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Wildebeest migration drives tourism demand in the Serengeti

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Abstract

We examine tourism demand for an iconic ecological resource – the migration of ~1.3 million wildebeest (*Connochaetes taurinus*) in the Serengeti-Mara ecosystem. The wildebeest migration generates economic benefits through ecotourism, which we investigated by combining quantitative tools from spatial ecology and environmental economics with wildebeest GPS collar data and lodge use data from Serengeti National Park. We used GLMMs and random utility models to quantify the effect of the distance from lodges to wildebeest hotspots on two important aspects of demand: the number of tourists visiting lodges in the park (participation); and the tourists' choice of where to stay during their visit (site choice). We find that longer distances between lodges and wildebeest hotspots significantly reduced tourist participation (i.e. the total number of tourists visiting lodges) and site choice (the probability of tourist groups choosing a lodge). Lodge price had a positive effect on participation, but it did not affect site choice for international tourist groups. Whilst our results are specific to the Serengeti, the methods presented here can be applied to any system in which non-consumptive wildlife viewing is the foundation of local ecotourism. As such, this novel approach provides a new perspective on the economics of wildlife management and strengthens the case for the continued conservation of ecosystems that contain wildlife resources. Due to the high value of the wildebeest migration to tourism, we suggest that future expansion of tourist infrastructure in the Serengeti should proceed in ways that minimise disturbance to this living resource.

Key words

Spatial ecology
Recreation demand
Ecotourism
Environmental economics
Ecosystem management

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1 Introduction

Ecosystems provide multiple goods and services on which economies and societies rely, but these are rarely fully valued by markets. The resulting failure to incorporate the economic value of environmental goods into management strategies and decision-making can undermine the resource itself and have detrimental future economic and ecological impacts (Hanley et al., 2007). The movement pattern of 1.3 million wildebeest (*Connochaetes taurinus*) migrating across a 20 000 km² landscape in the Serengeti-Mara Ecosystem is an example of such a resource. Wildebeest are more abundant in this ecosystem than all other large mammals combined (Hopcraft et al., 2015), and their migration has widespread effects on ecosystem functioning (McNaughton, 1976; Sinclair, 1979; McNaughton, 1985; Sinclair, 1995; Veldhuis et al., 2019). Through this role, wildebeest provide essential ecosystem services on which local communities rely, such as firewood, timber, bushmeat, medicinal plants, and wild foods (Jiao et al., 2019).

The migration also has far-reaching economic consequences through its impact on ecotourism. The Tanzanian tourism sector has grown rapidly in the past decades (Fig. 1). International arrivals to Tanzania reached a record 1.5 million in 2018, a number which the government of Tanzania aims to increase to 2 million by 2020 (International Travel & Health Insurance Journal, 2019). Currently tourism contributes about \$2,250 million USD per annum to the gross domestic product of Tanzania, which accounts for more than 14% of GDP, making tourism one of the largest foreign income earning sectors for the country (Government of Tanzania, 2018). Most international tourists visit East Africa to go on safari, and the 'wildlife watching market segment' is an extremely valuable, and growing, source of foreign revenue (Balmford et al., 2009; World Tourism Organisation, 2014). Serengeti National Park (SNP) in Tanzania was originally gazetted in 1951; its borders were subsequently re-aligned to protect the entire wildebeest migration route (Hopcraft et al., 2015). Today, the park remains an iconic safari destination due to its abundance of wildlife. In 2009, when tourism levels were substantially lower than at present (Fig. 1), the Greater Serengeti Ecosystem attracted 300 000 visitors annually, and the total expenditure from these tourists in Tanzania was US\$500 million in revenue per year which accounted for more than 50% of foreign tourism income (World Tourism Organisation, 2014).

In the Serengeti, wildlife plays a key role in safari-based marketing (Okello & Yerian, 2009; Borner, 2013), but the effect of wildebeest movement on tourism demand has not been explicitly measured. This is not unusual: trends in tourism-generated revenue in the African wildlife watching market are rarely quantified, which has been attributed to lack of suitable data (Balmford et al., 2009; World Tourism Organisation, 2014). As a result, past efforts to economically value wildlife viewing in Africa (e.g. Lindsey et al., 2005; Mladenov et al., 2007; Sekar et al., 2013; Lee & Du Preez, 2016; Saayman & Saayman, 2017), are relatively uncommon in terms of wildlife areas and species. However, quantifying ecotourism demand provides a powerful argument for conservation (Balmford et al., 2009) and helps to maximise ecotourism benefits (Sekar et al., 2013).

Economists rely on a variety of quantitative tools to estimate the economic value of specific recreational resources within non-market settings (Hanley et al., 2007). The non-market value of wildlife viewing is often inferred through revealed and stated preference approaches (e.g. Zawacki et al., 2000; Martín-López et al., 2008; Cerda et al., 2013; Richardson et al., 2017). Here, we employ recreation demand models within a revealed preference framework to relate the distance between lodges and wildebeest to tourism demand. Our novel approach combines data from wildebeest GPS collars and recreation demand data from occupancy rates of Serengeti lodgings with Geographic Information Systems and advanced statistical modelling. Specifically, we investigated the relationship between where wildebeest

were located in the park at a particular point in time, and tourism demand. Changes in wildebeest movement depend on a range of complex factors including changes in precipitation, land use and infrastructure (Veldhuis et al., 2019). Our work yields insights into how such changes could impact economically vital tourism spending in the park. Whilst our results are specific to the Serengeti, the methods presented here can be applied to any system in which non-consumptive wildlife viewing is the foundation of local eco-tourism.

[INSERT FIGURE 1]

2 Methods

2.1 Overview

We quantified the effects of distance from a lodge to the nearest wildebeest hotspot, i.e. a location with a high density of animals, in a given month (hereafter “distance to wildebeest”), lodge price, lodge capacity, and seasonality (defined as the annual periodicity of holidays) on tourism demand for all 19 Serengeti tourist lodges (Table 1). We investigated two aspects of tourism demand: (1) total recreational participation rates, measured as the weekly average number of beds occupied/unoccupied per lodge (hereafter “*Lodge occupancy*”) and (2) site choice, measured as tourist groups’ selection of a specific lodge to stay at (hereafter “*Lodge choice*”). Note that the distinction between models estimating changes in participation and site choice is common in recreational demand modelling (Hanley et al., 2003). We used generalized linear mixed models (GLMMs) to model *Lodge occupancy* and random utility models (RUMs) to model *Lodge choice*. The two analytical approaches provided different insights. The GLMMs of *Lodge occupancy* analysed how spatial variation in the distribution of wildebeest impacted the number of tourists visiting the lodges in the park whereas RUMs of *Lodge choice* allowed us to explore the distribution of a given (fixed total) number of tourists between lodges as a function of the spatial distribution of wildebeest. Analysing people’s recreational site choices with RUMs is a standard approach within recreation demand modelling in economics (Hynes et al., 2008).

In the *Lodge choice* models, we analysed data from residents of East Africa (Tanzania, Kenya and Uganda) and international tourists (non-residents) separately, as we expected their tourism demands to differ due to unequal availability of recreational choices, decision-making processes, travel costs prior to reaching the SNP, and fees for the same park services. However, because the number of occupied beds (and not individual tourists) was the observational unit in the *Lodge occupancy* model, we could not differentiate between resident and international tourists. In both analyses, we hypothesised that there would be a negative effect of increasing distance to wildebeest on lodge occupancy and lodge choice because tourists may come to the Serengeti specifically to witness the wildebeest migration during their safari.

2.2 Data collection and processing

2.2.1 Response variables

The study area was Serengeti National Park (SNP) in northern Tanzania (Fig. 2). The research relied on secondary data provided by the Serengeti Tourism Office, which was collected electronically by park staff through a gate entry database. The gate data provided information about the number of people in each tourist party entering the park, whether they were residents of East Africa or not, and in which of the 19 permanent Serengeti lodges the party stayed (Fig. 2). The availability of this lodge use data limited the sample size to 10 626 observations of tourist parties entering SNP over the course of 43 weeks from July 2017 to May 2018, of which 2240 were resident and 8386 were international parties. The 19 lodges in our dataset provided a total of 1490 beds which tourist parties could choose to stay in during their trip. We used the lodge use data to calculate the daily number of beds that were occupied in each lodge, i.e. our response variable *Lodge occupancy*. We modelled *Lodge occupancy* as a binomial process of successes and failures (i.e. bed spaces occupied and not occupied, respectively) and related this to a set of explanatory variables including distance to wildebeest. We minimized the effects of temporal autocorrelation, related to tourist parties staying more than one day, by modelling the weekly, rather than daily, mean occupancies for each lodge (n=817 lodge-weeks). Lodge use data were processed differently in order to analyse our second response variable *Lodge choice* using RUMs. The choice to stay in a given lodge on a particular trip was mutually exclusive (one cannot sleep in two locations simultaneously), so every tourist party was assigned a binary observation for each of the 19

lodges, either ‘1’ if that lodge had been chosen on a specific choice occasion (visit) or ‘0’ if it had not. The choice set for the RUMs thus comprised 19 lodges. Each choice to visit a given lodge on a given choice occasion was associated with a set of lodge attributes, including distance to wildebeest, which were used as explanatory variables. Due to planned closures during the wet season (typically March and April), some lodges were unavailable in the choice sets during certain periods.

2.2.2 Explanatory variables

The explanatory variables used in the models are outlined here and summarised in Table 1. To estimate the effect of distance to wildebeest on tourism demand, wildebeest GPS telemetry data were used to estimate monthly distributions of wildebeest in the SNP. Wildebeest are continuously moving between the southern plains in the wet season (December–April) and the northern woodlands in the dry season (August–November). This migration pattern is seasonally predictable at a large spatial scale and follows counter-gradients of soil fertility and rainfall (Holdo et al., 2009; Hopcraft et al., 2015), though the timing and small-scale pattern of movements vary from year to year (Pennycuik, 1975). We estimated aggregated monthly wildebeest distributions based on long-term (2008–2018) movement patterns rather than those from the specific months and year in which lodge use data were collected (2017–2018). Because lodge bookings are typically made several months to years ahead of safari dates, we assumed that lodging decisions were made based on long-term average wildebeest viewing opportunities rather than those from the year in which visitation occurred. We tested this assumption by comparing *Lodge occupancy* models using the 10-year (2008–2018) versus current year (2017–2018) wildebeest distribution and found that the 10-year average provided a substantially better fit ($\Delta AIC = 114.7$). To estimate wildebeest distributions, we fit Brownian bridge movement models (BBMMs) (Horne et al., 2007) to GPS telemetry data from 138 adult female wildebeest in each of the twelve months of the year. Utilisation distributions from each individual’s monthly BBMM were summed and normalized so that the resulting population-level utilisation distribution for each month summed to 1. The resulting rasters had a resolution of 180x180m. In the distributions, most parts of SNP had a low but non-zero probability of wildebeest use; thus we identified wildebeest hotspots as raster cells containing the upper 25% of utilisation distribution values. We calculated the minimum, direct-line Euclidean distance from each lodge to these wildebeest hotspots (*Dist_wildebeest* variable in our models). Examples of the monthly maps of wildebeest hotspots are shown in Fig 2.

[INSERT FIGURE 2]

A number of factors may affect tourism demand for a recreational resource and we expected the cost of staying in a given lodge to be one such factor. Lodge cost suppresses demand if tourists prefer cheaper options, and enhances demand if the price reflects un-measured lodge quality and visitors’ preference for higher levels of satisfaction or luxury, which they believe are signalled by higher prices. Lodge prices were retrieved by contacting lodges directly, requesting their “rack rates” for a single room including full board, for every month of the year. This information was contained in the variable *Lodge price*, which was included in both *Lodge occupancy* and *Lodge choice* models.

The total number of lodge beds imposed an upper limit on occupancy, so we controlled for *Capacity* in our analyses. Lodge capacities were retrieved from an infrastructure survey of SNP (Mafuru and Hongoa, 2019, unpublished data), but data processing revealed that 16 lodges occasionally exceeded their stated

capacities. In these cases, the maximum observed number of people in the lodge was taken as the true capacity.

Visitor preferences and decision-making processes are likely to differ according to varying levels of total tourism pressure. We expected that when the total number of tourists in the SNP was high, the saturation of lodges would cause wildebeest distributions to become less important as a trip determinant. To control for this potential interactive effect, we calculated the total number of visitors staying in the SNP every night (Fig. 3). The weekly mean of these values, our *Daily_visitors* variable, was then interacted with the *Dist_wildebeest* variable in the *Lodge occupancy* model. However, this continuous variable was not suitable for the *Lodge choice* RUMs as there was a lack of variation in the variable across the choice sets. Instead, in *Lodge choice* models we interacted the *Dist_wildebeest* variable with a seasonality factor (i.e. categorical variable) determined *a priori* to estimate the effect of wildebeest on lodge choice at different times of the year within the same model. The *Season* variable had two levels, “High” and “Low.” High season was defined based on northern hemisphere school holidays, most of which fall in the months of July and August, as well as from 15th December to 14th January. Entries not falling within these time periods were classified as low season.

[INSERT TABLE 1]

2.3 Analysis of lodge occupancy

We employed GLMMs in R (R Core Team, 2016) to analyse the effect of distance to wildebeest (*Dist_wildebeest*), lodge *Capacity*, lodge *Price*, and tourism pressure (*Daily_visitors*) on *Lodge occupancy*. We included *Lodge ID* as a random effect in the model because the data consisted of repeated samples within lodges, creating non-independence across observations. To test whether any linear effect of *Dist_wildebeest* levelled off at high distances, we included a quadratic *Dist_wildebeest* term, and we interacted *Dist_wildebeest* and *Daily_visitors* to test whether the overall number of tourists in SNP affected the relationship between wildebeest and occupancy. All variables were rescaled (standardised and centered by subtracting the mean, then dividing by the standard deviation) to allow convergence of the model. See Table 1 for the summary statistics of unscaled values for each variable. We used likelihood ratio tests (LRTs) to test whether each term improved model explanatory power and we found that no terms were non-significant (Table B, supplementary material).

2.4 Analysis of lodge choice

We analysed lodge choices in the statistical software package Stata (StataCorp., 2019). We explored the patterns in the reported lodge choices of tourist parties entering the park using the conditional logit (CL) RUM model, which allowed us to predict tourist party lodge choice based on *Dist_wildebeest*, *Season*, *Price*, and *Capacity*. We then fitted random parameter logit (RPL) models, which are also a type of RUM, with the same structure. When using CL models, we assume that all tourist party preferences for each site attribute (*Dist_wildebeest*, *Season*, *Price*, and *Capacity*) are identical, whereas with RPL models we recognise that individual preferences for each of these lodge attributes may differ across visitors. This is known as preference heterogeneity and is represented by computing parameter estimates of the standard deviations of each attribute. Thus, with RPL models two parameter estimates are obtained for each attribute: a mean effect (average preferences) and a standard deviation around this mean effect (how different people in the sample are compared to the average in their preferences for each

attribute). In addition to addressing unexplained preference heterogeneity within the sample, RPL models also account for error correlation across choice observations. We assumed a normal distribution for the random preference parameters because both positive and negative preferences were feasible for all attributes. Halton draws (500) were used to simulate the attribute distributions. Lodge ID (site dummies) were not included in the RUMs because this would mask the effects of the lodge attributes of interest. The results of a separate model predicting lodge choice using only site dummies are available in Table A1 and A2 (supplementary material).

3 Results

3.1 Data characteristics

The daily number of tourist parties that visited the SNP over the 43 weeks showed large variation, between a minimum of 25 per day in late April and a maximum of 2573 per day in late August, and lodge occupancy likewise varied greatly (Fig. A, supplementary material)

3.2 Analysis of lodge occupancy

Serengeti *Lodge occupancy* was strongly related to *Dist_wildebeest*, *Dist_wildebeest*², *Daily_visitors*, *Capacity*, *Price*, and an interaction between *Daily_visitors* and *Dist_wildebeest* (Table B, supplementary material). All model terms had significant effects on *Lodge occupancy* at the <1% level, except *Capacity* which had a significant effect at the 5% level (Table 2). Comparing the residuals-versus-fitted plot of the real data with the same plot of data simulated from our model, suggested that the model fitted the data well. The marginal R² (variation in the data explained by fixed effects) and conditional R² (variation in the data explained by fixed and random effects) with the delta method and obtained values of 0.434 and 0.963, respectively. Note that the variables were re-scaled, so parameter estimates in Table 2 should be interpreted as the mean change in the response variable resulting from a one standard deviation change in the independent variable when all other variables are held constant.

Lodge occupancy was negatively related to *Dist_wildebeest*: when lodges were farther away from a wildebeest hotspot, *Lodge occupancy* decreased (Table 2), but this effect levelled off at high distances because of the positive quadratic *Dist_wildebeest* term (Table 2). The interaction between *Dist_wildebeest* and tourism pressure (*Daily_visitors*) was negative, suggesting that higher tourism pressure amplifies the negative effect of increasing distances to wildebeest (Table 2; Fig. 3). Unsurprisingly, *Lodge occupancy* increased with the total number of *Daily_visitors* to the park, and this was the largest main effect (Table 2). Lodge *Capacity* had a positive effect on *Lodge occupancy*, suggesting that larger lodges tended to be fuller (Table 2). The effect of *Capacity* was smaller than the main effect of *Daily_visitors*, but slightly larger than the main effect of *Dist_wildebeest* (Table 2). *Lodge occupancy* was also positively affected by lodge *Price* (Table 2), though *Price* was the weakest of the main effects.

[INSERT TABLE 2]

[INSERT FIGURE 3]

3.3 Analysis of lodge choice

The RPL model results are presented in Table 3. The majority of the mean effects were significant, but the standard deviation estimates for all attributes, except lodge *Capacity* in the International Tourist Model, were not significant. This absence of preference heterogeneity across visitors implies that the tourist parties in our sample had very similar preferences for the lodge attributes, including distance to wildebeest. Under the assumption that attribute coefficients are normally distributed, a negative mean coefficient implies that visitors on average dislike higher values of the attribute. Therefore, the

Dist_wildebeest coefficient (in Table 3) suggests that increasing distance to wildebeest decreased the probability of a tourist party choosing a particular lodge, both for parties consisting of East African residents and international tourists. For international tourist parties, the effect of *Dist_wildebeest* on *Lodge choice* depended on *Season*, such that they had a stronger preference for (shorter) distance to wildebeest hotspots in low season. This was evidenced by a stronger avoidance of lodges far from wildebeest hotspots in the low season compared to the high season (Table 3). This seasonal effect was not significant in the Resident Tourist Model (Table 3). *Lodge Capacity* had a positive effect on choice for both resident and international tourist parties (Table 3), suggesting that larger lodges were preferred. However, the significant ‘Standard deviation of attribute’ estimate for lodge *Capacity* in the International Tourist Model (Table 3) showed that within our sample of international tourist parties there were significantly different preferences for lodge size. *Lodge Price* negatively affected resident tourist parties’ probability of choosing a lodge (Table 3). However, *Price* did not affect *Lodge choice* by international tourist parties (Table 3).

[INSERT TABLE 3]

4 Discussion

4.1 The wildebeest migration and tourism demand in Serengeti

We estimated the marginal effect of increasing distance to wildebeest (defined as distance from a lodge to the nearest wildebeest hotspot in a given month) on tourism demand for the Serengeti. Two aspects of tourism demand were investigated, namely (1) lodge occupancy and (2) lodge choice. Respectively, these were measures of two commonly analysed aspects of recreational demand, (1) total recreational participation and (2) the sites within a choice set that groups choose to visit. Our results show that increasing distance to wildebeest significantly decreased tourism demand, both when demand was modelled as lodge occupancy (Fig. 3) and lodge choice (Table 3).

The analysis revealed that lodge occupancy (our proxy for tourist participation) decreased when lodges were farther away from a wildebeest hotspot. For instance, our model predicted that during periods when the number of daily visitors to the park was high, increasing distance to wildebeest from 0 km to 80 km caused a reduction in lodge occupancy from 69% to 9% (Fig. 3). The significant positive quadratic parameter estimate provided evidence that the effect of distance to wildebeest levelled off at high distances. The relationship between distance to wildebeest and occupancy depended on the total number of tourists in the park (i.e. tourism pressure), suggesting that under relatively crowded conditions, being closer to wildebeest was an even stronger driver of lodge occupancy. We found that lodge price had a significant positive effect on occupancy which could suggest that occupancy increases when luxurious lodging is provided if luxury is signalled by higher prices. However, the relationship may also exist because lodges increase their rates during high season, in which occupancy is expected to be high, resulting in the co-occurrence of high prices and high occupancy.

The analysis of lodge choice revealed that although tourists preferred lodges that were close to wildebeest hotspots, the choice of lodging differed by season and between resident and international tourists. International tourists were less sensitive to distance to wildebeest during the high season than during the low season. This suggests that overseas tourists visiting during northern-hemisphere school holidays (July, August and mid-December to mid-January) were more willing to accept lodges that were farther from the wildebeest migration when the availability of beds in the national park was relatively low. This behaviour may be explained by the fact that many of the lodges were at or near full capacity, thus restricting lodge choices especially for people who did not book early. While lodge occupancy was positively affected by lodge price, we found that the cost of staying at a lodge had no effect on international tourist lodge choice. The lack of a response to price may suggest that international tourists would tolerate being charged higher prices, which is consistent with a past study showing Serengeti safari packages are undervalued (Sekar et al., 2013), but this conclusion remains speculative within the scope of our study since the effect was not significant. Conversely, resident tourists were more selective, preferring lodges that were less expensive and displayed a similar preference for (shorter) distance to wildebeest hotspots between high and low season. The fact that accommodation costs are likely to form a much larger fraction of total trip cost for resident compared to international tourists may account for this differential response to cost. The majority of tourists visiting the Serengeti were international (79%) and this is the most lucrative sector of tourism in Tanzania. Our results imply that international tourists are willing to accept lodges far from the migration during peak seasons when availability in prime locations is limited, which opens a range of alternative ecologically sustainable solutions to managing high tourist pressure. Nonetheless, while increasing prices charged by lodges might raise revenue, it would likely reduce the accessibility of the tourist experience to lower-income tourists (Thur, 2010; Baral et al., 2008).

4.2 Alternative management strategies and the threat of mass tourism

The large demand by tourists to witness the wildebeest migration raises concerns about the ecological sustainability of developing new infrastructure such as hotels, lodges and roads in the core protected area. For instance, a recent survey by the Serengeti National Park revealed a 4-fold increase in bed-night capacity in the last 7 years indicating substantial infrastructure development inside the protected area (Mafuru and Hongoa, 2019, unpublished data). Of particular concern is that high tourist pressure could compromise the habitats and resources on which the migration depends, and undermine the long-term sustainability of the resource. Mass tourism has been shown to have negative impacts on many ecosystems globally through its effect on animal physiology and behaviour, translating into reduced reproduction, survival, abundance, diversity, and altered interactions between species (Shannon et al., 2017). The challenge lies in finding solutions that are economically attractive while protecting the natural capital assets that support the generation of economic benefits (Dobson et al., 2010; May et al., 2019).

There are two ways in which the wildebeest-tourism relationship may be modified and managed; one is through changes to the distribution of the wildebeest migration, and the other is through changes to the distribution of tourism facilities. The distribution of wildebeest may change in density, timing, or spatial extent. There is evidence indicating that each of these three changes has occurred in response to anthropogenic factors. For example, intensifying human activity around the edges of, and within, the core protected area has caused habitat compression, thus increasing wildebeest densities in the core and pushing wildebeest distributions farther south and west (Veldhuis et al., 2019). Furthermore, a proposed highway bisecting SNP could exacerbate this effect, lowering ecosystem carrying capacity and “decoupling” wildebeest wet and dry season habitats (Dobson et al., 2010; Holdo et al., 2011). Second, since the wildebeest migration is driven in part by rainfall (Holdo et al., 2009), climate change-induced alterations to rainfall are likely to have large impacts on the spatio-temporal distributions and timing of wildebeest migration. The predicted increase in ENSO (El Niño–Southern Oscillation) events (Cai et al., 2014) will also cause more frequent extreme droughts and floods in the ecosystem, thus lowering carrying capacity and leading to a decline in wildebeest abundance (Ogutu et al., 2007).

The effects of climate variability on tourism are already evident; an unusually dry end of the rainy season was the suspected cause of the migration arriving one month early in the Maasai Mara in June 2019, when lodge occupancy was only 30-50% (Sayagie, 2019). Usually, hotels in this area fill to 90-100% of capacity when the migration arrives, so considerable revenue was lost as a result of the altered migration timing (Sayagie, 2019). It is difficult to predict the effect of altered wildebeest distributions on ecotourism revenue because the exact densities of wildebeest that tourists respond to are unknown. We analysed the response of tourist demand to wildebeest hotspots calculated as the 25th percentile of predicted probability landscapes and found a significant effect, but more research is needed to identify thresholds of wildebeest concentrations that satisfy tourism demand. However, given the effects of external anthropogenic and environmental factors on the wildebeest migration, it is not unreasonable to think that increases in tourist development inside the protected areas could alter the movement and distribution of wildebeest in the future.

An alternative way to manage the wildebeest-tourism relationship is by controlling the distribution of lodges, for instance following IUCN recommendations of locating large-scale infrastructure outside protected areas (Leung et al., 2018). Our result that tourists prefer being near to the wildebeest migration may, in fact, reflect a demand for easy access to see the migration rather than necessarily staying overnight near it. One solution would, therefore, be to build any new lodges on the park border while simultaneously improving road access to wildlife viewing areas, thereby minimising the ecological

footprint of lodgings and reducing the travel time to view the migration (note, the Serengeti planning department receives dozens of propositions for new tourist facilities every year so this could be a viable option in the future). The geometry of the park, with a large perimeter to area ratio, allows visitors choosing to stay on the perimeter to be within 10 to 30 km of prime game viewing circuits, which is easily commutable. If roads were to be upgraded, then the consequences of increased traffic such as restricted animal movement, road kills, or noise and environmental pollution would also need to be monitored and regulated (Caro et al., 2014). Additionally, small luxury mobile fly-camps with small ecological footprints could provide exclusive access to the migration for visitors willing to pay premium prices. A strategy which involves large permanent structures on the perimeter and small mobile high-end facilities in the core of the ecosystem confers several advantages: (i) it would improve employment opportunities for local people living around the ecosystem in the tourism-sector, (ii) it would improve access to supplies such as local produce, fuel, and transportation to lodges, and (iii) it could create a “tourist fence” effect around the perimeter of the ecosystem thereby reducing illegal incursions by hunters and livestock keepers who are intent on avoiding detection by rangers. One caveat here is that while our work focused only on lodges, future work should assess tourist choices between lodges and tented camps, as well as the potentially different effects of large permanent tourist structures as opposed to small mobile structures on wildebeest migration patterns.

Our results also suggest that international tourists have a stronger preference to be near the migration during the low season (i.e. outside the northern-hemisphere school holiday period) (Table 3) when wildebeest are typically on the southern short grass plains and western corridor of the Serengeti (see the wildebeest hotspot distribution for January in Fig. 2). While only 4 of the 19 permanent lodges in Serengeti are located in these areas, they are crucial feeding and calving grounds for the wildebeest and contain important resources for the migration (Pennycuick, 1975; Mduma, 1996; Holdo et al., 2009). This suggests that the southern short grass plains and western corridor may be particularly sensitive areas to build additional infrastructure. Lodges on the perimeter of the ecosystem, with reliable access to viewpoints, would ensure ecological sustainability and long-term economic returns and would be the most viable option.

4.3 Setting appropriate prices for tourism in Serengeti

We found that the choice of where to stay for international tourists was unaffected, on average, by the price of the lodge. This suggests that economic returns to the national park could be improved simply by increasing the lodge concession fee (i.e. the fee paid to the park by the lodge based on the number of bed-nights sold) without increasing the overall number of tourists. The added benefit of this approach is that it also caps the annual expenditure that national parks have to pay in order to maintain the infrastructure needed to support additional tourists (e.g. road repairs, guards, provisioning water, sewage and waste disposal, and fire breaks).

With additional information about visitors, the site choice models used in our study could be used to calculate the maximum tourists are willing to pay for accessing wildebeest watching. The difference between this value and the current cost of viewing the wildebeest migration (also called the consumer surplus), would allow us to quantify a feasible cost increase that would not compromise the popularity of wildlife watching. We did not estimate this maximum Willingness to Pay or consumer surplus in our analysis because there was no socio-demographic information associated with the lodge use data, and the cost of occupancy of the lodges is only a portion of a visitor’s travel cost to the SNP. However, it would be worthwhile to obtain these data in future research in order to estimate the dollar value of wildebeest viewing in the SNP.

4.4 Future work – reciprocally interacting ecological and economic models

The ability to capture the reciprocal relationship between tourists and the wildebeest migration in which each interacts with the other over time would provide additional insights into our ability to predict changes to the distribution of tourists within the SNP, and thus revenue. In this study, we assumed a uni-directional relationship between wildebeest and tourism demand (that is, our assumed causality runs from changes in wildebeest location to changes in tourist demand), but wildebeest are affected by a myriad of factors including tourism. This makes the dynamic relationship a complex one. Ideally, this would be modelled over time with a truly integrated (simultaneous) approach that firstly predicts the distribution of the wildebeest migration using all factors that affect it. These predictions would be supplied to models, like those presented in this study, to estimate tourist abundance, revenue generation, and distribution over the landscape, which would feed into wildebeest migration predictions for the following year. This is an appealing approach for future work: however, it is not possible with current data.

4.5 Conclusions

Our study demonstrates the links between wildlife conservation and sustainable economic development and illustrates the value of natural phenomena, such as large mammal migrations, for enhancing a country's economic potential. We found that longer distances between lodges and hotspots of the Serengeti wildebeest migration reduced lodge occupancy (our measure of total recreational participation rates) and influenced lodge choice (where these tourists chose to stay), such that lodges closer to wildebeest were strongly preferred. The consistently significant tourist preference for shorter distances to the migration highlights the economic potential of this resource for Tanzania and Kenya, but it also underscores its vulnerability to over-exposure. Anthropogenic activities are currently changing the timing, spatial distribution, and abundance of wildebeest in the Serengeti (Veldhuis et al., 2019). Given the strong relationship we demonstrated between the wildebeest migration and the tourism demand it generates, factors and actions that are likely to impact the migration should raise concern. If tourism and development in SNP are not carefully managed, the persistence of the Serengeti wildebeest migration is likely to be compromised, thus undermining this highly valuable economic resource. Understanding the economic value of wildlife, and the interplay between its persistence and the economic benefits it generates will enhance our ability to design optimal ecosystem management strategies in the future.

Acknowledgments

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Figures and tables

Figure 1. Print in black and white. Single column fitting image:

Figure 1 legend:

Fig. 1. The number of international tourist arrivals in Tanzania between 1972 and 2018. Colours correspond to the data sources specified: GovTZ 2012 (Government of Tanzania, 2014), GovTZ 2014 (Government of Tanzania, 2016), GovTZ 2017 (Government of Tanzania, 2018), IPPmedia (Kajubi, 2019), Knoema (Knoema, 2017), Wade et al. 2001 (Wade et al., 2001).

Figure 2. Print in black and white. Two column fitting image:

Figure 2 legend:

Fig. 2. The Serengeti National Park (SNP), shown on the map is the core of the Greater Serengeti-Mara Ecosystem that falls between Tanzania in the south, and Kenya to the north. The top left panel depicts tourism infrastructure, including the 19 permanent lodges analysed in this study (blue) and smaller tents and campsites (empty circles). Top right, bottom left, and bottom right panels show wildebeest hotspot distributions for May (late wet season), September (dry season) and January (early wet season), estimated using Brownian bridge movement models fit to GPS telemetry data from 2008-2018. Darker green colours correspond to higher probability of use. Wildebeest distributions outside of SNP (shown in transparent colours) were omitted from our models because tourists in the park did not have access to these areas for viewing and therefore the distances to wildebeest occupying them were irrelevant.

Table 1:

Table 1.

Variables used to model lodge occupancy and lodge choice and their means and standard deviations (SD), where relevant.

Variable	Description	Mean	SD
Dist_wildebeest	<i>Continuous</i> . The estimated distance from each lodge to the nearest wildebeest hotspot in a given month. Unit: km.	12.4	18.9
Price	<i>Continuous</i> . The price of one non-resident tourist staying a single night in the given lodge. Unit: US dollars (US\$).	593.5	455.5
Capacity	<i>Continuous</i> . The maximum number of people a given lodge can accommodate.	79.2	59.9
Daily_visitors	<i>Continuous</i> (only GLMMs). Weekly mean of the total daily number of overnight visitors in SNP.	333.9	159.6
Season	<i>Factor</i> (only RUMs) with two levels: "High" and "Low." School holidays were defined <i>a priori</i> as July, August, and from 15 th December to 14 th January.	-	-
Lodge ID	<i>Random effect</i> (only in GLMMs). A unique identifier for each lodge.	-	-

Table 2:

Table 2.

Estimates of variable coefficients for the full binomial GLMM predicting the proportion of a lodge occupied. All variables were rescaled (standardised and centered by subtracting the mean, then dividing by the standard deviation) to allow convergence of the model. Thus, the parameter estimates in the model should be interpreted as the mean change in the response variable resulting from a one standard deviation change in the independent variable, when all other variables are held constant.

Variable	Mean estimate	SE	z value	p
Intercept	-2.050	0.256	-8.018	<0.001
<i>Dist_wildebeest</i>	-0.548	0.043	-12.874	<0.001
<i>Dist_wildebeest</i> ²	0.407	0.053	7.654	<0.001
<i>Daily_visitors</i>	0.717	0.012	57.482	<0.001
<i>Capacity</i>	0.607	0.258	2.357	0.018
<i>Price</i>	0.401	0.039	10.307	<0.001
<i>Dist_wildebeest:Daily_visitors</i>	-0.064	0.015	-4.123	<0.001
Random effect (<i>Lodge ID</i>) variance				1.232
Model fit				
Number of observations				817
Log-likelihood				-3613.800

Figure 3. Print in black and white. 1.5 column fitting image:

Figure 3 legend:

Fig. 3. The predicted relationship between distance from a lodge to the nearest wildebeest hotspot and the weekly mean proportion of that lodge occupied by tourists (*Lodge occupancy*). The four lines show this relationship under different levels of tourism pressure in SNP, measured as the number of total daily visitors to the park. Raw data are shown by grey filled circles.

Table 3:

Table 3.

Parameter estimates and standard errors in the RPL models for the resident and non-resident data subsets, predicting the tourist party lodge choice. Significant coefficients are in bold. Variables were analysed in their original units (see Table 1). The “Standard deviations of attributes” parameter estimates quantify how different the sampled tourists were with regards to their preferences, which is termed preference heterogeneity. A nonsignificant “Standard deviations of attributes” parameter estimate indicates that the sample did not differ with respect to their preferences for that attribute.

Attribute/level	RESIDENT TOURIST MODEL			INTERNATIONAL TOURIST MODEL		
	Mean RPL model estimate	SE	p	Mean RPL model estimate	SE	p
<i>Mean effects</i>						
<i>Dist_wildebeest</i> ‡	-8.87×10⁻³	3.61×10 ⁻³	0.014	-1.46×10⁻²	1.56×10 ⁻³	<0.001
<i>Dist_wildebeest:Season^{high}</i>	4.50×10 ⁻³	4.03×10 ⁻³	0.264	8.21×10⁻³	2.02×10 ⁻³	<0.001
<i>Price</i>	-4.04×10⁻⁴	8.00 ×10 ⁻⁵	<0.001	-1.95×10 ⁻⁵	4.05×10 ⁻⁵	0.630
<i>Capacity</i>	9.66×10⁻³	3.99×10 ⁻⁴	<0.001	1.24×10⁻²	3.68×10 ⁻⁴	<0.001
<i>Standard deviations of attributes</i>						
<i>Dist_wildebeest</i> ‡	9.36×10 ⁻⁶	3.80×10 ⁻³	0.998	-2.49×10 ⁻⁵	3.22×10 ⁻³	0.994
<i>Dist_wildebeest: Season^{high}</i>	-1.52×10 ⁻⁵	4.23×10 ⁻³	0.997	3.19×10 ⁻⁵	6.14×10 ⁻³	0.996
<i>Price</i>	3.52×10 ⁻⁷	1.46×10 ⁻⁴	0.998	1.82×10 ⁻⁷	6.90×10 ⁻⁵	0.998
<i>Capacity</i>	1.97×10 ⁻⁴	5.95×10 ⁻³	0.974	-1.93×10⁻²	8.18×10 ⁻⁴	<0.001
Model fit						
	Log likelihood	-5076.404		Log likelihood	-18271.513	

‡ Reference level: Low season

Supplementary Material

Table A1 – International Tourist Site Dummy Model

Lodge	Mean conditional logit estimate for residents	SE	z	p	lower confidence interval	upper confidence interval
Intercept (Bushtops)	0 (baseline)	NA	NA	NA	NA	NA
Elewana	0.690	0.092	7.540	<0.001	0.511	0.870
FourSeasons	-0.580	0.124	-4.680	<0.001	-0.823	-0.337
Grumeti	0.587	0.094	6.240	<0.001	0.402	0.771
Kirawira	0.210	0.100	2.090	0.036	0.013	0.407
Kubukubu	1.812	0.081	22.410	<0.001	1.654	1.971
KuriaHills	0.396	0.098	4.030	<0.001	0.204	0.589
Kusini	-1.659	0.192	-8.640	<0.001	-2.036	-1.283
Lamai	0.587	0.095	6.160	<0.001	0.400	0.773
Lobo	0.581	0.093	6.230	<0.001	0.398	0.764
MaraRiverPost	-1.501	0.173	-8.660	<0.001	-1.841	-1.162
Mbalageti	-0.479	0.120	-3.990	<0.001	-0.714	-0.243
MbuziMawe	0.799	0.090	8.870	<0.001	0.622	0.975
Sayari	-0.013	0.108	-0.120	0.903	-0.225	0.199
Serena	2.441	0.078	31.180	<0.001	2.288	2.595
Seronera	-18.512	771.624	-0.020	0.981	-1530.867	1493.843
Singita	-2.258	0.254	-8.890	<0.001	-2.755	-1.760
Sopa	1.655	0.082	20.230	<0.001	1.495	1.815
Soroi	-18.512	771.624	-0.020	0.981	-1530.867	1493.843
Observations						130,318
Log likelihood						-15879.88

Table A2 – Resident Tourist Site Dummy Model

Lodge	Mean conditional logit estimate for residents	SE	z	p	lower confidence interval	upper confidence interval
Intercept (Bushtops)	0 (baseline)	NA	NA	NA	NA	NA
Elewana	0.666	0.191	3.480	0.001	0.291	1.041
FourSeasons	0.320	0.204	1.570	0.117	-0.080	0.720
Grumeti	-0.127	0.230	-0.550	0.580	-0.579	0.324
Kirawira	0.577	0.194	2.970	0.003	0.196	0.957
Kubukubu	2.275	0.164	13.890	<0.001	1.954	2.597
KuriaHills	-0.098	0.230	-0.430	0.669	-0.550	0.353
Kusini	-2.044	0.474	-4.320	<0.001	-2.973	-1.116
Lamai	0.320	0.210	1.530	0.127	-0.091	0.732
Lobo	1.630	0.170	9.560	<0.001	1.296	1.964
MaraRiverPost	-0.796	0.278	-2.870	0.004	-1.340	-0.252
Mbalageti	0.320	0.204	1.570	0.117	-0.080	0.720
MbuziMawe	1.021	0.182	5.630	<0.001	0.666	1.377
Sayari	-0.821	0.289	-2.840	0.004	-1.386	-0.255
Serena	2.388	0.163	14.650	<0.001	2.069	2.708
Seronera	-16.746	666.767	-0.030	0.980	-1323.585	1290.094
Singita	-1.532	0.387	-3.960	<0.001	-2.290	-0.774
Sopa	1.800	0.168	10.700	<0.001	1.471	2.130
Soroi	-16.746	666.767	-0.030	0.980	-1323.585	1290.094
Observations						35,822
Log likelihood						-4380.146

Figure A – Lodge Occupancy and Tourism Pressure Time Series

Variation in lodge occupancy (top) and tourism demand (bottom) from July 2017 to May 2018. In the top plot, grey lines show individual lodges occupancy, the blue line shows mean occupancy across lodge, and the black line shows median occupancy. In the bottom plot, the green line shows the total daily number of visitors in SNP.

Table B – Likelihood ratio test (LRT) statistics for single term deletions from the full binomial GLMM

Term(s) deleted	Log-likelihood	Df residuals	Chi-sq (LRT)	<i>p-value</i>
None (full model)	-3613.8	809	NA	NA
<i>Capacity</i>	-3616.2	810	4.899	0.027
<i>Price</i>	-3669.4	810	111.277	<0.001
<i>Dist_wildebeest:Daily_visitors</i>	-3622.1	810	16.704	<0.001
<i>Daily_visitors & Dist_wildebeest:Daily_visitors</i>	-5402.6	811	3577.609	<0.001
<i>Dist_wildebeest²</i>	-3642.0	810	56.447	<0.001
<i>Dist_wildebeest & Dist_wildebeest² & Dist_wildebeest:Daily_visitors</i>	-3776.2	812	324.959	<0.001