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# Original article Indication of a species in an extinction vortex: The ocellated turkey on the Yucatan peninsula, Mexico

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# ABSTRACT

The ocellated turkey Meleagris ocellata (OT) is a large, unmistakable endemic bird of the Yucatan peninsula. The species has suffered a considerable loss of distributional area as well as local abundance between 1980 and 2000 and is classified as endangered according to Mexican norms. We applied Classification Trees and Random Forests in order to determine the factors that most closely explain the observed patterns of distribution and abundance loss, and to develop hypotheses that may guide measures for the protection of the OT. Among the most important predictors of change were variables corresponding to aspects of forest cover and variables on human population and small settlements. OT abundance in 1980, however, was by far the most important predictor for OT abundance change. This is an indication that the OT dynamics are governed by internal rather than by external factors. Medium and low abundances in 1980 inevitably led to a further decrease during the following years, which gives rise to the conclusion that the OT might find itself in an extinction vortex. We suggest the following hypothetical scenario for OT decline: migrant people from other Mexican states colonise forested regions in Yucatan; they establish small settlements; bushmeat hunting is important for their survival; the naïve OT is easy prey; hunting-together with beginning deforestation-reaches a certain level, and local OT abundance falls below a critical threshold; OT continues declining regardless of current social and environmental changes except where there is total protection of both the species and its habitat.

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# 1. Introduction

The ocellated turkey Meleagris ocellata (henceforth, OT) is a large (3-5 kg), unmistakable bird endemic to the Yucatan peninsula. Its geographic range encompasses the Mexican states of Yucatán, Campeche and Quintana Roo, as well as the Guatemalan department of El Petén, and the Northern portion of Belize (Howell and Webb, 1995). This region, especially along the borders between countries, represents the last agricultural frontier in Central America (Turner et al., 2001). Despite the scale and rate of land-use change throughout its geographic range, little is known about the actual distribution of OT. The first comprehensive assessment of its

distribution in Mexico was performed by Calmé and co-workers (Calmé and Sanvicente, 2000; Calmé et al., in press); previously, only anecdotal distributional data had been collected (e.g., Brodkorb, 1943: Leopold, 1948).

The lack of attention to the status of the OT is surprising since it has been a longstanding cultural symbol of life among peninsular Maya (De la Garza, 1995). The OT has also long been recognised as an important gallinaceous species for subsistence hunting in poor rural areas (Escamilla et al., 2000; Jorgenson, 1993; Quijano-Hernández and Calmé, 2002). González et al. (1998a) reported that two-thirds of the subsistence hunters in northern Guatemala had hunted OT, with one-third killing more than 10 individuals per year. Moreover, like the North American wild turkey Meleagris gallopavo, the OT is a prized game species for Mexican and American sport hunters, who hunt for trophy males (Branton and Berryhill, 2007; NWTF, 2005).

The OT is very similar in its biology, ecology and behaviour to the wild turkey (González et al., 1998a, 1998b; Sugihara and Heston, 1981; Steadman et al., 1979). Like wild turkey, OT is gregarious,

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except for nesting females during incubation and early chick life. Unlike wild turkey, the OT is prey for a suite of very diverse predators, ranging from snakes and birds of prey to canids and felines (González et al., 1998a). Also, the OT is presently an endangered species, unlike the wild turkey.

In the most recent IUCN Red List of Threatened Species (IUCN, 2009), the OT has been assigned "nearly threatened" status. This listing is mostly due to the lack of recent information on the precarious situation of the species. According to the Mexican list of endangered species (NOM-059-SEMARNAT-2001, 2002), the OT is indeed "endangered." To support this classification, the assessment by Calmé et al. (in press) demonstrated considerable losses of distributional area and decreases in local abundance of the OT between 1980 and 2000, except for a few notable exceptions (Table 1, Fig. 1). Over this 20-year time period, the species vanished from 114 (16.6%), and its local abundance decreased in 238 (34.6%) of 688 map grid cells ( $10 \times 10$  km) with available data. We hypothesise that this is mostly due to corresponding changes in land occupation by migrant peasants. The most obvious example is southern Yucatan, which experienced increasing human colonisation between the early 1970's and late 1990's (Ericson et al., 1999). The largest corresponding rates of deforestation came in the late 1980's when the Calakmul Biosphere Reserve (CBR) was close to being established (Turner et al., 2001). Settlers from all over Mexico have settled in the southern peninsula because of land scarcity, lack of employment, ecological disasters or social unrest in their original communities (Ericson et al., 1999). Their settlements have been characterised by fast population growth and extreme poverty, and bushmeat is an important component of their diet. Within the same region, another unexpected change occurred: OT abundance increased in the CBR, at least in the vicinity of archaeological sites. Here, any extractive activity was prohibited after the reserve was declared. Therefore, it can be assumed that ongoing habitat loss and forest fragmentation, together with increased levels of subsistence hunting, are most likely responsible for the decrease of the OT. However, there has been no attempt to closely analyse the relationships between these factors and OT abundance and distribution.

The toolbox available for the identification of species distributions and species-habitat relationships has recently been augmented by a number of novel methods, which come from artificial intelligence and machine learning (see comparisons of methods by Benito-Garzón et al., 2006; Segurado and Araújo, 2004; Kampichler et al., in press; among others). In the present study, we make use of a classical method, the automated induction of classification trees (Breiman et al., 1984; De'ath and Fabricius, 2000), and proceed with its further development into an ensemble forecasting method, which is called random forests (Breiman, 2001; Cutler et al., 2007; Hastie et al., 2009). While classification trees have the appeal of explicitly representing the relationships

#### Table 1

Abundance change matrix of the ocellated turkey (OT) on the Yucatan peninsula between 1980 and 2000 in 688 cells of a  $10 \times 10$  km grid. For example, of the 130 squares without OT in 1980, there was no change observed in 118, an increase to low abundance in nine, an increase to medium abundance in three squares, and an increase to high abundance in none of them.

2000	1980				
	Absent	Low abundance	Medium abundance	High abundance	Row total
Absent	118	30	30	54	232
Low abundance	9	26	63	59	157
Medium abundance	3	0	34	116	153
High abundance	0	1	9	136	146
Column total	130	57	136	365	688



**Fig. 1.** Distribution of the ocellated turkey (*Meleagris ocellata*) in the Yucatan peninsula in (A) 1980 and (B) 2000 on a grid of  $10 \times 10$  km cells (after Calmé et al., in press).  $\circ$ , OT absent;  $\bullet$ , low abundance;  $\bullet$ , medium abundance;  $\bullet$ , high abundance; empty cells, no data available. State borders between Yucatán (N), Campeche (W) and Quintana Roo (E) are shown. CBR, core area of the southern part of the Calakmul Biosphere Reserve; LO, Laguna Om communal farming system.

between the state variable (for example, local abundance class) and its explanatory variables in an intuitively comprehensible tree-like structure, random forests are superior to classification trees with regard to accuracy of model predictions and stability (Breiman, 2001; Kampichler et al., in press). Instead of specifying explicit relationships between variables, random forests yield a ranked list of explanatory variables according to their importance in predicting the state variable. The generalisation error converges to a limit as the number of trees in the forest gets large; therefore, in contrast to other machine-learning methods, overfitting is not a problem in random forests (Breiman, 2001). Both methods are non-parametric approaches and do not depend on statistical distributions of the explanatory variables, and are able to model noisy and non-linear relationships in high-dimension data sets. Random forests are competitive with the best available classification methods and can outcompete most of the commonly used ones (Cutler et al., 2007; Prasad et al., 2006).

In this paper, we applied classification trees and random forests to determine which factors most closely explained the observed patterns of distribution and abundance loss of the OT. We are aware that these factors are not necessarily the proximate causes of the observed losses since the relationships between distribution and abundance of the OT and the explanatory variables are purely correlative. Nevertheless, the modelling results permitted us to develop testable hypotheses, and may guide measures for the protection of the OT.

## 2. Materials and methods

# 2.1. Data origin and definition of response and explanatory variables

#### 2.1.1. Ocellated turkey

Data were collected between February and November 1999 in the Yucatan peninsula of Mexico, which encompasses the states of Yucatán, Quintana Roo and Campeche. We covered the study region with a reference grid of  $10 \times 10$  km cells, which was the basis for data collection. This resolution is commonly used to map species distributions in bird atlases. Moreover, female OT dispersal remains within the resolution of the 10  $\times$  10 km cells (González et al., 1998b). Information was gathered for cells corresponding to human settlements (e.g., communally owned land, private ranches, ranger stations). More details on how information was obtained can be found in Calmé et al. (in press). Because the purpose of our study was to obtain reliable information within a short time frame and at low cost, we used the local ecological knowledge of the subsistence hunters and peasants whom we interviewed. Confidence in the information was based on the fact that OT is well-known and unmistakable (Howell and Webb, 1995), and because local rural people, especially hunters and gum-tappers, make use of the whole territory to which they have access during the course of their numerous activities (González-Abraham et al., 2007). The interview was divided into two sections. The first section allowed us to evaluate the validity of answers provided by informants, while the second was designed to collect information on sightings of OT over the past two years (present) and 20 years ago. Informants were asked about the presence of the species and the maximum number of birds in flocks, among other information. The maximum number of birds in flocks was used as a surrogate for species abundance, as group size varies with local abundance in gregarious species. Detailed information on the rationale for using local ecological knowledge, and how informants were approached and information was validated, is provided by Calmé et al. (in press). Also, recent studies have found that local ecological knowledge of well-known, conspicuous species is more efficient, and as exact in determining distributional and abundance changes, compared to traditional ecological methods (Anadón et al., 2009; Liu et al., 2009). We defined the response variable "change in OT abundance between 1980 and 2000" in two ways: (1) we classified abundance changes in three classes (increase, decrease, no change), irrespective of prior abundance in 1980. For example, a cell with low OT abundance in 1980 that went extinct falls into the same class "decrease" as does a cell with high OT abundance in 1980 that dropped to medium abundance. (2) We resolved abundance changes at a finer grain, using 16 classes, with each one defined by abundance classes absent, low, medium, or high in 1980 and by abundance classes absent, low, medium, or high in 2000. The corresponding abbreviations are derived by their first letters; abundance change class ML, for example, means that the OT decreased from medium abundance in 1980 to low abundance in 2000. There were no observations for classes AH and LM, so the number of classes was actually 14. We have referred to the two approaches as the "coarse" (3 abundance change classes) and the "fine" (14 abundance change classes) models, respectively, throughout the paper.

### 2.1.2. Environmental and social data

Due to our hypothesis, we limited the range of explanatory variables to vegetation properties and land-use types, and to characteristics of the human population. Climate and physiography were not considered since temperature and elevation gradients across the Yucatan peninsula appeared to be negligible (Mexican National Meteorological Service, URL http://smn.cna.gob.mx/ climatologia/normales/normales.htm; Soler-Bientz et al., 2010). Moreover, meteorological data were scarce, spatially irregular, and at a scale much coarser than the 10  $\times$  10 km cell unit. Main data sources were the results of the Mexican national forest inventories of 1980 and 2000 (URL http://www.conafor.gob.mx), and the human population census of 2000 (INEGI, 2002). Earlier censuses (the Mexican population is counted every 10 years) were not available in digital form and could not be included in the analysis. All data were converted to a  $10 \times 10$  km grid format corresponding to the OT distribution maps. For every explanatory variable, we determined the local value, i.e., in each  $10 \times 10$  km cell (100 km<sup>2</sup>), and the corresponding mean value for the Moore neighbourhood, i.e., the lattice of eight cells that surrounds the first, thereby characterising the regional level (800 km<sup>2</sup>) in which the local cell is embedded. To include relationships between local abundance and regional status of the OT, we included OT data from the Moore neighbourhood in 1980 to the explanatory variables. We added geographic variables (coordinates of the cells within the grid) to identify regions where the chosen predictors were not efficient enough for a successful classification of OT abundance change. The complete list of explanatory variables is presented in Table A (electronic supplementary material).

#### 2.2. Modelling

A total of 688 cells of the grid contained complete information on OT abundance changes and explanatory variables and were used for the induction of classification trees and random forests.

We applied the R packages tree (Ripley, 2007; R Development Core Team, 2008) for classification tree (CT in the rest of the paper) induction and randomForest (Liaw and Wiener, 2002) for growing the random forests (RF in the rest of the paper). Briefly, CT represents the relationships between the attributes (i.e., the environmental and social variables in a given cell) and the class of an object (i.e., abundance class of OT in that cell) as a dichotomously branching tree (Breiman et al., 1984; De'ath and Fabricius, 2000), which is intuitively easy to understand. Each node (or internal branching point) of the CT is defined by one of the attributes, which best partitions the data into two purer subsets as measured by the Gini index or entropy (Breiman et al., 1984). The algorithm continues by hierarchical, recursive binary partitioning of subsequent nodes until further subdivision does not reduce the Gini index (or entropy). RF constitutes a substantial modification of the CT approach towards ensemble learning: many classifiers are constructed and predict a class by a majority vote (Breiman, 2001; Liaw and Wiener, 2002). Each tree is grown independently by using a bootstrap sample (with replacement) of the entire data set, a procedure called bootstrap aggregating, or bagging for short (Breiman, 1996). Aside from the use of bootstrap samples, RFs are special in their construction in that each node is split using only a subset of the explanatory variables chosen randomly for each node. Breiman (2001) showed that the error of RF converges on a limit as the number of trees in a forest becomes larger; thus, the method is robust against overfitting. This property makes RF an extremely useful tool in ecological modelling. In addition, there is no need to set aside test data for the estimation of the error on unseen data, since at each bootstrap iteration the prediction for the cases not included in the bootstrap sample (the so-called out-of-bag C. Kampichler et al. / Acta Oecologica 36 (2010) 561-568

cases, or *OOB* cases, for short) can be compared with the observed data. All OOB predictions of an RF are aggregated and yield the OOB estimate of error rate, that is, the proportion of cases that are not correctly classified. The parameters that have to be tuned for growing an RF are the number of attributes chosen at each split (*mtry*) and the number of trees to be grown (*ntree*). For a given number of trees (in this study: *ntree* = 2000), the randomForest package permits the search for an optimal number of randomly selected explanatory variables per tree (in this study: *mtry* = 15).

Each RF differs from the next because of the process of bootstrap sampling during induction, and consequently, each differs in its predictive success. We grew ten RF and saved the best one. To determine predictive success, we evaluated the confusion matrix **C** obtained for each RF by determining the OOB estimate of error rate.

Variable importance was determined for the best RF (one for the coarse, one for the fine model) and evaluated in randomForest by looking at prediction error increases when the OOB data were permuted for a certain variable, while keeping all others constant. Among the various possible criteria for variable importance, we selected the mean decrease in accuracy from splitting on the variable, averaged over all trees.

Model residuals were mapped onto the grid of  $10 \times 10$  km cells of the Yucatan peninsula and checked for spatial autocorrelation. We used Moran's *I* adjusted for a ranked continuous variable (Bivand et al., 2008) by applying the R package spdep (Bivand et al., 2007).

# 3. Results

Both the fine and the coarse RF models classified all 688 grid cells into the correct abundance change classes; thus, all residuals were equal to zero. The fine and coarse CT models yielded a less efficient classifier, but still 72% (coarse model) and 54% (fine model) of the cells were correctly classified (see Table B, electronic supplementary material, for confusion matrices). CT model residuals were neither spatially autocorrelated for the coarse nor the fine model (Moran's *I*, *p* > 0.05).

In both fine and coarse RF models, OT abundance in 1980 was by far the most important predictor of OT abundance changes between 1980 and 2000 (Fig. 2); all other explanatory variables had considerably less predictive power. Among the ten most important variables, most were regional variables corresponding to various aspects of forest cover (Fig. A.I, electronic supplementary material). Two variables that were related to human population were of some importance in both the fine and coarse models, i.e., total regional human population and the number of small settlements with 10 or fewer inhabitants (Fig. 2). The probability of OT population decline increased sharply with human population size at already very moderate densities of less than 20 individuals per square kilometre (Fig. A.II, electronic supplementary material). The geographical coordinate variables were among the ten most important predictors, indicating that in certain parts of Yucatan OT abundance changes could not be modelled by considering the environmental and social variables alone. Closer examination of the relationships between these predictors and OT abundance change revealed that the corresponding regions were the southeast of the study area (where OT suffered extreme losses, Fig. 1) and the northernmost parts of the peninsula (Fig. A.III, electronic supplementary material).

CT explicitly illustrated the relationships between explanatory variables and OT abundance changes. In the fine model, no explanatory variables other than OT abundance in 1980 were necessary to classify those cells where OT abundance in 1980 was medium or less: existing populations were predicted to decrease, and cells without OT were predicted to remain without it (Fig. 3A). Forest and human population-related variables were relevant only in case of high OT abundance in 1980; threshold levels of forest

#### Δ





2.5



**Fig. 2.** Importance of explanatory variables in the (A) coarse and (B) fine random forest models of decrease in the distribution and abundance of the ocellated turkey (*Meleagris ocellata*) in the Yucatan peninsula between 1980 and 2000. Only the 10 most important variables are shown.

cover and local settlement cover were required that would allow the persistence of large OT populations and resembled the results of the fine RF model. The inclusion of a geographic coordinate (the position of a cell on the East-West gradient is measured in km from the easternmost to the westernmost extension of the study area) again hints of a region where the environmental and humanrelated variables were not sufficient to predict OT change successfully; OT abundance decreased in that region (southeastern part of the Yucatan peninsula). The coarse CT model differed from the fine one insofar as the main bifurcation at the root of the tree distinguishes only between cells with and without OT in 1980 (Fig. 3B); however, the rest of the coarse CT showed elements similar to the fine CT model. OT abundance was constant only when forest cover did not fall below a minimum threshold (total cover 81%, cover of low forest 62%) and settlement cover did not exceed a maximum threshold (0.2%) (Fig. 3B).

# 4. Discussion

## 4.1. Importance of forest cover thresholds

Between 1980 and 2000, total forest cover in the study area decreased by 14%, according to data collected by CONAFOR (the

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Fig. 3. Classification trees modelling the decrease in distribution and abundance of the ocellated turkey (*Meleagris ocellata*) in the Yucatan peninsula between 1980 and 2000. (A) coarse model (3 classes of abundance change); (B) fine model (14 classes of abundance change).

Mexican National Forest Commission). Most of the 1209 grid cells ( $10 \times 10$  km each) showed a decrease in forest cover of less than 10%; some, however, were completely deforested (Fig. B, electronic supplementary material). Increased forest cover was only observed in 190 grid cells, which was mostly due to natural succession after land-use changes. These changes included cessation of henequen (agave fibre) production in Yucatan state (Mizrahi-Perkulis et al., 1997), and the general trend of decreasing areas under maize cultivation after the 1994 North American Free Trade Agreement (NAFTA) caused a marked decline in maize prices (Schmook and Vance, 2009).

Although OT uses savannah and other open vegetation types during courtship, it remains within forested areas the rest of the time, especially during nesting and brood-rearing (S. Calmé, pers. obs. 1999–2002; González et al., 1998b). Most nests are directly on the ground and are found within dense forest, where nesting females remain inconspicuous. During brood-rearing, young hide from predators and find abundant sources of insects on the forest floor of mature forests (González et al., 1998b). In contrast, adults feed in the forest on fruits and leaves, as well as on seeds and flowers of herbs and vines found in forest clearings, and even forage along the edges of cultivated areas, picking bean flowers in summer and maize in fall (Williams et al., 2010). While OT behaves as a generalist, it also depends on forest habitat for many critical resources.

Very detailed knowledge about the closely related wild turkey provides even more information regarding habitat requirements of OT. Optimal habitat for wild turkeys consists of at least 40% forest with the remainder consisting of other vegetation types, including pastures and croplands (Backs and Eisfelder, 1990; Donovan, 1985). Schroeder (1985) also determined that wild turkeys are reluctant to cross open areas of more than 180 m wide. Forest cover and connectivity among patches are thus important landscape characteristics which allow wild turkeys to persist.

The fine CT model that showed OT cannot persist below 50% forest cover in the landscape (Fig. 3A) hints at the negative relationship between forest cover in the Yucatan and other variables such as forest connectivity and human density, together with their own respective ensembles of associated variables (see Harrison and Bruna, 1999). One of these effects is increased predation by both humans and medium-sized, generalist predators such as the grey fox *Urocyon cinereoargentus* (Tewksbury et al., 1998; Thogmartin and Schaeffer, 2000), which are favoured by the disappearance of large predators such as the jaguar *Panthera onca* (Sieving and Karr, 1997; Terborgh and Winter, 1980). It might well be that, in our 100 km<sup>2</sup> "landscapes," forest behaves as an ecological trap (*sensu* Gates and Gysel, 1978) when its cover decreases below 50%, even if the amount of forest is large enough to support flocks.

# 4.2. Importance of small settlements

The importance of very small settlements and low human population density in the models corroborates our expectation that subsistence hunting causes a major threat to OT populations. Whereas in larger settlements (>1000 inhabitants) or towns there are several possibilities guaranteeing more stable family income and nourishment (employment or informal work contracts), the small settlements were characterised by considerable poverty and a strong reliance on bushmeat (Escamilla et al., 2000; Jorgenson, 1993; Quijano-Hernández and Calmé, 2002).

There is additional evidence that the founding of new settlements affected OT distribution, based on the relationship between settlement age and the minimum walking distance from the settlement required to encounter an OT (Fig. C, electronic supplementary material). Although there is large variation for any given settlement age, an upper limit can be fitted to the data. For settlements  $\geq$  30-years-old, there appeared to be a constant upper distance threshold of 15 km (except for very old settlements, including larger towns with highly impacted surroundings), whereas for recently founded settlements, there was a distinct and statistically significant relationship (Fig. C, electronic supplementary material). Immediately following settlement establishment, OT can be found in the immediate vicinity; with increasing settlement age and corresponding increases in hunting pressure and decreases in prey naiveté, the minimum distance threshold for OT encounter progressively increases to 15 km. In this context, settlers act like alien predators that prey upon a naïve prey species and which have the potential for heavily affecting the prey population (Banks and Dickman, 2007; Cox and Lima, 2006). Although we did not directly observe what the respondents reported (i.e., OT appearing almost within village boundaries, being easy prev. and progressive disappearance from closer areas and increased wariness), we observed that OT became less wary in CBR after the hunting ban of 1989. Consequently, some flocks now remain almost permanently stationed around human installations, such as the residences of CBR personnel or touristic infrastructure.

### 4.3. Indications of an extinction vortex

OT abundance in 1980 was expected *a priori* to be the most important explanatory variable in the fine models. This is due to the fact that information on prior abundance appears as a part of the abundance change classes. If OT abundance in 1980 was H, for example, then the only possible abundance change classes were HH, HM, HL and HA. OT abundance in 1980 was also the most important explanatory in the coarse models, where information regarding prior abundance was not integrated into the abundance change classes. In both the fine and the coarse models, classification accuracy decreased considerably when OT abundance in 1980 was excluded from the list of explanatory variables: in the fine RF model, for example, the OOB error rate increased from 42.88% to 59.30%, while in the coarse RF model it increased from 26.60% to 37.06%.

All conclusions based on the importance of OT abundance as a predictor depend heavily on the reliability of the data, particularly when they were collected in recent inquiries regarding the status of a bird population 20 years ago. Despite having no way to corroborate these data which otherwise would not exist, we would like to stress that: 1) interviewees had no cues to determine whether it would be better or worse to report a positive or a negative trend; 2) each interview was led as an informal conversation in which most information was provided by the informant prior to even being asked; and 3) present day data that were verified in the field proved to be accurate. Also, using categories rather than exact numbers of maximum bird number per flock made the data more robust to errors.

The preeminent importance of OT abundance in 1980 as an explanatory variable for abundance changes between 1980 and 2000 (Figs. 2 and 3) indicates that OT dynamics have been governed by internal rather than by external factors. Medium and low abundances in 1980 inevitably led to a further decrease during subsequent years, which leads us to conclude that the OT might well find itself in what Gilpin and Soulé (1986) have termed an extinction vortex. When human colonisation, subsequent hunting, and habitat loss reach certain thresholds (Fig. 3; Fig. A.I and A.II, electronic supplementary material), OT abundance would decrease so that its populations become increasingly small and

isolated. These populations are thus vulnerable to processes such as reduction in gene flow, genetic drift, inbreeding, the Allee effect, or environmental stochasticity, all of which reinforce the trend towards extinction.

Conservation biology traditionally has concentrated on the extinction risk of small populations (Fagan and Holmes, 2006; Primack, 1998). However, Oborny et al. (2005) showed through simulation that low abundances also can be dangerous. They pointed out that, below critical thresholds, a population spontaneously fragments into discrete subpopulations even if the population is very large and that this fragmentation is an abrupt rather than a steady process. This situation might well apply to OT, which still is distributed over the entire Yucatan peninsula and far from being a "small population." The observed population thinning between 1980 and 2000 (Fig. 1) and the lack of an obvious relationship between environmental/social variables and population decline correspond quite well to the kind of population erosion modelled by Oborny et al. (2005).

The model proposed by Oborny et al. (2005) is based on the dispersal abilities of a species: the lower the dispersal ability, the higher the critical threshold. Turkeys are not considered good dispersers (Schroeder, 1985). Consequently, failures of wild turkey reintroductions are often due to their limited capacity in reaching more favourable parts of the North American landscape (Backs and Eisfelder, 1990). For OT, the few data that exist for females come from the protected area of Tikal, Guatemala, where the species is not exposed to human predators. While one female dispersed eight km from her nest, the average distance travelled by radio-collared female OTs is only 2.4 km (González et al., 1998b), thereby characterising the OT as a weak disperser. Since female OT dispersal remains within the resolution of the  $10 \times 10$  km grain we applied, dispersal would be very rare to observe at the spatial scale of our study.

An extinction vortex is only averted with the complete cessation of hunting and deforestation, and when species and habitats are effectively protected. This is the case in the conversion of Calakmul to CBR, with the result that OT abundance increased from medium to high abundance (Fig. 1) in 1989. Another example is the forest reserve of the communal area of Laguna Om (Fig. 1). This community was founded more than 80 years ago for gum tappers, but eventually its forest was depleted by bad management practices in the 1960's and 1970's. Most of its inhabitants turned to cattle ranching and let the vegetation recover in the forest reserve, thereby permitting OT populations to re-establish.

# 5. Conclusions

Our survey results suggest a hypothetical scenario for OT decline, as follows: migrants from other Mexican states settle forested regions in Yucatan; they establish small settlements, and in their initial phase, bushmeat hunting is important for survival; the naïve OT is easy prey; when hunting, together with the initiation of land-use changes (deforestation), reaches a certain level, local OT abundance falls below a critical threshold and enters an extinction vortex; and finally, OT keeps declining over its entire distribution regardless of current social and environmental changes, according to the Oborny population thinning model, except when there is complete protection of both the species and its habitat.

As a consequence of abundance decreases and the loss of distributional area, hunting of OT has been officially forbidden since 2001, except in dedicated wildlife management units. However, subsistence hunting persists and is widespread. Moreover, deforestation and conversion of forests to agricultural land and cattle ranches has not halted. Since large parts of the distributional area of the OT have already shown low or medium abundances in 2000, we suspect that the OT has continued to decrease since then. If the OT actually finds itself in an extinction vortex and OT decrease goes on, then only a network of well-protected reserves will be able to locally conserve the species.

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### Appendix. Supplementary material

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.actao.2010.08.004.

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