was modeled.

When a population is very near to extinction individuals may become significantly influenced by processes such as the Allee effect and inbreeding depression, which were not modeled (Simberloff, 1988). These processes combine to form extinction vortices which tend to drive the population to extinction sooner than would otherwise be expected (Gilpin and Soulé, 1986). The quasi-extinction threshold of 20 females which was used as an alternative outcome in this study is therefore likely to be a more reliable measure, and is also more reasonable than extinction as the minimum tolerable population size in a management context.

Three qualitatively different forms of dynamic behavior leading to extinction were delineated during the investigation of

the model system. The first was deterministic extinction, resulting when parameter combinations were in the region of parameter space where the population growth rate was negative. Our estimates of the threshold for deterministic extinction in terms of mortality rate should be reasonable for populations on good quality habitat (e.g.  $OTS \leq 2.0$ ), where the upper limit on reproduction is set by the physiological capacity of the species. On poor quality habitat, however, there is greater uncertainty. Territories are larger, presumably entailing greater energetic cost, leading to some degree of reduction in the maximum potential reproduction and a lower mortality rate threshold (Thompson, in press).

The magnitude of this difference between habitat types is dependent on the function relating territory size and energetic cost. The two forms that were used represent extremes, bounding the possible behavior of the system. Evidence for the extreme nature of the linear increase form is in the false prediction that marten populations cannot persist when the OTS is greater than 3.4 (Bissonette et al., 1988). The high sensitivity of the model to this function indicates that further empirical research to better define it is required.

The second form of dynamic behavior was associated with parameter combinations leading to a population growth rate that was clearly positive. The defining feature of these models was strong density dependent control of the population size, restricting annual fluctuations to a well defined range. The minimum population size over time was therefore a fairly consistent linear

function of the mean population size, resulting in an abrupt transition between persistence and quasi-extinction when the habitat size (and hence carrying capacity) was decreased. This transition occurred at a population size of between 75 to 125 females for models representing a broad region of parameter space (but see caveats below).

The final form of dynamic behavior occurred in models with parameter combinations in the vicinity of the deterministic threshold (e.g., juvenile mortality rate = 0.7; Fig. 8). The behavior of these models was similar to a random walk, subject to an upper limit set by the lowest prey densities routinely encountered. The transition from persistence to quasi-extinction with decreasing habitat size was gradual in these models and even relatively large populations had non-trivial probabilities of quasi-extinction (and total extinction). It is anticipated that all of these populations would eventually go extinct if followed for a long enough time period, in contrast to the populations with strong positive growth rates.

Based on the analytical analysis of birth-death models it has been suggested that when environmental stochasticity is incorporated, the average persistence time of a population is a linear function of its size (Goodman, 1987). This is not consistent with our finding, in many fully stochastic models, of a discrete population size threshold beyond which the probability of extinction was negligible. The difference is due to the absence of density dependence in the analytical models, and suggests that the

earlier results may have restricted applicability. Some of our models did conform to the analytical predictions, however, so the suggestion by Ginzburg et al. (1990) that models without density dependence are useful for conservatively estimating extinction risk when the form of density dependence is unknown, seems valid.

Sensitivity testing the model with respect to secondary parameters did not result in any appreciable changes to the results presented. The exception to this was the function for the cost of territoriality, which was an important factor in poor quality habitats and needs to be characterized empirically. We conclude that these results are sufficiently robust to serve as a broad foundation for the understanding of extinction dynamics in the marten; however, for site-specific applications a number of other factors must be considered.

Foremost is the fact that the model did not take catastrophes, such as fire or disease epidemics, into account. The reported probabilities of extinction refer to the effects of demographic and environmental stochasticity only. Furthermore, in some systems of even-aged forest, large-scale reversion to an earlier successional stage through disease or wind-throw is possible as individuals of the dominant tree species reach the end of their lifespan (Thompson, 1991). We anticipate that landscape-level habitat management and a system of multiple marten populations will be necessary to ensure marten persistence within a given region over long time periods. The minimum size of each subpopulation could be estimated using the methodology presented here; their number and

location would depend on the site-specific catastrophe regime (Ewens et al., 1987). Further modeling would be of use if the catastrophes can be characterized.

Other model refinements for site-specific application include the incorporation of fine-scale data concerning habitat quality and its spatial configuration, possibly through the use of habitat suitability index models (Lofroth and Banci, 1991). If the habitat is not contiguous then the issues of dispersal and edge effects must be addressed. Marten will move out into cutover areas during the summer to hunt (Steventon and Major, 1982), and therefore more edge would imply more food for the population, but more edge may also imply greater access by terrestrial predators, increasing the mortality rate. Reports of marten dispersal between 40 and 100 Km are common (Bissonette et al., 1988; Slough, 1989), but beyond this dispersal distance may become a limiting factor. Empirical research on both of these factors is required.

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## Appendix A

Assumptions concerning basic marten biology used to construct the model.

1. Marten maintain exclusive territories within each sex (Powell, 1979).

2. Territory size is a function of prey availability (which is a function of prey density and habitat type) and intraspecific competition (Weckwerth and Hawley, 1962; Soutiere, 1979; Thompson and Colgan, 1987).

3. There is a minimum limit to territory size set by the minimum quantity of prey necessary to meet maintenance requirements, and by behavioral factors once territories reach a certain minimum size. Marten that are unable to acquire the minimum territory size enter a reproductively inactive "transient" class (Powell, 1979; Thompson and Colgan, 1987).

4. The energetic cost of territoriality, related to hunting efficiency and cost of defence, is proportional to territory size (Thompson, in press). As a consequence, there is a maximum limit to territory size.

5. Marten compete annually for the establishment of territories, with residents having primary access to the available habitat (as the best competitors), followed by transients and then young of the year (Weckwerth and Hawley, 1962; Bissonette, 1988).

6. Marten that are unable to establish a territory locally will disperse to the nearest patch of unoccupied habitat (Archibald

and Jessup, 1984). Dispersal distance is not a limiting factor for marten within the habitat sizes being modeled (Slough, 1989).

7. Reproduction only occurs once per year, and marten females do not produce litters until they are at least two years of age (Strickland and Douglas, 1987).

8. Males and females are born in approximately equal numbers (Strickland and Douglas, 1987).

9. There is a physiological upper limit to the mean reproductive output that marten are capable of. Below this limit, reproductive output is primarily a function of a female's energy balance (Weckwerth and Hawley, 1962; Thompson and Colgan, 1987; Bissonette et al., 1988).

10. The amount of energy available for reproduction is the amount derived from eating prey (primarily a function of prey availability) less a constant quantity for maintenance requirements, and a variable quantity associated with territoriality.

11. In addition to the above deterministic processes, there are stochastic elements involved in reproduction reflecting processes operating at the individual-animal level (Simberloff, 1988).

12. Mortality is primarily a stochastic process, except for juveniles which are influenced by their mother's energy balance during and after gestation (Strickland and Douglas, 1987).

## Appendix B

### Derivation of the Analytical Model

The model was based on the following equation:

$$\Delta N = \text{Recruits} + \text{Survivors} - N_0$$

Assuming that all available habitat is divided equally among residents and the population growth rate is positive, the equilibrium population size is:

$$N_{EQ} = RMAX + \frac{AREA [RMORT - MALE \cdot OVUL (1 - JMORT) (1 - RMORT)]}{OTS [MALE \cdot OVUL (1 - JMORT) (1 - TMORT) - TMORT]}$$

Where:

- AREA = the size of the habitat patch (Km<sup>2</sup>).
- OTS = the optimum territory size for the region (Km<sup>2</sup>).
- RMAX = the maximum number of residents (AREA/OTS)
- RMORT = the per capita adult resident mortality rate.
- JMORT = the per capita juvenile mortality rate.
- TMORT = the per capita transient mortality rate.
- OVUL = the per capita ovulation rate.
- MALE = the percentage of males born.

This function is discontinuous, however, as recruitment reaches a maximum constant if there are more adults surviving than there are available territories. The equilibrium population size then becomes:

$$N_{EQ} = RMAX + \frac{AREA [MALE \cdot OVUL (1 - JMORT) - RMORT]}{OTS \cdot TMORT}$$

## Literature Cited

- Archibald, W.R. and R.H. Jessup. 1984. Population dynamics of the pine marten in the Yukon territory. Pages 81-97 in R. Olsen, R. Hastings and F. Geddes, editors. Northern ecology and resource management. University of Alberta Press, Edmonton, Alberta.
- Bateman, M.C. 1986. Winter habitat use, food habits and home range size of the marten in Western Newfoundland. Canadian Field Naturalist. 100:58-62.
- Bissonette, J.A., R.J. Fredrickson and B.J. Tucker. 1988. The effects of forest harvesting on marten and small mammals in Western Newfoundland. Utah Cooperative Fish and Wildlife Research Unit., Logan, UT.
- Boss, J., G. Deveau and C. Drysdale. 1987. Kejimikujik National Park. American marten reintroduction program. Parks Canada, Atlantic Region, Interim Report., Halifax, Nova Scotia.
- Boyce, M.S. 1992. Population viability analysis. Annual Review of Ecology and Systematics. 23:481-506.
- Buskirk, S.W. 1992. Conserving circumboreal forests for martens and fishers. Conservation Biology 6:318-320.
- Buskirk, S.W. and L.L. McDonald. 1989. Analysis of variability in home-range size of the American marten. Journal of Wildlife Management 53:997-1004.
- Ewens, W.J., P.J. Brockwell, J.M. Gani and S.I. Resnick. 1987. Minimum viable population size in the presence of catastrophes. Pages 59-68 in M.E. Soulé, editor. Viable populations for conservation. Cambridge University Press, Cambridge, England.
- Falls, B. 1986. Small mammal populations in Algonquin park. Report submitted to the Ontario Ministry of Natural Resources.
- Francis, G.R. and A.B. Stephenson. 1972. Marten ranges and food habits in Algonquin Park, Ontario. Resource report #91. Ontario Ministry of Natural Resources, Ottawa, Ontario.
- Gilpin, M.E. and M.E. Soulé. 1986. Minimum viable populations: processes of species extinction. Pages 19-35 in M.E. Soulé, editor. Conservation biology: the science of scarcity and diversity. Sinauer Assoc., Sunderland, Massachusetts.
- Ginzburg, L.R., S. Ferson and H.R. Akcakaya. 1990. Reconstructibility of density dependence and the conservative assessment of extinction risks. Conservation Biology 4:63-70.

- Goodman, D.. 1987. The demography of chance extinction. Pages 11-34 in M.E. Soulé, editor. Viable populations for conservation. Cambridge University Press, Cambridge, England.
- Krebs, C.J. and J.H. Myers. 1974. Population cycles in small mammals. *Advances in Ecological Research* 8:268-400.
- Lofroth, E.C. and V. Banci. 1991. Marten habitat suitability research project working plan. Pages 1-26 in Wildlife working report No. WR-50. B.C. Ministry of the Environment, Victoria, British Columbia.
- Markley, M.H. and C.F. Bassett. 1942. Habits of captive marten. *American Midland Naturalist* 28:605-616.
- Ontario Ministry of Natural Resources (OMNR). 1992. Marten harvests, Algonquin region.
- Pimm, S.L. and A. Redfern. 1988. The variability of population densities. *Nature* 334:613-614.
- Powell, R.A. 1979. Mustelid spacing patterns: variations on a theme by *Mustela*. *Z. Tierpsychologia* 50:153-165.
- RENEW (Recovery of Nationally Endangered Wildlife). 1990. Annual report (1989/1990). Canadian Wildlife Service, Ottawa, Ontario.
- Ritchie, J.W. 1953. Raising marten for twenty-four years. *Fur Trade Journal of Canada* 30:10-24.
- Saitoh, T. 1987. A time series and geographical analysis of population dynamics of the red-backed vole in Hokkaido, Japan. *Oecologia* 73:382-388.
- Simberloff, D. 1988. The contribution of population and community biology to conservation science. *Annual Review of Ecology and Systematics* 19:473-511.
- Slough, B.G. 1989. Movements and habitat use by transplanted marten in the Yukon territory. *Journal of Wildlife Management* 53:991-997.
- Snedecor, G.W. and W.G. Cochran. 1980. *Statistical methods*, seventh edition. Iowa State University Press, Ames, Iowa.
- Soutiere, E.C. 1979. Effects of timber harvesting on marten in Maine. *Journal of Wildlife Management* 43:850-860.
- Steventon, J.D. and J.T. Major. 1982. Marten use of habitat in a commercially clear-cut forest. *Journal of Wildlife Management* 46:175-182.

Strickland, M.A. and C.W. Douglas. 1987. Marten. Pages 531-546 in M. Novak, J.A. Baker, M.E. Obbard and B. Malloch, editors, Wildfurbearer management and conservation in north America. Ontario Trapper's Assoc., Toronto, Ontario.

Thomas, C.D. 1990. What do real population dynamics tell us about minimum viable population sizes. Conservation Biology 4:324-327.

Thompson, I.D. In press. Marten activity in mature and post-logging boreal forest in Ontario. Journal of Wildlife Management.

Thompson, I.D. 1991. Could marten become the spotted owl of eastern Canada? Forestry Chronical 67:136-140.

Thompson, I.D. and P.W. Colgan. 1987. Numerical responses of martens to a food shortage in northcentral Ontario. Journal of Wildlife Management 51:824-835.

Weckwerth, R.P. and V.D. Hawley. 1962. Marten food habits and population fluctuations in Montana. Journal of Wildlife Management 26:55-74.

Table 1. Parameter values used in the model, including the maximum and minimum range used in sensitivity testing. The values represent pooled estimates from the studies cited in the introduction and in Appendix A.

Parameter	Base Model Estimate	Minimum	Maximum
Juvenile Mortality Rate <sup>1</sup>	0.60	0.50	0.75
Adult Resident Mortality Rate	0.35	0.25	0.50
Adult Transient Mortality Rate	0.60	0.40	0.75
Maximum Ovulation per Female <sup>2</sup>	4.0	4.0	4.0
Minimum Territory Size (Km <sup>2</sup> )	0.75	0.50	0.75
Maximum Territory Size (Km <sup>2</sup> )	12.0	6.0	12.0
Minimum % OTS for Reproduction <sup>3</sup>	15.0	15.0	40.0
Energetic Cost of Territory Size (%) <sup>4</sup>	0.0	0.0	100.0

<sup>1</sup>Minimum mortality rate, in juveniles with mothers that achieved 100% OTS.

<sup>2</sup>Mean physiological maximum ovulation rate for the species (i.e. for females not limited by energetic constraints).

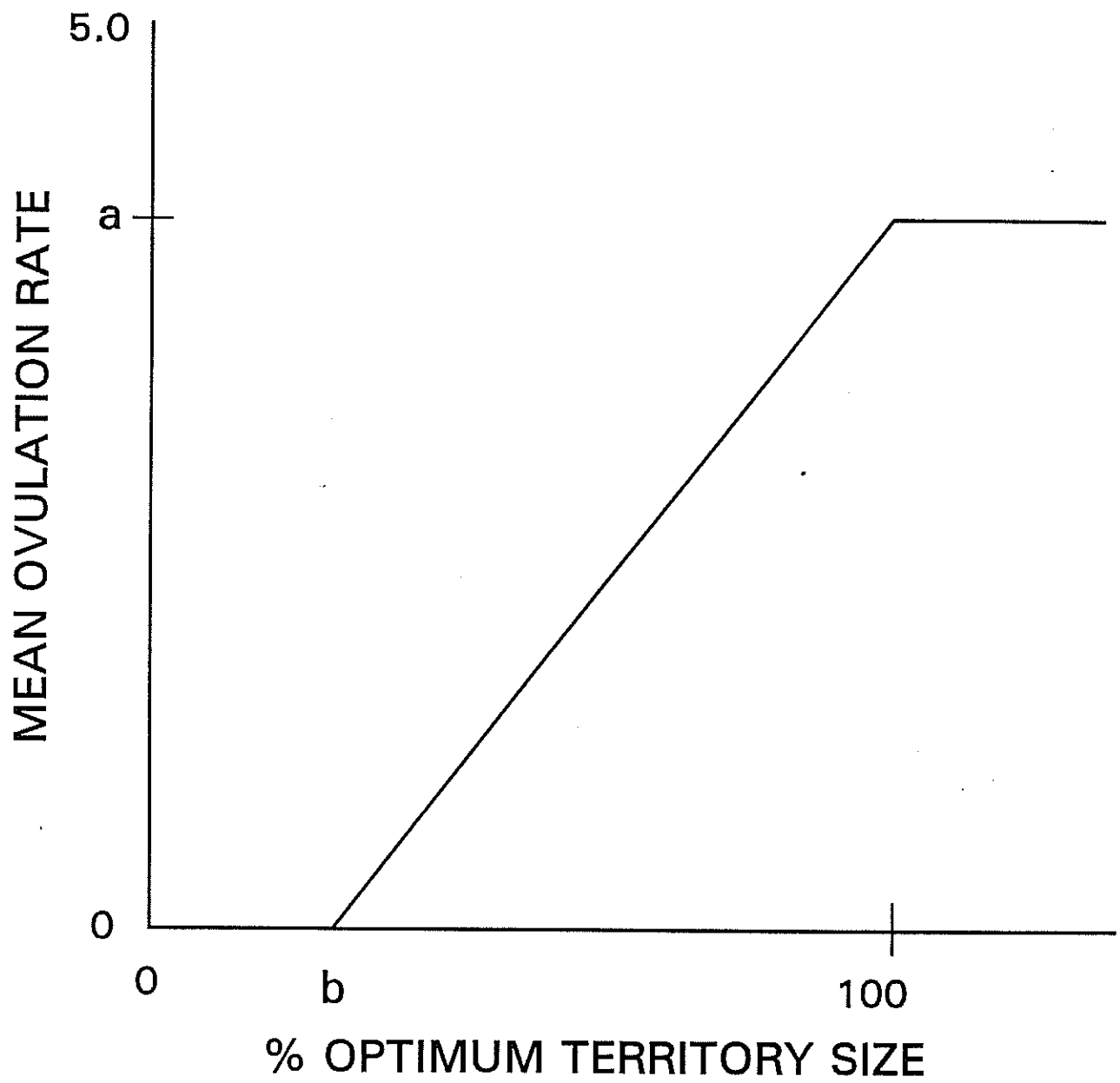
<sup>3</sup>Reproduction will not occur unless sufficient territory has been acquired to meet this percentage of OTS.

<sup>4</sup>Reflects the percentage reduction in ovulation rate at the maximum territory size.

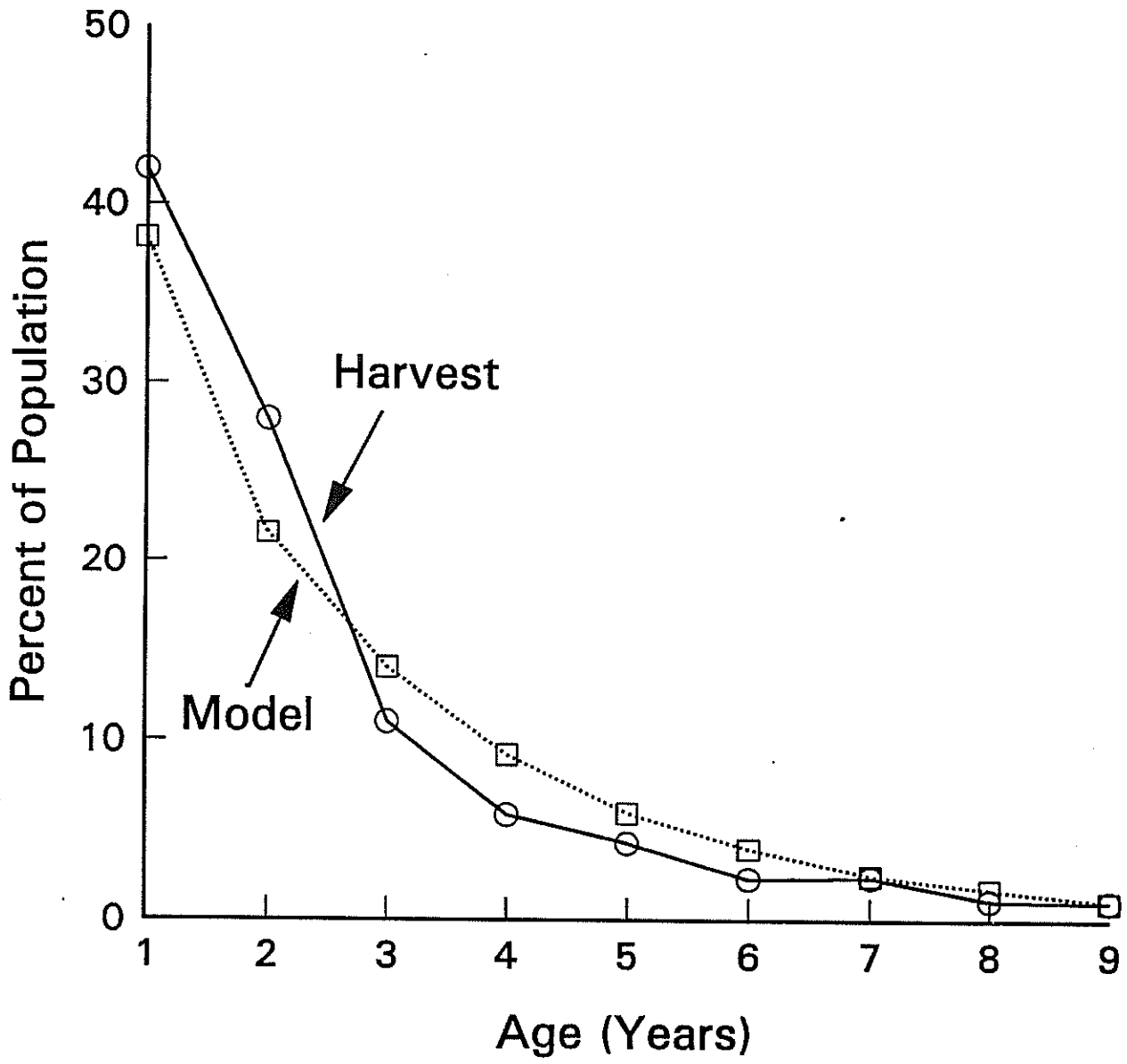
## Legends for illustrations

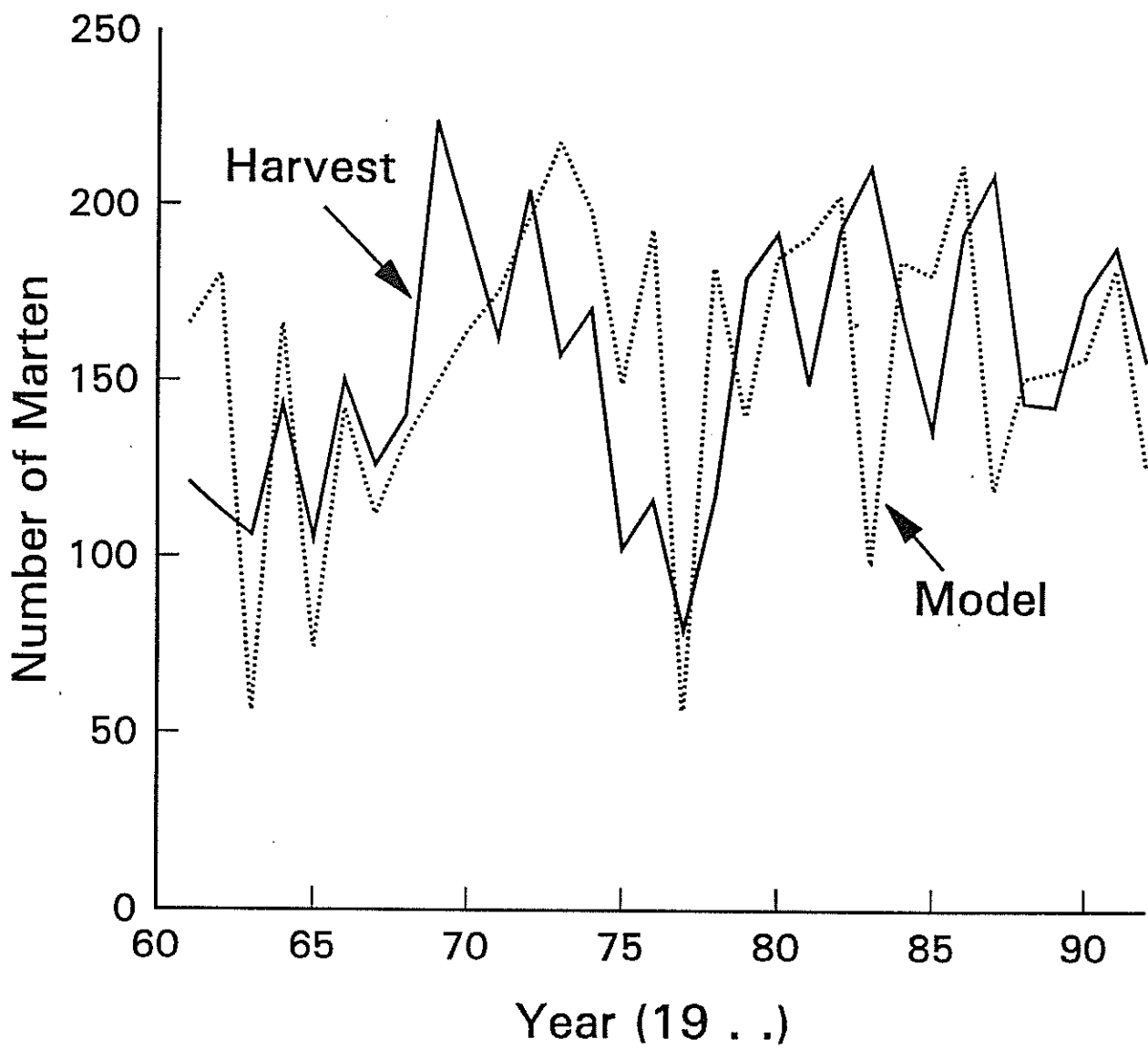
1. Functional relationship between the percentage of OTS achieved and the mean ovulation rate, for individual females ("a" = physiological maximum; "b" = minimum %OTS for ovulation to occur).
2. Average age distribution of the modeled population over 500 years with parameters at their base levels, and of 829 female marten harvested over a 12 year period in central Ontario, Canada (Strickland and Douglas, 1987).
3. Number of marten harvested from 1960 to 1992 on traplines adjacent to Algonquin Park, Ontario, Canada (OMNR, 1992) and annual size of the modeled population, averaged over 10 runs, using 1960 to 1992 prey density estimates from Algonquin Park (Falls, 1986; Falls, pers. comm.). The mean size of the modeled population was scaled to the mean of the harvested population as the densities for the latter were unknown.
4. Mean marten density over 500 years versus OTS for 5 model types. A= analytical model; B= demographic stochasticity only; C= same as B with cost of territoriality proportional to territory size; D= demographic and environmental stochasticity; E= same as D with proportional territory cost.
5. Deterministic extinction threshold for mortality rate as a function of OTS for 4 model types. A= demographic stochasticity only; B= demographic and environmental stochasticity; C= same as A with cost of territoriality proportional to territory size; D= same as B with proportional territory cost. The upper 4 lines refer to juveniles and the lower 4 lines to adults.
6. Probability of extinction over 500 years as a function of habitat size and OTS. A, demographic and environmental stochasticity with constant territory cost. Outcome is quasi-extinction. B, same as A, except outcome is total extinction. C, same as A, but using random numbers as prey input, with range = 15% to 190% of mean. D, same as A but with demographic stochasticity only.
7. Probability of extinction over 500 years as a function of habitat size and juvenile mortality rate. Outcome is quasi-extinction threshold incorporating both demographic and environmental stochasticity.
8. Probability of extinction over 500 years as a function of mean population size for 3 levels of juvenile mortality rate.
9. Coefficient of variation (dashed line = demographic stochasticity only; solid line = demographic and environmental stochasticity) and minimum population size (dotted line) over 500 years as functions of mean population size.

Fig. 1.

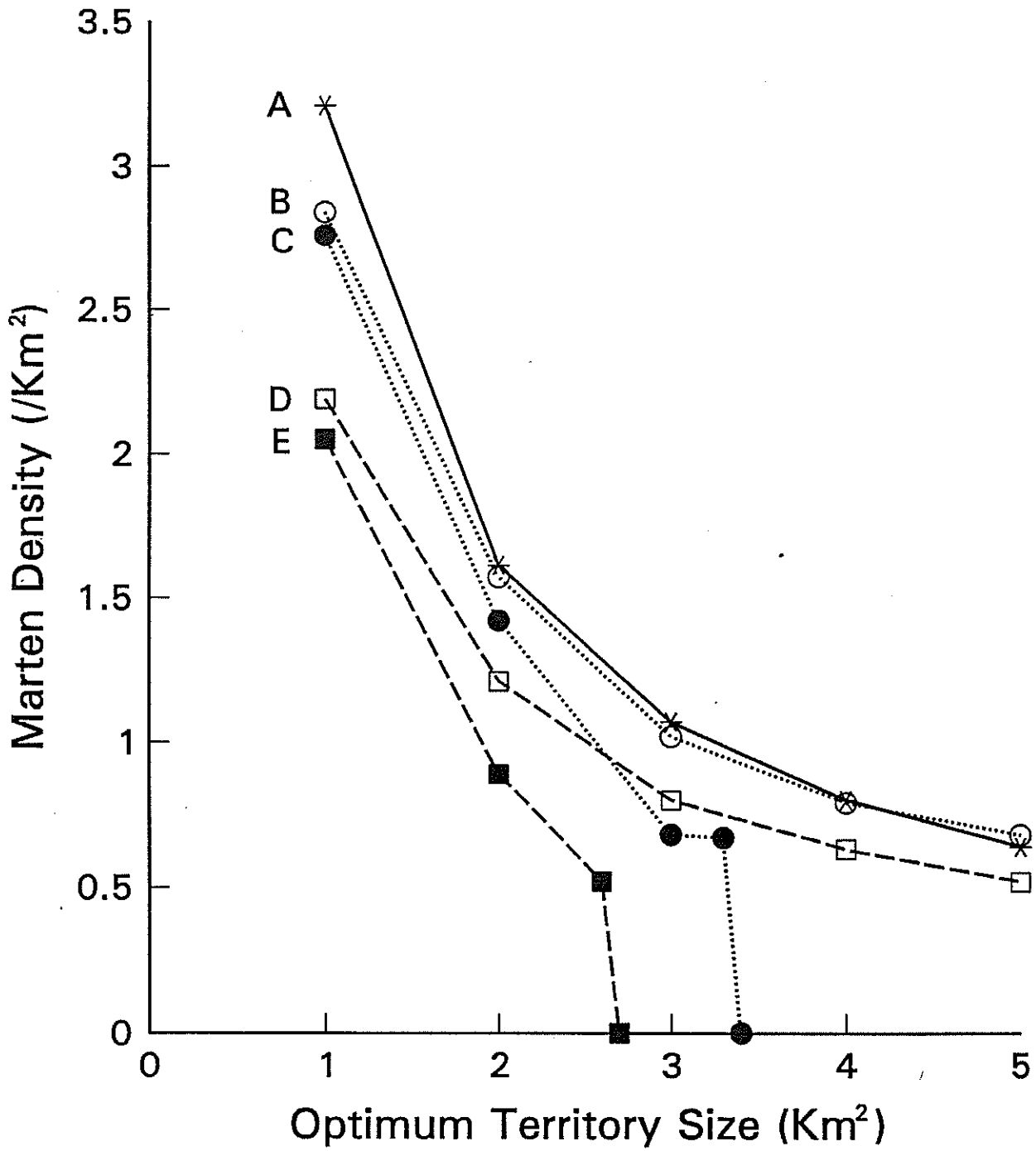


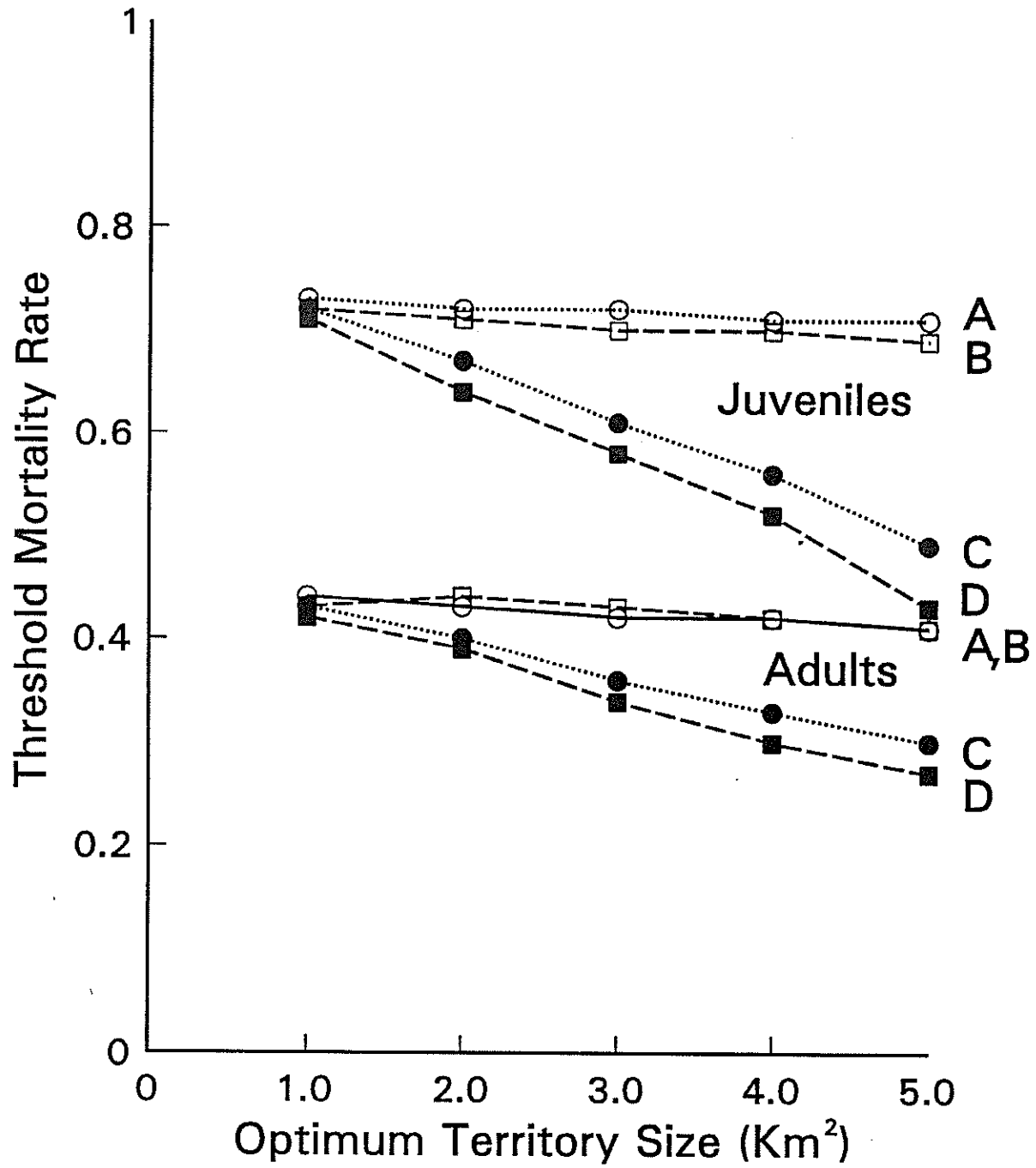
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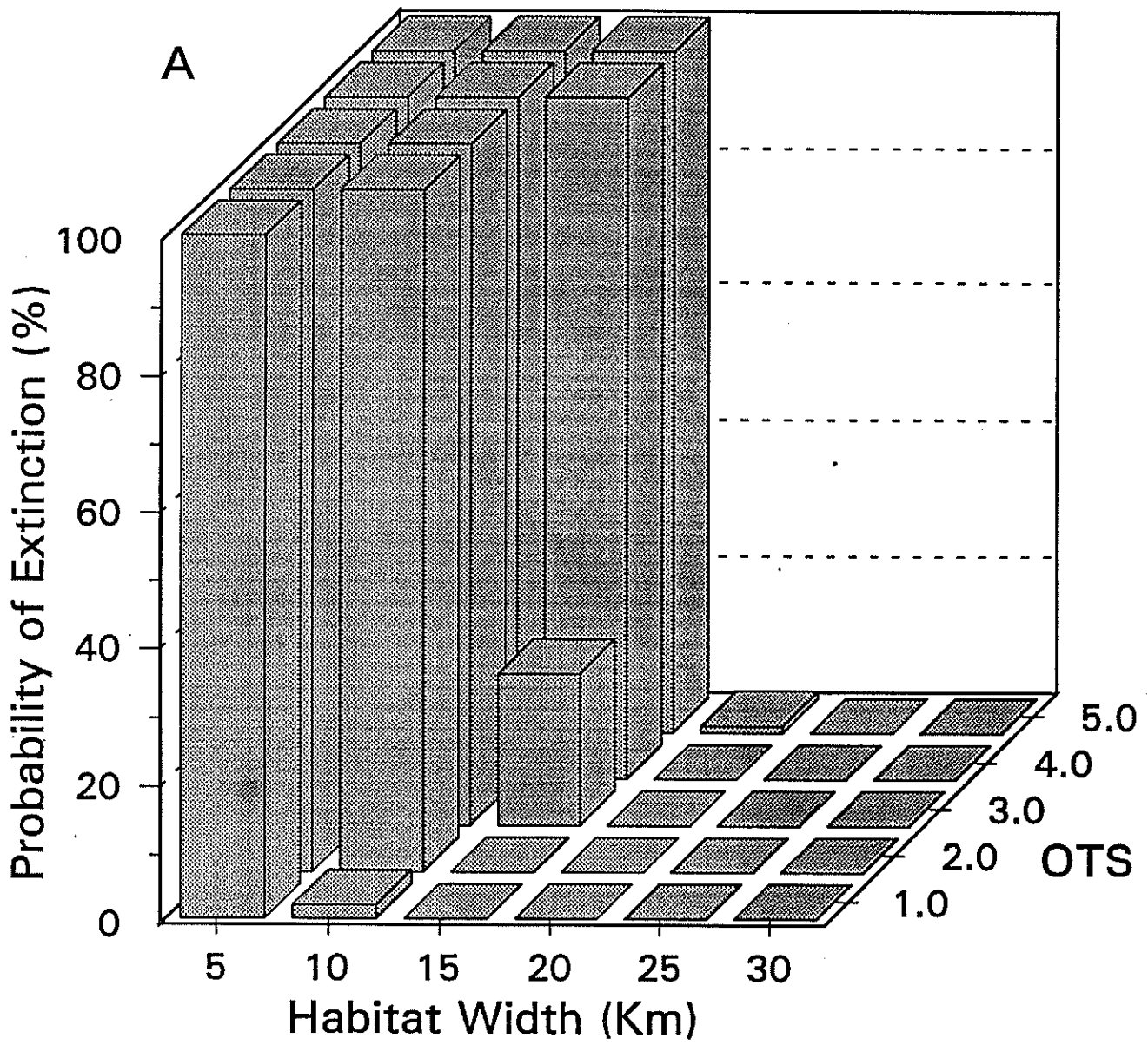


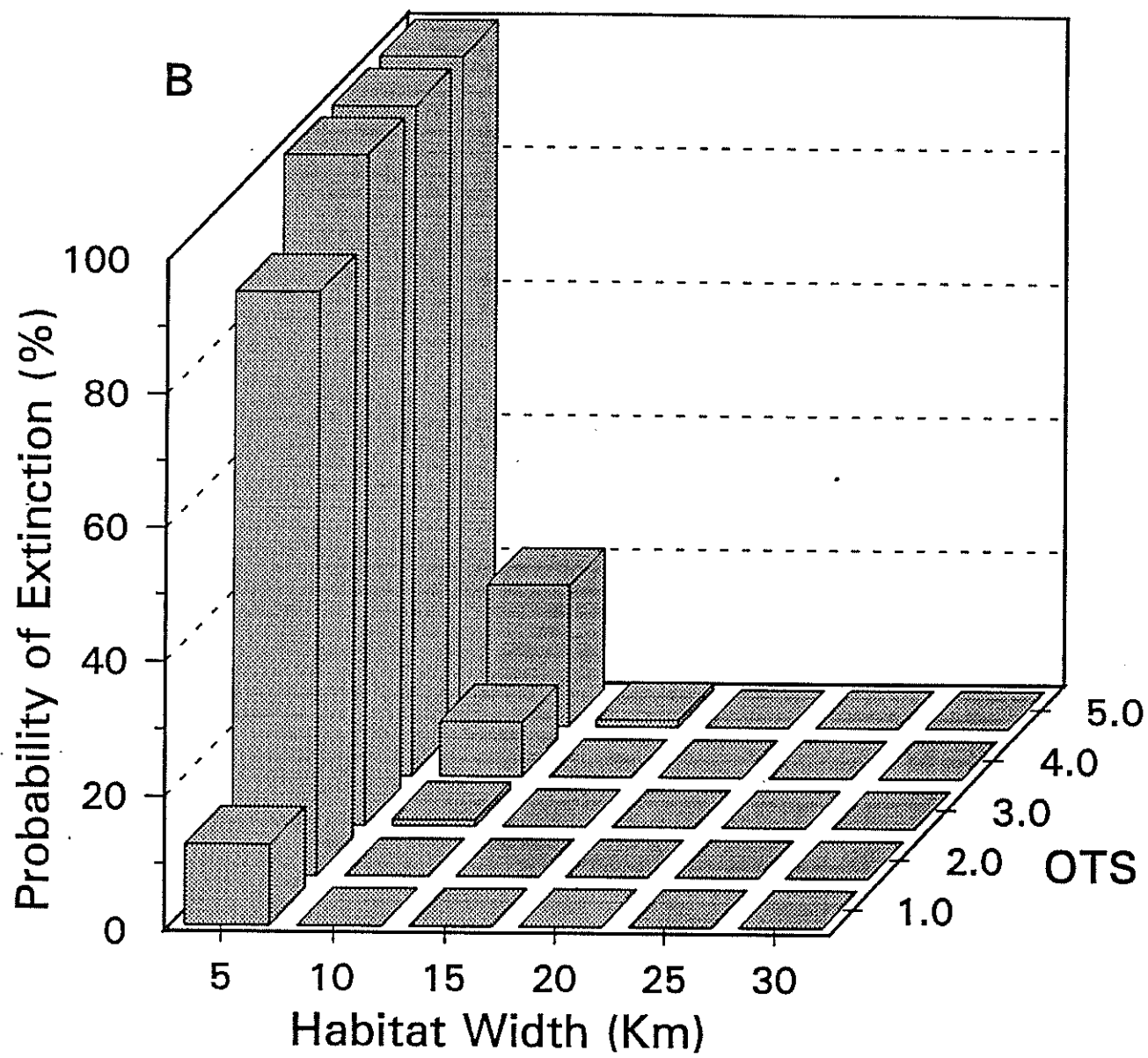
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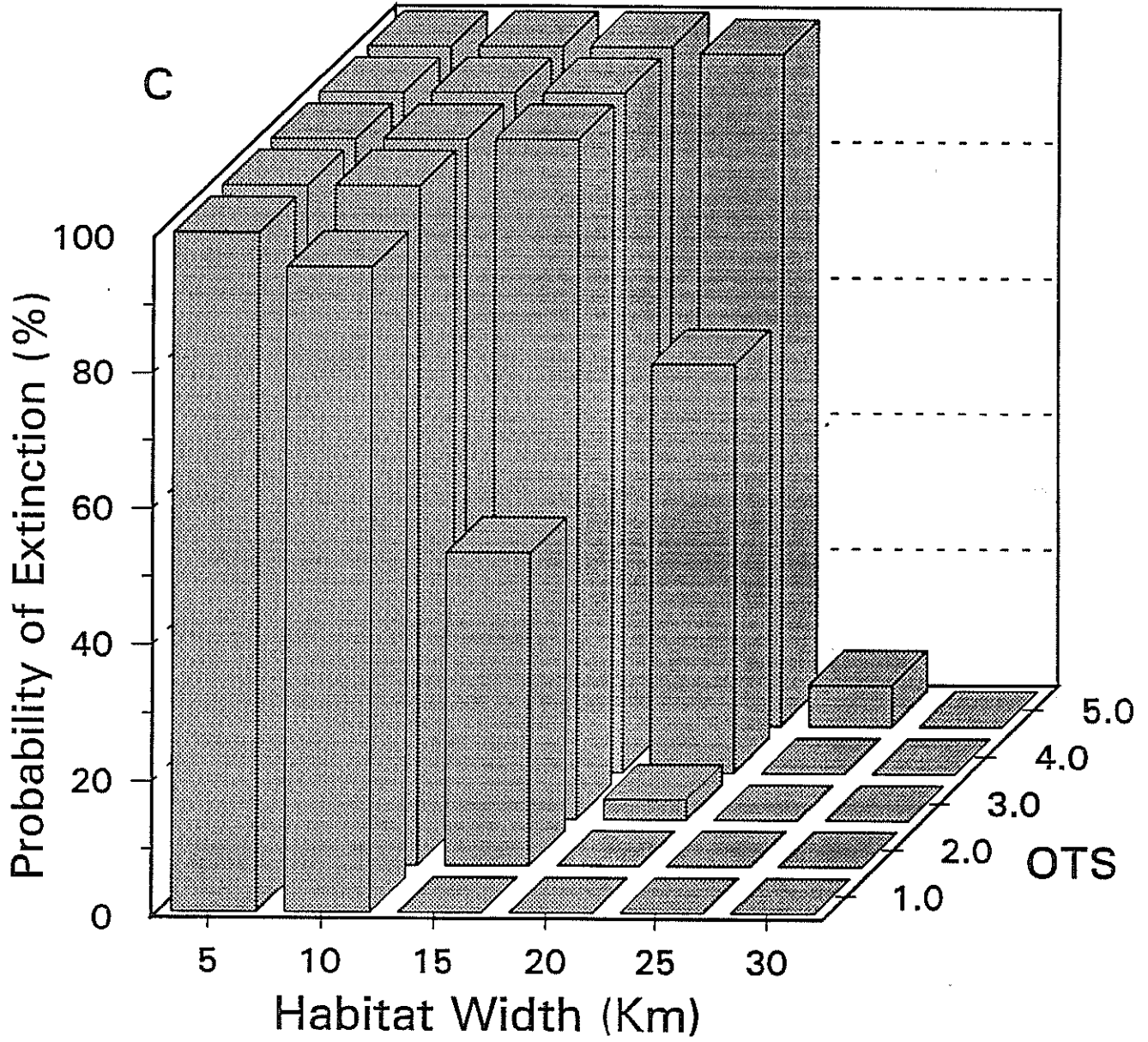


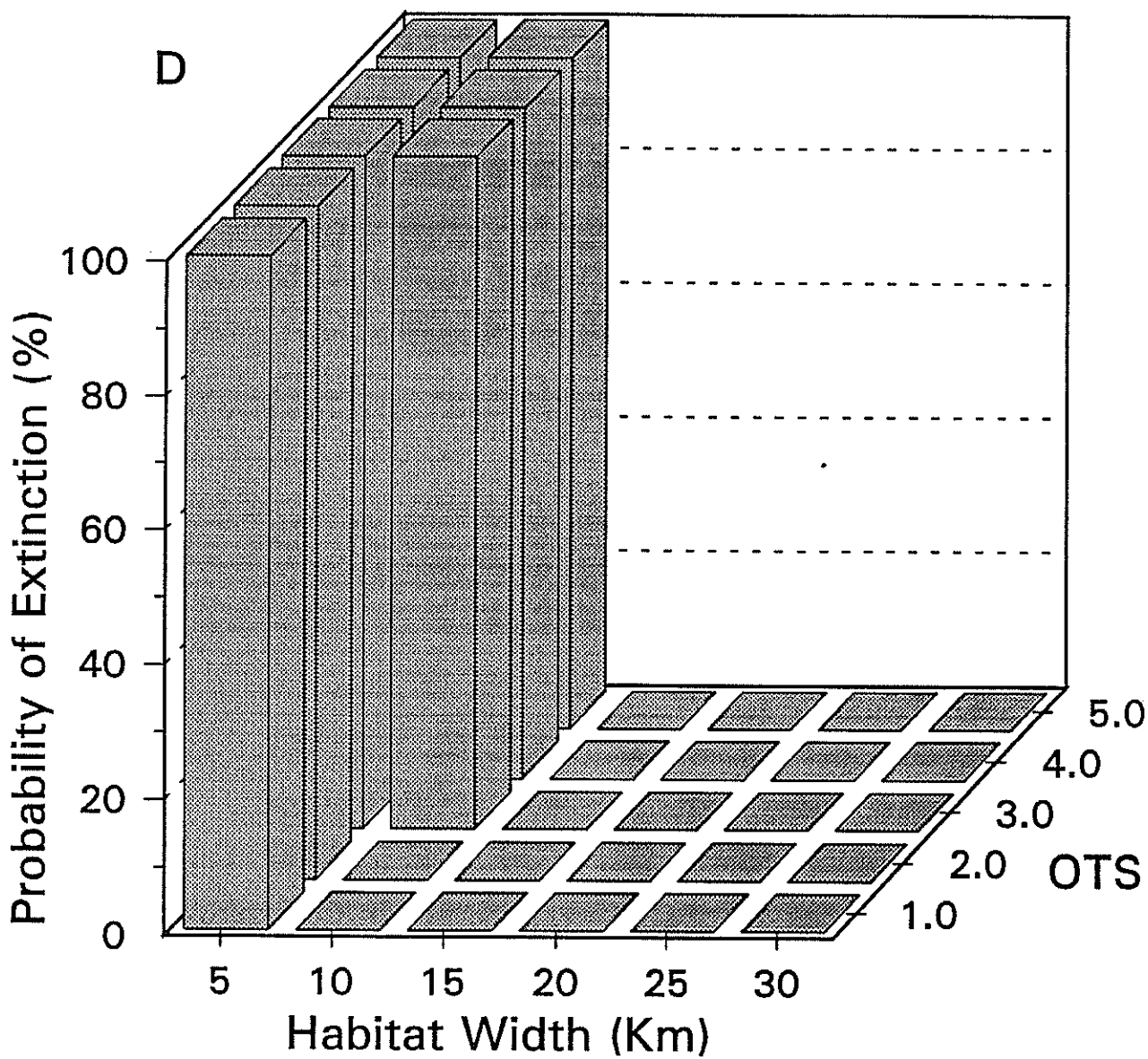
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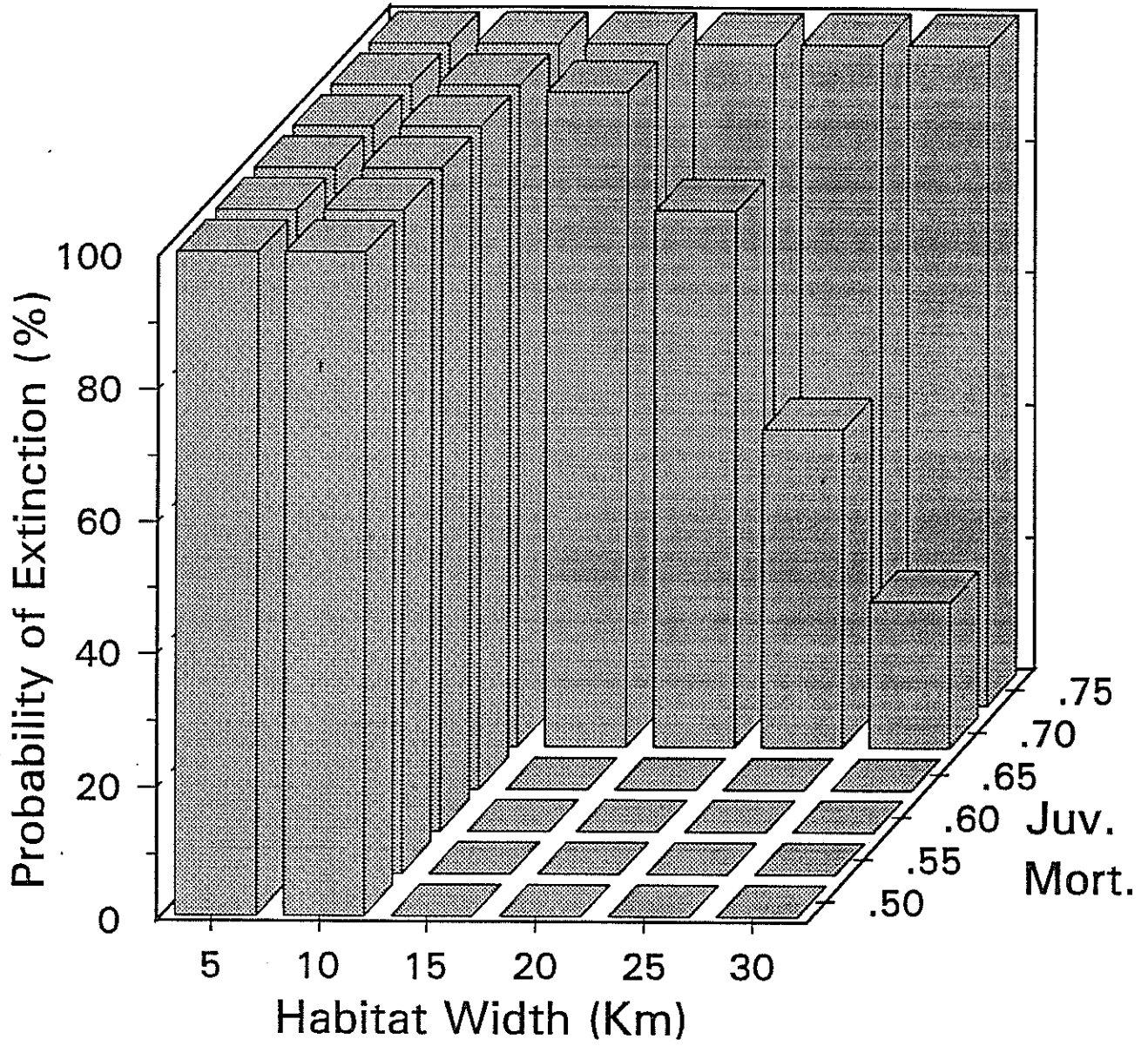


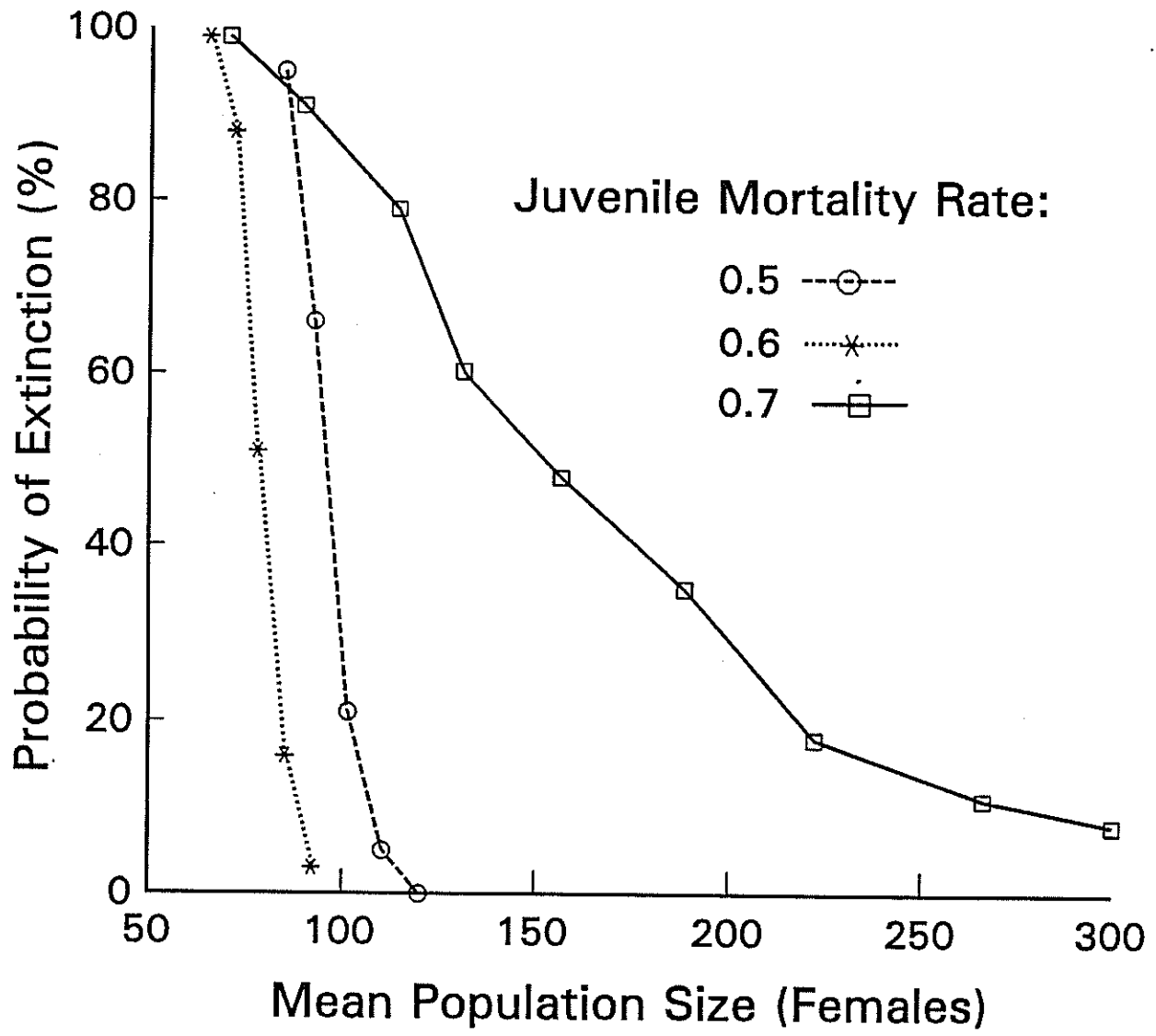
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F7





F9

