A Frontier Model for Landscape Ecology: The Tapir in Honduras

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Abstract. We borrow a frontier specification from the econometrics literature to make inferences about the tolerance of the tapir to human settlements. We estimate the width of an invisible band surrounding human settlements which would act as a frontier or *exclusion* zone to the tapir to be around 290 meters.

Keywords. Habitat fragmentation, extinction, mammalian persistence models.

1. Introduction

Baird's tapir (*Tapirus bairdii*), the largest mammal of the neotropics, is a generalist herbivore weighing between 150–300 kilograms (Emmons, 1990; pp. 156-157). Once having a broad distribution throughout the rain forest from Mexico to Ecuador this ancient perissodactyl is now threatened with extinction (IUCN, 1982; Part I, pp. 447–450). The tapir's decline is largely attributed to habitat destruction caused by logging, pastoral, and agricultural pressures which increasingly fragment tapir populations isolating them in dwindling forest patches. (Overhunting is another important cause of the decline; see, *e.g.*, Eisenberg, Groves and Mackinnon, 1990; vol. 4, pp. 598–608.)

The departments of Olancho and Colón in northeastern Honduras —where the data used in this study were collected— is a rugged mountainous area still supporting 10,000–11,500 square kilometers of contiguous tropical evergreen rain forest. Over the last twenty years, subsistence farmers fleeing environmental degradation in other parts of Honduras have been colonizing the study area and threaten to fragment this contiguous forest into disconnected patches. The implication for the tapir is that the resulting habitat fragmentation would shatter a large connected population into smaller isolated ones. Small isolated populations run increased risks of inbreeding depression, genetic drift, and stochastic events which reduce their chance of long term persistence (Wilson, 1992).

95% Persistence for 100 years.   95% Persistence for 1000 years.

Kgs   Kgs
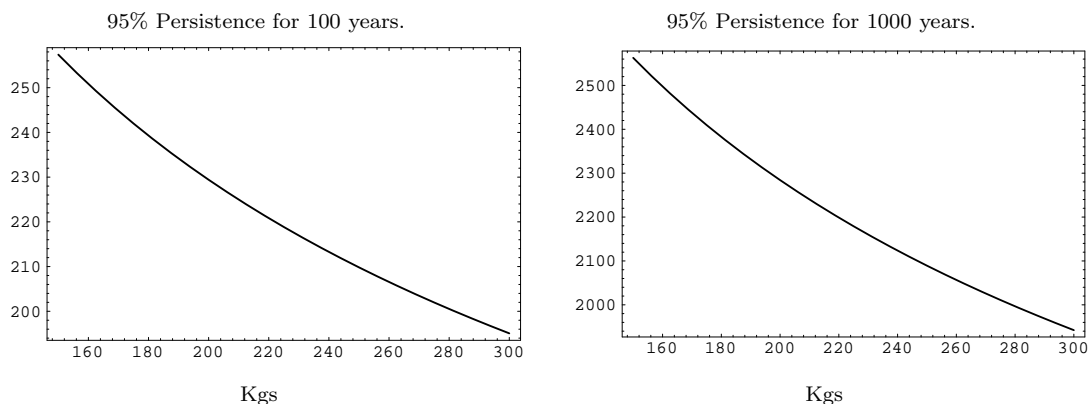
Fig. 1. Tapir body weight (horizontal axis) vs population size (vertical axis).

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Figure 1 shows the population size needed to prevent extinction. It is constructed using Belovsky's (1987) application of Goodman's (1987) mammalian persistence model. Instead of using a single population size, we plot the population size (vertical axis) for the whole tapir weight range (150–300 kilograms) versus body weight (horizontal axis). The left panel represents the number of individuals required for a 95% chance of persistence for 100 years, the right panel for 1000 years. Calculations using Janzen's (1982) lowest tapir density figures for Corcovado National Park in Costa Rica (0.24 tapirs per square kilometer) yield a total population of 2496–2760 tapirs for the area of Olancho and Colón. From the right panel of Figure 1, we calculate that this population is large enough to have a 95% chance persistence for 1000 years. This makes it an important population for any conservation strategy aimed at saving this endangered species as few of the remaining forest tracts in Central America are large enough to support a population of this size. However, the integrity of this population is in jeopardy as much of the forest lies outside protected reserves and is under increasing pressure from subsistence farmers. If continued clearing reduces forest cover to the seven disjunct reserves in the area, only two of the isolated reserves will be large enough to support viable tapir populations in the short run (see Figure 1, left panel) and none will be large enough to support the tapir in the long run.

The key to the long term survival of this population is to protect it as a single unit and thus avoid the deleterious effects of isolation. To do this it is vital to maintain links between the forest reserves which will allow tapirs to pass from one reserve to another. Continued human colonization in the area is likely but if settlement is managed in a way that preserves tapir movement corridors between the reserves, perhaps both human and wildlife can be accommodated. To accomplish this we need to know how human settlements affect tapir movements. Preliminary study suggests that clustered human settlements create barriers to tapir movement whereas dispersed settlements allow it. We must establish the parameters which define this phenomenon in order to design movement corridors capable of maintaining this population as a single unit.
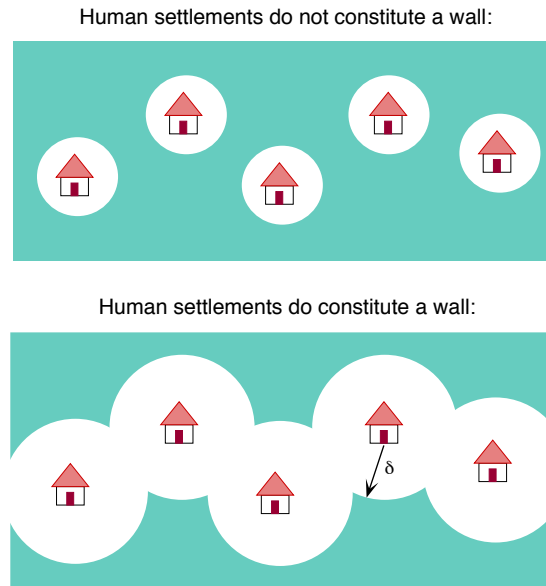
Fig. 2. Same layout of human settlements for different values of δ.

The objective of this paper is to investigate the effect of human settlements on tapir movements by estimating the closest distance that a tapir will approach a human settlement, δ. To allow for a tapir to pass between two human settlements, these settlements must be at least 2δ apart. Figure 2 illustrates this idea. The upper panel shows a distribution of settlements that does not

constitute a movement barrier because δ is sufficiently small. With a large δ, the same settlements would constitute a movement barrier as shown in the lower panel.

2. The Sampling Model

The field research consisted of searching for evidence (tracks) of tapirs in the vicinity of human settlements. (The area covered in this study was the northeastern part of Olancho and the eastern part of Colón, northeastern Honduras: longitude 85–86W, latitude 14–16N. The field research was conducted between April and August 1994.) Areas chosen to search were selected on the basis of interviews with local farmers. Typically, the field researcher (K. Flesher) hiked through an area engaging people in conversation and asking if tapirs occurred nearby. If they said yes, he would then try to find some one to show him the tracks. All searches commenced at the guide's house (and therefore from a settlement). It was explicitly stated that the researcher wished to see the tapir tracks closest to the settlement and would pay a flat day rate of 20 lempiras for the service (equivalent to US $2.50; Honduran labor rates were typically 10–12 lempiras a day). It was emphasized that the guide would receive this pay even if the foray lasted ten minutes, but stipulating that the search would continue until sunset if necessary. The data collected are shown in Table 1.

Table 1. Measured Distances (in meters) to the nearest Human settlement.

i	Distance	Size of Settlement
1	3,000	1–5 Households
2	3,750	6–20 Households
3	3,000	6–20 Households
4	600	6–20 Households
5	1,000	1–5 Households
6	1,500	6–20 Households

Since a *fixed* reward was offered, regardless of the time it would take to find the tracks, the guide had a powerful incentive to find the tracks closest to the starting point (which, as noted before, was always a human settlement). This characteristic of the sampling method will be reflected in the model specification through the error density. (Perhaps a more plausible model would have the guide attempting to minimize *search time* rather than *distance*. However, such a model can also be accommodated in the specification below.) Once found, tracks were marked on 1:50,000 scale topographic maps and the distance between the tracks and the settlement were measured by drawing a straight line on the map between them.

Measurements of distances from a human settlement to the closest tapir track are assumed to follow the model:

$$d_i = \delta + \varepsilon_i, \qquad \varepsilon_i \geq 0; \tag{1}$$

where δ is the closest that a tapir would ever get to a human settlement. Thus, we assume that a tapir will never venture within the band of width δ around a human settlement —which would act as an invisible barrier or frontier. Equation (1) is similar to the deterministic frontier models used in econometrics to study productive efficiency (Schmidt, 1985). In a production context, the technology determines the feasible set and deviations (shortcomings) from the technological frontier are attributed to managerial inefficiency. It is important to note that assuming a density with much of its mass close to zero for ε_i in (1), as in production frontier models, follows from the sampling procedure, *not* from any assumptions on the distribution of the tapir population. It is in the guide's interest to *minimize ε_i* in equation (1) as it is in the manager's interest to minimize inefficiency in production-frontier models.

Assuming a particular distribution for the error term in (1), we could proceed then to maximize the resulting likelihood function to obtain estimates of the relevant parameters. However, the usual maximum likelihood properties do not automatically follow since one of the regularity conditions needed to obtain them is violated; namely, the independence of the support of the random variable with respect to the values of the parameters to be estimated. Here, there is no guarantee that the error term in equation (1) will always be positive. In other words, for the error term to be always positive, the range of the left-hand side variables is bounded below by δ, one of the parameters of interest. This is something that the usual regularity conditions assume away. This problem in the context of production frontier estimation was pointed out by Schmidt (1975) —in particular, the Exponential and Half-Normal specifications do not meet the regularity conditions. Not being able to rely on general results available for maximum likelihood estimators, their properties would need to be investigated in a case-by-case basis. Greene (1980) partially solved this problem finding sufficient conditions on the error density such that maximum likelihood methods yield consistent and asymptotically efficient estimators (and standard errors for the estimates can be computed from the information matrix). (An alternative approach is to consider the frontier itself to be random. Aigner, Lovell and Schmidt (1977) introduced such stochastic formulation for estimating frontier production function models. Although stochastic frontiers are appealing in the production-function context, we do not use them in the present application because they would involve a larger number of parameters and we have a small number of observations.) A useful error specification that meets the regularity conditions is a Gamma density:

$$p(\varepsilon|\mu,\theta) = \frac{\theta^\mu \varepsilon^{\mu-1} e^{-\theta\varepsilon}}{\Gamma(\mu)}, \qquad \mu > 2,\, \theta > 0 \tag{2}$$

where we must restrict the range of the shape parameter, $\mu > 2$, in order to satisfy the regularity conditions (see Greene, 1980). We have that $\mathrm{E}[\varepsilon] = \mu/\theta$ and $\mathrm{Var}[\varepsilon] = \mu/\theta^2$. Also note that direct integration yields $\mathrm{E}[\varepsilon^{-2}] = \theta^2/((\mu-1)(\mu-2))$, which will be useful later to compute the information matrix.
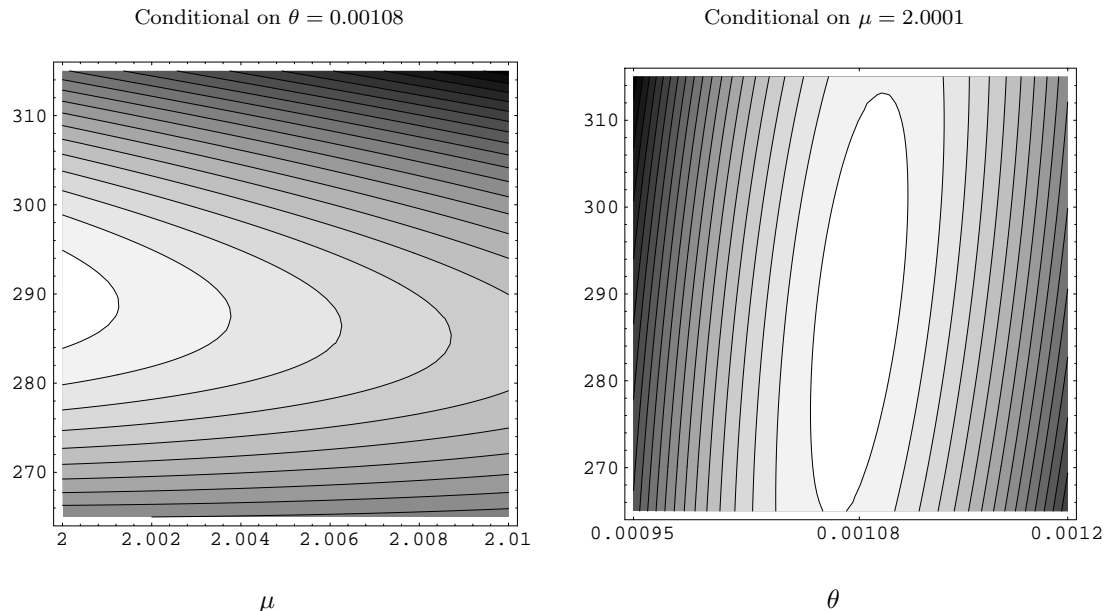
3. Estimation Results

Under the assumption that the sample collected is i.i.d. according to (1)–(2), the log-likelihood function is given by:

$$\mathcal{L}(\delta, \theta, \mu|\text{data}) = N(\mu \log \theta - \log \Gamma(\mu)) + (\mu - 1) \sum_{i=1}^{N} \log(\delta - d_i) - \theta \sum_{i=1}^{N} (\delta - d_i). \tag{3}$$

We obtain maximum-likelihood estimates by maximizing (3) using steepest-descent methods. We have 3 parameters to estimate and only $N = 6$ —we shall recover one degree of freedom by fixing one of the parameters as discussed below. We show equally spaced contour levels of the log-likelihood function (3) in Figure 3. On the left, θ is set to its maximum-likelihood estimate, 0.00108, the 'barrier' δ is shown (in meters) on the vertical axis and μ is shown on the horizontal axis. The right panel depicts the contour levels when we set $\mu = 2.0001$, δ is shown, again, on the vertical axis and θ on the horizontal axis.

We fix $\mu = 2.0001$ since this parameter would tend to move arbitrarily close to 2, its lower bound for the model to satisfy the regularity conditions (Greene, 1980). The parameters shown on Table 2 are obtained then by maximizing the conditional log-likelihood, $\mathcal{L}(\delta, \theta|\mu = 2.0001, \text{data})$, using steepest-descent methods. The standard errors are obtained from the information matrix, which has an analytical expression since:

$$-\mathrm{E}\left[\frac{\partial^2 \mathcal{L}}{\partial \delta^2}\right] = \frac{N\theta^2}{\mu - 2}, \quad -\mathrm{E}\left[\frac{\partial^2 \mathcal{L}}{\partial \theta^2}\right] = \frac{N\mu}{\theta^2}, \quad \text{and} \quad -\mathrm{E}\left[\frac{\partial^2 \mathcal{L}}{\partial \theta \partial \delta}\right] = N.$$

Conditional on $\theta = 0.00108$ Conditional on $\mu = 2.0001$

μ θ

Fig. 3. Contour levels of the log-likelihood function: δ on the vertical axis.

Table 2. Maximum Likelihood Estimates

| Parameter	Estimate	S.E.
δ	289.29	3.78
θ	0.00108	0.0003
μ	2.0001	(fixed)

3.1. Interpretation

The width of the 'exclusion' band around human settlements, δ seems to be around 290 meters (0.18 miles). The tapir tracks are expected to be found approximately 2 kilometers (1.24 miles) away from the boundary —*i.e.*, the maximum likelihood estimate of $E[\varepsilon]$ is 2000 meters, approximately. See Figure 4 where a Gamma density parametrized with the maximum-likelihood estimates is shown. These values are estimated with good precision and they are very credible. This simple model does a good job at describing the data.

4. Concluding Remarks

We have borrowed a frontier model from the econometrics literature to interpret a small ecological dataset. The model proves useful to make inferences about the parameter of interest, δ, and the estimates have very plausible values.

A larger dataset would allow us more sophisticated specifications and richer inference. This parsimonious model could be extended in a number of ways. In particular, different δ's depending on human population density, or different land uses, is a natural extension. Also, a more sophisticated model incorporating terrain characteristics would improve our understanding of the tolerance of the tapir to human land use.

Landscape designs which incorporate both human and wildlife needs are of critical importance in unprotected areas. The spatial arrangement of human land use practices could determine whether wildlife persist or perish. This paper attempts to provide a model to address this issue
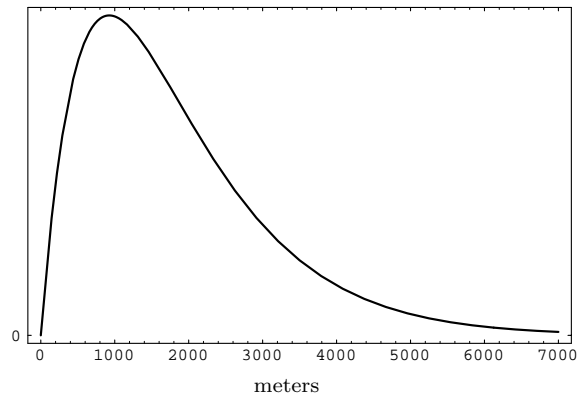
Fig. 4. Gamma density: $p(\varepsilon|\mu = 2.0001, \theta = 0.00108)$.

in a case study concerning the tapir in Honduras.

Acknowledgement

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