

Release

**A SPATIALLY EXPLICIT INDIVIDUAL-BASED MODEL
FOR FLORIDA PANTHER IN THE EVERGLADES LANDSCAPE**

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I. Introduction

This report describes the basic components of a preliminary model for the Florida panther. The dynamics of a population, particularly very small populations, with highly complex internal structure on a heterogeneous landscape can be more accurately described by individual-based models than by highly aggregated ones. Individual-based models offer the capability to simulate the life cycles of all individuals comprising the population, their interactions, and their response to environmental changes. As the population of Florida panther, an endangered species, is very low in the Everglades and surrounding landscape, we propose to carry out an individual-based modeling approach to analyze the behavior of this species on the Everglades landscape.

This model will be constructed to couple with SIMDEL, a spatially-explicit individual-based model for white-tailed deer in the Everglades landscape. It is proposed to simulated the interactions among Florida panther, white-tailed deer, climate change, hydrology, vegetation dynamics, habitat fragmentation, and human activities. This manuscript describe the structure, algorithm, and parameterization of the procedure PANTHER in SIMDEL.

II. Model Overview

The procedure has as a goal to simulate the dynamics of a panther population with a highly complex internal structure in

the Everglades landscape. PANTHER is projected to be used to understand and predict the viability of the population by representing the life cycles of panther individuals explicitly in a heterogenous environment. The procedure is composed of four subroutines; PREPRO, PGROW, PREDAT, and POPUL.

Subroutine PREPRO concerns the reproduction of panther. The impacts of habitat change, prey density, and population structure on panther reproduction are the focus in this subroutine. The sex ratio, pregnancy rate and age, and survivorship of the newborn are the important parameters.

PGROW is the subroutine for panther growth. Daily energy balance is calculated in PGROW. Body weight gain and lost depend largely on metabolic energy cost, energy cost for movement and predation, and energy gained from prey. The energetic gain and loss may be different from sexes and ages.

PREDAT simulates predation. The predation strategy, moving distance, frequency of predation, habitat preference, home range size, den sites, interactions between panther and deer, and the spatial distribution are the basic components in the subroutine.

POPUL focuses on the population dynamics by simulating the mortality and reproduction. Mortality is caused by old age, disease, nutrition, mercury poisoning, hunting, and highway killing. The sex and age structure of the population will depend upon the output of this routine.

III. Key Model Components

Procedure PANTHER simulates the population dynamics of the Florida panther in the Everglades landscape and the interactions with white-tailed deer. A genetic submodel and simulations of effects of mercury intake on panther are planned as well, but no description of these components is included below. A set of behavior rules, algorithms, and parameterization for each submodel is discussed as followings.

3.1 Subroutine PREPRO

Subroutine PREPRO models the reproduction processes and the factors influencing panther reproduction. The main concerns are the age for first breeding, number of litters in life time, number of kittens for each litter, birth weight, sex ratio, mating behavior, and factors affecting reproduction.

Observations from Maehr et al. (1989) indicate a female panthers older than 18 months can become pregnant as soon as it has established its own territory (Hornocker 1971); but a male needs to be 2.5, being estimated between 2 (Seal et al. 1989) or 3 (Hornocker 1971), years old for the first sexual encounters to occur. The subroutine includes an array (PNAG(jj), jj=1, ..., NP; NP=total number of panther) for recording the age of each panther and another array (PNSX(jj), jj=1, ..., NP) for identifying the sex.

A female can rear approximately four successful litters in their lifespan with birth intervals ranging from 16 to 37 months

(Russell 1978). There are two alternatives for simulations of panther pregnancy: (1) Since there are no data to determine the effects of age and nutrition on pregnancy available to us, we will randomly distribute four pregnancies between an age of 18 months to 10 years old with an interval of 16 to 37 months. (2) There is a probability of pregnancy for a female older than 18 months. The probability will depend on age, nutrition, male availability. The model simulates a male encountering the first mating after it is 2.5 years old. Since the proportion of adult males and females breeding each year is about 50% of adult females and perhaps fewer adult males (Seal et al. 1989), a male will be selected to mate or not at a probability (PMM) of 0.50. The probability for female to mate (PFM) varies from ages, which is modified from Maehr and Moore (1992) and Seal et al. (1989) (Table 1). A probability of effects of nutrition on breeding

Table 1. Probability of mating (PFM) for different age of female panther based on Maehr and Moore (1992) and Seal et al. (1989).

Age	<1	2	3	4	5	6
PFM	0.00	0.25	0.50	0.75	0.75	0.75
Age	7	8	9	10	11	>11
PFM	0.50	0.25	0.25	0.10	0.05	0.00

(PNB) will be used for the consideration of nutrition effects. PNB is estimated by the body weight of a female (PBW) divided by mean body weight of individuals with the same age (PMBW, Table 2, Maehr and Moore 1992). If PBW is greater than PMBW, PNB will be set to 1.

Table 2. Estimated mean body weights (kg) and 95% confidence intervals by sex and age classes (Maehr and Moore 1992).

Age	1	2	3	4	5	>5
F	21	34	37	39	40	41
±	6	9	9	10	11	12
M	29	49	54	55	56	56
±	5	12	12	12	12	12

Panthers can have litters in any month of the year (Russell 1978), but eighty-one percent of births occur between March and July (Maehr 1990). The period of gestation is 90-96 days (Anderson 1983). The model simulates a normal distribution of time periods of panther pregnancy with a mean of February 15 and 81% of pregnancies occurring within the period of December 1 to April 30. After 90 days of gestation, a panther will give birth. The mean or the birth peak will be May 15. If a female is simulated to be pregnant in the year, a day should be selected based on the mean of February 15 and 81% of probability within

the period of December 1 to April 30. As the pregnant day is determined, mating is simulated. A male will company with a female without hunting or food as long as 4 days (LIKE BOBCAT?). (DISCUSSION: 1. How about if there is no male available? 2. How many females can a male service? 3. Will a female lose a chance of being pregnant or another estrus is expected and what is the number and interval in a year?). The date for giving birth is the day of pregnant plus 90 days. Though the mean birth interval is 2 years but a female can rebreed with loss of litter. Reproductive life-span is about 7-9 years with maximum longevity of about 15 years. Few records of breeding after 11 years (Seal et al. 1989).

Based on Russell's research (1978) the sexual ratio at birth is estimated as 1.2-1.3:1.00 of males to females and litter sizes may be 1-6 kittens with a mean of 2.6. The probability of the number of kittens for a litter is determined by a triangle function and the probabilities are listed in Table 3. In the model, the number of a litter is determined by calling a random number and the probability distribution in Table 3 (DISCUSSION: if the number of kittens may be affected by any means?).

Table 3. The probabilities of having the number of kittens in a litter.

No. of Kittens	1	2	3	4	5	6
Probabilities	0.11	0.23	0.28	0.19	0.13	0.06

The sex at birth is determined randomly in the model with a probability of 0.56 for males and 0.44 for females (DISCUSSION: It was estimated as 1:1 by Seal et al. 1989). The body weight at birth will be estimated as 1.25 kg (Maehr et al. 1989).

Care of young is also simulated in the model. A kitten will company with its mother for about 12-18 months (Seal et al. 1989). The lactating period lasts 45 to 90 days (Seal et al. 1989). The model uses 60 days for average. A natural mortality rate can be estimated as 0.50 at birth (Seal et al. 1989).

Model components for which we are still finding information to estimate include: 1) Has distance been a problem for a male to mate with a female? 2) How does habitat fragmentation (separation) may affect mating opportunity? 3) Is age a factor for males in mating competition? 4) What else are important to reproduction?

3.2 Subroutine PGROW

This subroutine projects the growth and daily energy balance of an individual panther. It simulates each individual panther from the day of birth through its whole life cycle. Two important points are 1) to simulate the growth of kittens during the lactating period and 2) to model the asymptote growth function of body weight increases.

Body weights of newborn kittens are 1.25 kg (Maehr et al. 1989). During the lactating period if the female is healthy, a kitten should grow at a constant rate of about 82 g/day and 62

g/day for male and female kittens, respectively (Maehr and Moor 1992). The model assumes that the growth rates (PKGR) for a kitten will be retarded or enhanced by the health conditions of the mother. This will be done by a linear function of percent of female body weight (PBW) divided by panther mean body weight (PMBW) as,

$$PKGR = PSKGR * (PBW / PMBW) \quad (1)$$

where,

PSKGR = 62 g for female kittens and 82 g for male ones.

Also required for the simulation are energy cost (PNC) and energy gain (PNG) data, such as traveling and predation energy costs (PNCT), maintenance energy cost (PNCM), and energy gained (PNG) from prey (deer). Daily energy balance (PNB) are computed at the end of each simulation time step (day) as followings,

$$PNB = PNG - PNC \quad (2)$$

$$PNG = PDMI * NKCKG \quad (3)$$

$$PNC = PNCT + PNCM \quad (4)$$

where,

PDMI = daily meat intakes (kg)

NKCKG = energy content per kg meat (kcal/kg)

Several assumptions, which are discussed below, are necessary to estimate these energetic costs and intakes.

(1) Daily meat intakes (PDMI): According to Hornocker (1970), a panther may require 2.3 kg of meat each day. If we

assume that an average body weight for a female panther is 40 kg (Seal et al. 1989) and PDMI can be calculated using equation 2,

$$\text{PDMI} = \text{MCC} * \text{BW}^{0.75} \quad (5)$$

where,

MCC = meat consumption coefficient,

then,

$$\text{MCC} = \text{PDMI} / \text{BW}^{0.75} = 2.3 * / 40^{0.75} = 0.1446 \text{ (kg)} \quad (6)$$

Then, equation 2 can be written as,

$$\text{PDMI} = 0.1446 * \text{BW}^{0.75} \quad (7)$$

(2) Converting rate (PCR) of net energy ($\text{PNB}^+ = \text{PNG} - \text{PNC}$) contributing to body weight: Based on the characteristics of asymptote body weight growth function (Maehr and Moore 1992), which means that there is a limit of body weight increases up to a certain age, we assume that not all the net energy goes to body weights and use a converting rate (PCR) for calculating energy gained from food used to build up body weight. The model will set PCR as a step function based on body weight classes listed in Table 4. It is assumed that a panther will convert 100% of its daily positive energy balance (PNB^+) to body weight gain as it is younger than 1.5 years ($\text{PCR} = 1.00$). As the panther is growing up and its body weight increases, less PNB^+ will be converted to body weight gain, which will keep body weight close to asymptote function. As a result, PCR is used as a step function in the model for different body weight classes.

Table 4. Relationships among age (yr), body weight (kg), and daily growth rate (g) modified from Maehr and Moore (1992) and the converting rates (PCR) based on assuming daily growth rate of 62 g as 100% converting rate (Female/Male).

Age	Body Weight	Daily Growth Rate	PCR
0.2	5.7/ 7.2	62.0/82.0	1.00/1.00
1.5	27.5/39.0	35.6/54.8	0.58/0.67
2.5	35.5/51.5	8.2/13.7	0.13/0.17
3.5	38.0/54.5	5.5/ 2.7	0.09/0.03
4.5	39.5/55.5	2.7/ 2.7	0.04/0.03
>4.5	40.5/56.0	2.7/ 1.4	0.04/0.02

(3) Traveling Energy Costs (PNCT) -- Daily maximum travel distance (PMTD) is found to be about 15 to 20 km (Seal et al. 1989), as 40 km reported by Russell (1978), but the average is 2.4 km (Maehr et al. 1989). The model sets a daily maximum travel distance as 20 km for adult males, 15 km for adult females, and 10 km for kittens. If we assume that a panther travels an average distance of 2.4 km, it will costs all the energy for body weight growth, which means that a 27.5-kg female traveling 2.4 km will cost 121.8 kcal. Then, using Parker et al.'s (1984) equation, the energy cost for traveling one km (PTKC) may be estimated as,

$$\begin{aligned}
 \text{PTKC} &= \text{PNCT} / (\text{PBW}^{0.66} * \text{PTKM}) \\
 &= 121.8 / (27.5^{0.66} * 2.4) = 5.695
 \end{aligned}
 \tag{12}$$

where,

PTKM = travel distance in km.

Then, the energy costs for traveling (PNCT) can be calculated as,

$$\text{PNCT} = 5.695 * \text{BW}^{0.66} * \text{PTKM} \quad (13)$$

(3) Daily maintenance energy costs (PNCM): We assume that a 1.5-year-old female panther can add an average of 35.6 g per day to its body weight (Maehr and Moore 1992). The mean body weight for a 1.5-year-old female panther is 27.5 kg. Using equation 7, daily meat intake will be 1.736 kg and total energy gained from 1.736 kg of meat is 3407 kcal (Turner et al. 1992). It was assumed 0.1 of fat and 0.9 of lean body weight, 75% of water and 25% of protein for the lean body weight, and 9500 kcal/kg for fat and 4800 kcal/kg for protein. Then for 1.736 kg of meat from deer, the energy content is calculated as,

$$(1.736 * 0.1 * 9500) + (1.736 * 0.9 * 0.25 * 4800) = 3407 \text{ kcal} \quad (8)$$

If we assume that there is no difference of meat energy content between panther and deer, 35.6 g of increasing in body weight of the panther individual contents 69.9 kcal energy (Equation 8). But it needs 121.8 kcal of net energy (Table 4). According to Thompson et al. (1983) the maintenance energy costs (PNCM) may be calculated as:

$$\text{PNCM} = \text{MEC} * \text{BW}^{0.75} \quad (9)$$

where,

MEC = metabolizable energy needed per kg body weight
(kcal/kg)

If we assume that the animal does not hunt and travel in the day,

the total energy gained of 3407 kcal from food may surplus 121.8 kcal for body weight gain and another 121.8 kcal for an average of 2.4 km of travel energy cost, then the rest 3163.4 kcal goes to the maintenance energy, then MEC can be calculated as,

$$MEC = PNCM / BW^{0.75} = 3163.4 / 27.5^{0.75} = 263.4 \quad (10)$$

Then, Equation 9 can be re-written as,

$$PNCM = 263.4 * BW^{0.75} \quad (11)$$

During the lactating period, a female may be costed more energy. It is calculated as body weight gain for all the kittens the female panther has. For example, if the female has 3 kittens, one male and two female. Each day the 3 kittens will gain 206 g (404 kcal) in total. The energy will be added to the daily meat intake and the maintenance energy cost for the adult female. If there is no enough food, the mother will lose body weight.

3.3 Subroutine PREDAT

PREDAT emphasizes the predation behavior (roles), movement strategy, social behavior (territory defence), and home range of panther in the Everglades landscape. Female panthers seem to have a smaller home range (193 km²) comparing to that the home range of a male panther can be as large as 519 km² (Maehr et al. 1989). Because of the capability of traveling long distance and large home range, single panther may be able to hunt on deer or other species across the entire Everglades landscape. Also,

overlaps of panther home ranges are not unusual (Maehr et al. 1991). Therefore, the model does not include a strict home range as defended territory for panther. However the model will simulate panther establishing their own dens in a 500 x 500 pixel with a radius of 1.5 km and an area of 625 ha as its defended territory. Other panthers will not establish a den in this area except that kittens younger than 18 months can company with their mother.

Cover and vegetation types are important to panther temporal utilization of their home range and to the establishment of den sites. Panther utilization of alternative habitat types in the model initially is based upon a preference ranking as reported by Maehr et al. (1989) to be (based upon the number of observations of panther in these habitat types): hardwood hammocks (29%), pine flatwoods (24%), cabbage palm (20%), cypress swamp (19%), and other vegetation types (about 8%) . The average length of home range tenure for residents is 26 months (Maehr et al. 1989). Home range overlaps and shifts are usually observed. A kitten may be independent when it is 18 months old (Maehr et al. 1989, Hornocker 1979).

The strategy of predation may be important to energy costs on predation. Large prey include white-tailed deer, wild hog (Sus scrofa), raccoon (Procyon lotor), and armadillo (Dasypus novemcinctus). Deer and hogs accounted for 85.7% of consumed biomass in the northern Everglades and 66.1% in the southern Everglades. As the simulation of interactions between panther

and deer, panther have a high probability to find and encounter a deer in the den pixel ($P = 0.8$) and a lower probability to the eight adjacent pixels ($P = 0.2$). Panther have now knowledge about prey beyond the adjacent pixels. A deer has a probability ($P = 0.1$) of knowing that there is a panther in an adjacent pixel and prevent itself to forage in a pixel with panther near by. And a deer may have high probability ($P = 0.4$) to know a pixel with a panther in and avoid to go in that pixel.

The predation activity may depend on daily energy requirements, for example, if a panther needs 2.3 kg of meat in a day and a deer can provide 23 kg of meat (usually it is 70% of the total body weight of a deer), the next potential deer preyed upon is 10 days later. The next predation day is also affected by how long the meat can be preserved. Rapid spoilage of meat during the hot, wet season is one of the possible causes of increased kill frequencies, reported during this time since panthers generally refuse to eat tainted meat (Russell 1978). In the summer, it may not last longer than 4 days, spring and fall 6 days, and winter 6 days. There is an array for the time period for meat preservation days ($DPMT(i)$, $i=1,2,3,4$).

The predation process is simulated using a set of behavior roles and the probabilities). Since hearing and sight are important regarding stimuli eliciting and directing behavior toward prey (Leyhausen 1979), we assume that a panther has a probability ($P_s = 0.8$, average? or depends on habitat?) of being aware of deer or other prey in the eight adjacent 500 x 500

pixels (searching probability). The model assumes that the panther will search eight adjacent pixels and move directly towards the nearest prey (Leyhausen 1979). If there are no deer or other prey in the adjacent pixels, the panther moves to one of the pixels at random (or with a higher probability to move to a preferable habitat pixel?). If there are more than one pixel with prey being aware of, the panther goes to one of those at random. The model includes a probability of deer escaping from predation ($P_{DLS}=0.40$; Muckenhirn and Eisenberg). P_{DLS} will be different from different ages of panther (high for kittens and the old) and from different habitats (for example high in open grassland). If a panther does not need to hunt in a day, it will not move. As long as an individual has not caught prey, it will keep searching and moving until it catches prey or it meets its maximum daily movement distance, whichever comes first.

Hunting probability will depend on the time since last hunt, on the seasons (warmer season, food gets spoil quicker). Predation rates depend upon prey density or resource availability in the model.

(DISCUSSION: 1. what kind of ~~the~~ movement patterns do panther^s have? 2. Do panther^s change their dens often, and ^{what} is the frequency? 3. what are the factors affect^{ing} panther's changing their dens (prey density? habitat fragmentation? vegetation dynamics? panther population density?) 4. Do panther^s defend their territory and if yes, then ^{to} ~~on~~ what degree?)

The maximum daily movement distance for male will be 20 km,

for female 15 km, and for kitten less than 18 months old 10 km (Seal et al. 1989). (DISCUSSION: if a panther searching reaches half of its daily maximum movement distance, which means that the prey density is low in the area, then the individual will find a new den close to where it is, sine the available prey and the extent to which it is subject to hunting pressure are two of the most important factors that determine the home range -- den location?). If an individual daily movement distance is less than the maximum, the animal will keep the same den.

Panther will not move in agricultural and residential areas.

3.4 Subroutine POPUL

Subroutine POPUL simulates the population dynamics of panther, which includes a populations age and sex structure, spatial distribution, reproduction and mortality. Mortality rate is estimated as 17.2% in the Everglades landscape, in which highway collisions caused 46.9%, and natural events caused 28.1%. Other mortality is caused by illegal shooting and unknown reasons (Maehr et al. 1991).

Based on Seal et al.'s (1989) observations, highway kills are an important factor contributed to panther mortality. In an un hunted population, it is estimated as 10-30% of total mortality. An annual mortality of 4% (27% of annual total mortality for adult panther * 15% caused by highway kills) is simulated for highway kills in the model. The model assumes a

probability of 0.02 since about one animal per year (Maehr et al. (1991) was killed and the total population was estimated as 50 (Schortemeyer et al. 1991) for highway deaths each year (HWKL). If highways are included in the landscape, the deaths may be simulated close to the highway. In another approach, the deaths will be chosen at random. In the winter, highway deaths are higher than in summer due to increased travel on the highways during this season. At the end of each month, the model will simulate highway kills with a probability of 0.0008 ($0.02/12/2$) for May-October and 0.0016 ($0.02/12*2$) for November-April. Shooting is included as an option for study of the effects of this on population dynamics (HTKL). The probability of kills by shooting can be an chosen for simulations.

According to Hornocker (1970), there seem to be two periods within its first year after birth when the panthers are most likely to have a high mortality rate. The first period occurs during postnatal mortality as a result of intralitter competition for nursing. The second period is during the weeks following independence when young panthers have not yet become proficient in stalking and killing prey. Within this time period (12-18 months, Seal et al. 1989), the presence of small animals is very important. For the postnatal mortality, the model assumes it to be a function of the health of the female and the number of kittens in a litter. The more the female loses body weight and the greater the number in a litter, the higher probability a kitten dies. We assume that a panther dies if it loses 30% of

its lean body weight from the previous highest body weight (PHBW(jj), jj=1, ..., NP). The current body weight (PNBW(jj), jj=1, ..., NP) is recorded in the model for each panther. We assume that 70% of the PNBW(jj) is lean body weight, therefore the probability of kitten mortality caused by female health (PKMH) may be calculated as

$$PKMH = [(PHBW(jj) - PNBW(jj)) / PHBW(jj)] / 0.30 \quad (7)$$

The effect of the litter size on mortality rate, due to the higher expenditure of a females energy with larger litters, includes a possible loss of female body weight. The mortality of a specific kitten is determined by PKMH.

The high mortality rates caused by low ability to capture suitable prey is considered in subroutine PREDAT. As mentioned above, a panther dies if it loses 30% of its lean body weight, which is caused by negative energy balance (either gaining too little or expending too much energy).

For natural mortality, there is evidence of 15-18 year lifespans in the wild, but 8-12 years is considered old for panther (Young and Golman 1946). The subroutine uses different probabilities for natural mortality rates as a panther ages from birth day to 15 years old. Modified from Seal et al.'s (1989) model, we use following natural mortality rates in the our mode (Table 5).

Table 5. Natural mortality rate (PMR) for different age classes.

Age	<1	2	3	4	5	6
MR	0.50	0.15	0.10	0.10	0.10	0.10
Age	7	8	9	10	11	12
MR	0.15	0.25	0.50	0.80	0.95	
Age	13	14	15	>15		
MR	0.985	0.999	0.9999	1.0000		

IV. Model Initialization

Since the panther is endangered and numbers no more than 50 individuals residing south of Lake Okeechobee (Maehr 1990), the model will allow the initial number of panthers on the landscape to vary in a range based upon empirical data and estimates of maximum carrying capacity (Smith and Bass, 1992). Each panther will be located in a spatially random manner (DISCUSSION: 1. if we need to consider the distance from highway or human activity area? 2. if panther behave territory defense, individuals should be distributed separately in a distance -- what is the distance?), constrained by being placed in a pixel with the highest habitat preference based on data in Smith and Bass (1992)--1.5 km far away from human activity area and away from another panther's den site (1.5 km is the average distance for

panther activity from a den, Maehr et al. 1989). Also, initiated individuals should be located in the areas as indicated present documented range of the Florida panther by Seal et al. 1989 p9). The preference index of vegetation types for den sites is based on Friedman's test for habitat selection in South Florida from December 1985 to January 1989 (Table 6). Kittens younger than 18 months will be simulated in the same den with their mothers and those older than 18 months may have their own dens.

Table 6. The preference index of vegetation types for den sites is based on Friedman's ranking values for habitat selection in South Florida from December 1985 to January 1989 (in Maehr et al.'s 1990).

Habitat	Ranking Value	Preference Index
Agriculture/disturbed	21	6
Freshwater marshes	21	6
Thicket swamp	24	7
Mixed swamp	28	9
Cypress swam	47	15
Cabbage palm	50	16
Pine flatwoods	61	19
Hardwood hammock	72	22

Based on Seal et al. (1989), the sex ratio is even for male and female panther. The age structure will based on the data from Seal et al. (1989) as listed in Table 7.

Table 7. Florida panther age structure based on data from Seal et al. (1989).

Age	<1	1-4	5-8	9-13	>13
%	0.23	0.34	0.31	0.08	0.04

Body weight distribution is based on Maehr and Moore's (1992) equation to sign body weight to each individual related to its age. Adult body weight of males is 53-67 kg and female 34-48 kg (Seal et al. 1989). The body weight for a specific individual will be initiated based on its age, sex, mean body weight, and standard errors from Maehr and Moore's (1992, p703)) research (Table 2).

Literature Cited