Chapter 2

Why are wildebeest the most abundant herbivore in the Serengeti ecosystem?

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**INTRODUCTION**

Wildebeest are the cornerstone of the Serengeti ecosystem and influence virtually every single dynamic we observe. There are 29 large herbivore species in Serengeti and yet the wildebeest population outnumbers all other herbivores combined. It is 6 times larger than the next most abundant herbivore (zebra) and 100 times more abundant than their closest taxonomic relative (hartebeest). In this chapter we ask why do wildebeest dominate the ecosystem? The chapter is divided into three sections, each of which compares specific attributes of wildebeest with other sympatric species. In so doing we piece together a complete story that combines biology, behavior and the geomorphology of the ecosystem to explain how a single species can outnumber all other species in the Serengeti.

First, we compare wildebeest biology with that of their closest taxonomic relatives, topi and hartebeest. If specific aspects of wildebeest biology give them a competitive advantage over other species, then we expect other sub-populations of wildebeest in Serengeti should be equally large. However, the differences in abundance between the resident and migrant population suggest that wildebeest biology alone does not explain their dominance. Second, we compare the migratory population of wildebeest with four resident sub-populations in the Serengeti-Mara ecosystem. Migration potentially enables a population to escape local regulation, however 4 other herbivore species in Serengeti also migrate, and yet these species are far less abundant than wildebeest. Nevertheless, these migratory species are an order of magnitude greater than any resident species which suggests that migration could partially explain why wildebeest are so abundant. In the third section we compare migratory wildebeest with migratory zebra to investigate how migration can lead to greater abundance. We conclude that a combination of wildebeest biology and their adaptive migratory behavior only partially explains their abundance. The unique geomorphological and landscape features of the Serengeti make it particularly well suited for wildebeest. Therefore, the super-abundance of wildebeest in Serengeti is probably a function of a well-suited animal living in a system that closely matches its requirements.

**DOES WILDEBEEST BIOLOGY EXPLAIN THEIR ABUNDANCE OVER OTHER ACELAPHINES?**

The closest taxonomic relatives to wildebeest (*Connochaetes taurinus*) occurring in Serengeti are topi (*Damaliscus korrigum*) and Coke’s hartebeest (*Alcelaphus buselaphus*). The tribe Alcelaphini, to which these species belong, is at least 10 million years old (Vrba 1979; Georgiadis 1995), however wildebeest diverged from topi and Coke’s hartebeest about 4 million years ago. Topi in southern Sudan (where they are called tiang) migrate in large numbers in the Boma-Jonglei system, and kongoni previously migrated on the Athi-Kapiti plains of Kenya. However, neither species migrate in Serengeti. In this section we compare aspects of wildebeest diet and reproduction with topi and Coke’s hartebeest to understand how wildebeest biology might provide them with a competitive advantage in Serengeti.

**Digestion and intake rates**

All members of the ruminant suborder, which includes alcelaphines, use a complex fermentation process harnessing the microbial decomposition of symbiotic bacteria in the rumen to break down cellulose into volatile fatty acids. These are readily absorbed through the stomach wall leaving the fiber to be excreted. The digestive efficiency of the rumen varies between species, which imposes restrictions on the quality and abundance of food the animal ingests. Wildebeest and topi ingest approximately equal quantities of grass per unit of metabolic body weight (65.7 g/kg $W^{0.75}$/ day, and 67.0 g/kg $W^{0.75}$/ day, respectively), whereas the slightly larger Coke’s hartebeest consumes less (56.5 g/kg $W^{0.75}$/ day) but has greater digestive efficiency (Murray 1993). Therefore, we expect wildebeest, topi and Coke’s hartebeest to compete for the same food resources.
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The rate at which each species can ingest forage varies based on the mouth architecture and the structure of the grass sward. The wide dental pad and incisor row of wildebeest enable them to maximize their intake rates on prostrate mat-forming grasses that are approximately 3 cm high (Wilmshurst et al. 1999), which tend to have the highest protein content (Fryxell 1995; Gordon, Illius, and Milne 1996; Wilmshurst et al. 1999). This differs from both topi and Coke’s hartebeest. The narrower muzzle breadth and dental arcade of topi and hartebeest means they consume forage faster when grazing in taller grass swards than wildebeest (Murray and Brown 1993). Therefore, wildebeest specialize on grasses growing on the horizontal plane and can forage optimally on sub-mature grass in its early growth stages when it is most nutritious. Topi and Coke’s hartebeest specialize on grasses growing in the vertical plane and forage optimally on taller lower-quality grasses (Murray and Brown 1993; Murray 1993; Murray and Illius 2000), which suggests that competition for forage has lead to these species to divide the resource based on the architecture of the grass.

**Diet and water requirements**

Wildebeest, topi and Coke’s hartebeest are all obligate grazers. Between 90 and 100% of their diet is dominated by C₄ grasses with the remainder consisting of C₃ forbs and legumes (Cerling et al. 1997; Codron et al. 2007; Tieszen and Imbamba 1980; Casebeer and Koss 1970). Although there is no evidence that wildebeest, topi or Coke’s hartebeest select specific grass species, wildebeest tend to seek the most nutrient rich grass patches (Ben-Shahar and Coe 1992; Hopcraft et al. in prep; Wilmshurst et al. 1999). The analysis of stomach contents from wildebeest suggests they select a greater proportion of leaf material over stems or sheaths than either topi or Coke’s hartebeest (Bell 1970; Gwynne and Bell 1968; Casebeer and Koss 1970) (Figure 1). The population dynamics of wildebeest, topi and Coke’s hartebeest are closely linked with rainfall and the availability of drinking water (Ogutu et al. 2008; Mduma, Sinclair, and Hilborn 1999; Gereta, Mwangomo, and Wolanski 2009), which is critical for all alcelaphines.

![Figure 1. Analysis of the stomach contents from wildebeest (open squares), topi (closed circles) and zebra (open circles) illustrates the selection for different components of the grass structure (data from (Bell 1970; Gwynne and Bell 1968)).](image)
An analysis of resource selection for topi and Coke’s hartebeest suggests that both species select areas in proximity to water, however topi select areas with greater grass biomass rather than grass quality (Hopcraft et al. submitted). Topi are more abundant in the high rainfall areas in Western Corridor and the northern woodlands, while hartebeest distribution is shifted further to the east where they are more abundant in the drier central and eastern woodlands (Figure 2). Wildebeest essentially move between all these habitats.

![Figure 2](image.jpg)

Figure 2. The distribution of (a) topi and (b) Coke’s hartebeest is segregated roughly by rainfall. Topi tend to select areas with higher grass biomass in the wetter areas of the western corridor and northern woodlands, while hartebeest are more common in the drier central woodlands (Hopcraft et al. submitted). Resident herds of wildebeest occur sympatrically with topi and Coke’s hartebeest (compare to Figure 8).

**Reproduction**

**Calving synchrony**

Perhaps the most striking feature about wildebeest reproduction is the synchrony of calving of the Serengeti migrant population. Over 250,000 calves are born within a 3 week period starting in mid February, which accounts for approximately 80% of the year’s calves. This equates to 500 calves being born every hour, or 12,000 calves born a day. The Serengeti has approximately 2,500 lions of which only about 300 might have access to the calving grounds, and about 7,000 hyena which commute across the ecosystem (Hanby, Bygott, and Packer 1995; Hofer and East 1995). The huge synchronous pulse of wildebeest calves in the wet season completely outstrips the predators’ ability to regulate wildebeest recruitment.

The calving period for topi and hartebeest is much less synchronized than wildebeest (Figure 3). Approximately 70% of topi calves are born over a 3 month period at the very end of the dry season (Sindair, Mduma, and Arcese 2000). Peak calving for topi generally occurs in October and November but this varies between years. For instance, topi calving can be delayed or advanced by up to 3 months as a result of rainfall conditions during the proceeding season.
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(Ogutu et al. 2010). Hartebeest are even less synchronous and calve throughout the year, although there is a vague peak in August and September during the height of the dry season (Sinclair, Mduma, and Arcese 2000; Ogutu et al. 2008).

What are the biological mechanisms that enable wildebeest to synchronize the female conception so precisely? Female wildebeest undergo consecutive estrus cycles each lasting approximately 23 days and are repeated for up to 203 days if they remain un-mated. Following this extended period of estrus cycling (termed diestrus), non-pregnant females shed the lining of the uterus during a period of ovarian quiescence (Clay et al.). The first estrus starts about 102 days post-partum and evidence suggests the first ovulation might be silent (i.e. cows ovulate normally but do not display overt behavioral signs) (Watson 1967; Clay et al.). The beginning of the diestrus cycle is probably triggered by declining rainfall and reduced concentration of crude protein in the diet (Sinclair 1977; Clay et al.).

Figure 3. The number of calves per month (displayed as a percentage of the entire year) illustrates the strong calving synchrony in wildebeest. Topi are less synchronous and there is no discernable calving peak for Coke's hartebeest which tend to be asynchronous (data from (Sinclair, Mduma, and Arcese 2000)). Dark shading indicates wet season months, light shading indicates dry season months.

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The diestrus cycle of female wildebeest is an imperative feature of their biology that leads to synchronous calving (Watson 1967) and is illustrated in Figure 4. The most plausible physiological explanation was proposed by Watson (1967) but remains unproven. Watson suggested if the first ovulation in the diestrus cycle was silent (i.e. with no overt behavioral signals), this would cue the bulls without engaging them in copulation while simultaneously inducing other females to begin ovulating (con-specific cueing is common in several synchronously breeding species (Ims 1990)). Males cued by early estrus females become more territorial and start to separate small harems from the main herd. This social disruption could also lead higher endocrine function in both males and females (Mysterud, Coulson, and Stenseth 2002). Watson suggests that as the number of females in the first silent ovulation increases, the intensity of the rut builds in a positive feedback loop and males become more excited. Only during the second ovulation do females become behaviorally receptive to copulation and allow the males to mount (i.e. a non-silent ovulation), at which point the rut approaches its climax. Bulls mate rapidly with any and all receptive females. At this point, the competition between bulls becomes so intense that they no longer wait for overt behavioral cues from females and will also copulate with females in their first silent ovulation which they detect by smell.

The rut demands a huge amount of energy from bulls and selects for the fittest males. Males commonly lose up to 80% of their kidney fat and as much as 26% of their bone marrow fat (Figure 5) (Sinclair 1977). Furthermore, bulls can only sustain this level of activity for short periods of time. Exhausted bulls will stop competing and are quickly replaced by fresh bulls, meaning females are constantly harassed until they are bred. The result is that during the peak of the rut 80% of reproductively active females (approximately 200,000 females) are mated within a 2 to 3 week period (post-mortem data from (Watson 1967)), giving the rut the unique distinction of being the greatest mating show on earth (Estes and East 2008). More practically, this mass breeding event leads to synchronous calving 8 months later (Figure 6), which has important implications for calf survival through predator swamping and which partially explains the super-abundance of wildebeest in Serengeti.

Breeding and the rut

The wildebeest rut occurs as the herds are moving off the plains and into the western corridor (Figure 6). Males do not defend a stationary territory during the rut, but rather a moving arena around themselves to which they recruit as many females as possible. Presumably most mating occurs at night around the first full moon in late May or early June (Sinclair 1977) because it is not commonly observed.

In comparison, the topi rut typically occurs between March and May and lasts about 1.5 months. Males form leks from which they display and compete for female copulation, although some satellite males opt to defend territories and coerce females into copulation through harassment (Bro-Jørgensen 2003; Bro-Jørgensen and Durant 2003). By contrast, female Coke’s hartebeest are typically receptive only for a single day and will mate several times within a few minutes during this period (Estes and Wilson 1992).

The main difference is that wildebeest and topi reproduction is associated with leks (wildebeest essentially have a moving lek), while Coke’s hartebeest do not. It is the competitive mating displays by sexually mature bulls associated with the leking behavior that leads to breeding synchrony and thus predator swamping when the calves are born.

Gestation and calving

Wildebeest gestation lasts 8 months (240 days) which is approximately the same in all alcelaphines (Estes and Wilson 1992; Clay et al.). Wildebeest, topi and Coke’s hartebeest only produce a single calf per season (Ogutu et al. 2010; Watson 1967; Clay et al.). There are no reliable reports of twinning, although this is sometimes confused with small crèches or the strong follower instincts of lost orphans. There is no evidence that orphaned calves are adopted by other cows even if the female has lost her own calf (Estes and Estes 1979). There-
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Therefore, neither gestation nor the number of offspring can explain why wildebeest are more abundant than topi or Coke’s hartebeest.

Female wildebeest rarely calve in isolation but instead prefer to form crèches which are joined by other expecting females. Calves born in crèches are defended against small predators by co-operative females (Estes and Wilson 1992). Studies from the Ngorongoro Crater suggest that calf survival declines drastically from 84% to 50% in smaller herds, suggesting communal calving is an effective anti-predation strategy for wildebeest (Figure 7) (Estes 1976; Sinclair, Mduma, and Arcese 2000). Unlike wildebeest, topi and hartebeest do not

![Figure 4. The diestrus cycle of female wildebeest could lead to intense male competition which might account for their high degree of breeding synchrony (about 80% of calves are born within a 3 week period approximately 8 months later). The first ovulation in the diestrus cycle is silent (dotted line) in which females do not display overt behavioural signs and do not permit the males to mate. The first ovulation cues the bulls and increases male-male competition as well as inducing other females to start ovulating. During the second ovulation (dashed line) females display overt mating behaviours and permit bulls to mate. The fertilization rate (solid line) increases synchronously with the second ovulation (between points AB) during which time the competition between bulls increases in intensity. Between BC the inter-male competition becomes so intense that bulls no longer wait for overt behavioural signals from females. During this time, both females in their first and second ovulation are harassed until they are mated, resulting in a peak fertilization rate at point C. From CD the fertilization rate declines as the number of unmated females decreases. By the end of the rut (DE) only the remaining second ovulating females are fertilized (as suggested by (Watson 1967)).](image)
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Instead, they give birth in secret isolation and discretely visit their hidden calves periodically for many days before re-joining the herd.

Wildebeest calves express two important behaviours almost immediately postpartum which are different to topi and Coke’s hartebeest, and both of which are critically important to their survival in large herds: imprinting and a “follower” instinct (Estes and Estes 1979). Mothers and calves imprint on each other within a matter of minutes and are capable of individually recognizing each others’ calls (Estes and Estes 1979). Their mutual recognition is confirmed by smell. The “follower” instinct in young wildebeest is so great that calves will often

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**Figure 5.** The seasonal fluctuations of (a) kidney fat and (b) bone marrow fat for lactating females, non-lactating females and male wildebeest in comparison to the weight of the mammary glands. Lactating females consistently have lower amounts of kidney fat than non-lactating and male wildebeest. Declines in male kidney fat are associated with the large energy demands of the rut in June. The loss of bone marrow fat, which are the final reserves of fat in the body, occurs in females during peak lactation and illustrates the extreme nutritional demands of reproduction especially in April and May (data from (Sinclair 1977; Watson 1967)). Dark shading indicates wet season months, light shading indicates dry season months.
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Topi and hartebeest calves are not as precocial as wildebeest calves and take up to 30 minutes or more before they stand, and as long as 45 minutes before they can follow their mothers for short distances. By comparison, wildebeest calves are able to stand within an average of 6 minutes and walk within 30 minutes, which is an adaptive trait for such a mobile species (Estes and Wilson 1992; Sinclair, Mduma, and Arcese 2000). Wildebeest calves can outrun hyena within a day, whereas hartebeest calves are unable to keep up with their mothers until they are more than a week old (Kruuk 1972; Estes and Estes 1979).

**Lactation**

The peak lactation for wildebeest is between February and May which coincides with the greatest amount of rainfall and fresh grazing on the short-grass plains (Figure 6) (Kreulen...
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However, females continue to lactate until September, which is the core of the dry season resulting in large energetic costs (Watson 1967). Wildebeest females lose up to 60% of their bone marrow fat in the first 3 months of lactation and consistently have lower amounts of kidney fat than non-lactating females or males (Figure 5). For 4 months (June to October) female wildebeest are both pregnant and lactating, as illustrated in Figure 6. This extended demand means all the females must constantly have access to water and sufficient grazing. Lactating females require 30% more energy per day, 5 times more Ca, 3 times more P, and twice as much Na than females in early pregnancy (Table 1) (Murray 1995). Females are especially vulnerable to predation and starvation during the last stages of pregnancy and peak lactation (Sinclair and Arcese 1995). Because topi and Coke’s hartebeest reproduce less synchronously than wildebeest, their nutritional demands associated with lactation are spread through-out the year. Therefore, there is no synchronous demand for the same resources by all females of the population, which means individual topi and hartebeest can find sufficient resources locally rather than being forced to migrate long distances, unlike wildebeest.

**Sexual maturity**

The age of sexual maturity does not differ significantly between wildebeest, topi and Coke’s hartebeest (Estes and Wilson 1992). Females are sexually mature by 3 years old, while males are mature by 2 years old. However, most males do not become sexually active until their 5th year because they are excluded from breeding by intense male competition. Therefore, difference in the age of sexual maturity cannot account for the differences in abundance between wildebeest, topi and Coke’s hartebeest.
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Summary: Wildebeest biology partially accounts for their dominance in the Serengeti

There are several aspects of wildebeest biology which might explain why they are more abundant than topi or Coke’s hartebeest in Serengeti. First, their flat and wide dental arcade enables wildebeest to rapidly select leaves from mat-forming grasses while avoiding the lower quality stems and sheaths, where as topi and hartebeest are better suited to pick individual leaves from vertically complex grasses. The prostrate grasses selected by wildebeest are typically in a young and nutritious growth stage which means they are easier to digest and provide more energy than taller grasses (Wilmshurst et al. 1999).

Second, the breeding and calving synchrony of wildebeest coincides with the wet season when grass supply on the short-grass plains is the most nutritious (Kreulen 1975; McNaughton 1985) (Figure 6). In addition, the strong synchrony of wildebeest calving swamps the predator guild and reduces the overall predation rates on neonates (Sinclair, Mduma, and Arcese 2000; Ims 1990). The peak calving in topi varies interannually but is somewhat synchronized with the early green flush in long grass areas. Historically, very large concentrations of topi (up to 14,000 animals in a single herd (A. Sinclair, pers. comm.) breeding somewhat synchronously would have had a predator swamping effect, however there is no evidence for this in smaller herds. Coke’s hartebeest also occur in small herds and are completely asynchronous. Hartebeest gain no advantage from the seasonal abundance of high quality food (Sinclair, Mduma, and Arcese 2000; Ogutu et al. 2008), nor do they gain any predator swamping advantages of synchronous breeders (Ogutu et al. 2010). Therefore, the advantage of predator swamping is only realized by synchronous breeders living in large herds.

Wildebeest calves are more precocial than either topi or hartebeest calves and have a strong “follower” instinct which provides them with additional protection of large herds. Wildebeest calves are exposed to predators for a brief period of time post-partum after which they accompany their mother and can escape predators by losing themselves in large herds. By comparison, the “hider” calves of topi and wildebeest do not gain the protection afforded by a large herd (Ims 1990).

However, if biology alone explains the abundance of wildebeest in the Serengeti, then we would expect the resident sub-population of wildebeest to exist at a similar density to that of the migrants, which is not the case. Therefore, wildebeest biology might partially account for their dominance in the ecosystem, but not entirely.

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Table 1. The dietary requirements of adult female wildebeest during early pregnancy as opposed to peak lactation (Murray 1995).

<table>
<thead>
<tr>
<th>Reproductive phase</th>
<th>MJ/day (kg equivalent of (T.) triandra)</th>
<th>Ca g/day</th>
<th>P g/day</th>
<th>Na g/day</th>
</tr>
</thead>
<tbody>
<tr>
<td>Early pregnancy</td>
<td>22.3 (~3.10 kg)</td>
<td>3.59</td>
<td>5.76</td>
<td>1.07</td>
</tr>
<tr>
<td>Peak lactation</td>
<td>32.7 (~4.54 kg)</td>
<td>15.51</td>
<td>17.61</td>
<td>2.35</td>
</tr>
</tbody>
</table>

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Summary: Wildebeest biology partially accounts for their dominance in the Serengeti

Second, the breeding and calving synchrony of wildebeest coincides with the wet season when grass supply on the short-grass plains is the most nutritious (Kreulen 1975; McNaughton 1985) (Figure 6). In addition, the strong synchrony of wildebeest calving swamps the predator guild and reduces the overall predation rates on neonates (Sinclair, Mduma, and Arcese 2000; Ims 1990). The peak calving in topi varies interannually but is somewhat synchronized with the early green flush in long grass areas. Historically, very large concentrations of topi (up to 14,000 animals in a single herd (A. Sinclair, pers. comm.) breeding somewhat synchronously would have had a predator swamping effect, however there is no evidence for this in smaller herds. Coke’s hartebeest also occur in small herds and are completely asynchronous. Hartebeest gain no advantage from the seasonal abundance of high quality food (Sinclair, Mduma, and Arcese 2000; Ogutu et al. 2008), nor do they gain any predator swamping advantages of synchronous breeders (Ogutu et al. 2010). Therefore, the advantage of predator swamping is only realized by synchronous breeders living in large herds.

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**Why are there so few resident wildebeest in Serengeti?**

In this section we compare the attributes of the main migratory wildebeest population with four other resident sub-populations of wildebeest in the Serengeti ecosystem. Specifically, we ask what accounts for the differences in abundance between the resident and migratory herds, given their comparable biology?

**Four populations of resident wildebeest in Serengeti**

There are four resident sub-populations of wildebeest, which are distinct yet seasonally sympatric with the main migratory population. These resident sub-populations are the Kirawira, Masai Mara, Loliondo and Ngorongoro Crater wildebeest herds (Figure 8a). Genetic evidence suggests these smaller sub-populations were once part of a larger interbreeding pool, which included the main Serengeti migratory population (Georgiadis 1995).

The Kirawira residents in the Western Corridor move seasonally between the open grasslands of Ndabaka, Ndoha, Musabi and Sibora plains but do not move beyond the western arm of the ecosystem (Figure 8). The separate population of semi-migratory wildebeest in the Masai Mara moves a short distance to the Loita Plains during the wet season. The Mara wildebeest could be the remnants of a larger pre-rinderpest population that perhaps migrated further to the north-east. The Loliondo wildebeest are resident around the Ngata Kheri plains near Waso (Pennycuick 1975; Watson 1967).

The wildebeest in the Ngorongoro Crater are primarily resident although some members of the population emigrate out of the crater during the wet season (Talbot 1964; Watson 1967; Estes and Small 1981), and observations by Tony Mence as referenced by (Grzimek and Grzimek 1960) (Figure 8a). As much as 35% of the Ngorongoro population leave the crater and potentially mix with migrants in the Olbalbal Depression and the base of the Crater Highlands between February and April (from unpublished tagging studies by Orr and Watson (Watson 1967)), however the true percentage is probably much less than this (Estes and Estes 1979).

The distance between the Selai Plains (where the Serengeti migrants occasionally graze during the wet season) and the Natron-Lengai area (the northern extent of the Tarangire migrants (Bolger et al. 2008)) is only 30 km (Figure 8a). However, the steep escarpment of the Rift Valley and the thick forests of the Ngorongoro highlands act as a barrier between these populations, which have not interbred for thousands of years. Instead, the Tarangire wildebeest are more related to Nairobi National Park wildebeest 300 km north (Georgiadis 1995), which suggests they were once part of a single breeding population east of the Rift Valley and have been separated from the Serengeti populations for thousands of years.

**Constraints on the extent of resident wildebeest distributions**

A comparison of the habitat attributes in the ranges of the 4 resident sub-populations to the average habitat across the Serengeti ecosystem (i.e. the habitat available to the migratory population) suggests that resident wildebeest only occur in areas that receive approximately 900mm or more of rainfall per year and areas with access to permanent water (Table 2). The concentration of grass nitrogen in the ranges of resident wildebeest is no greater than what is available to migrants (Table 2). However, grass nitrogen occurs much more heterogeneously within the ranges of resident wildebeest than beyond their ranges, as can be seen by the juxtaposition of high and low quality patches in Figure 8b. When resources are distributed between small localized patches herbivore populations tend to stabilize (Owen-Smith 2004), which might explain why resident herbivores only persist in areas where water and good grazing occurs adjacently at fine scales. Local access to resources negates the need to migrate between distant patches.

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Differences between resident and migrant wildebeest

There are 4 key differences between the resident and migratory wildebeest populations in Serengeti. First, migrant wildebeest have a significantly smaller stature than individuals from the resident sub-populations in the ecosystem. The average male and female body sizes for Serengeti migrants are 160 ±13.4kg and 120 ±10.5kg, followed by the semi-migratory Masai Mara wildebeest which average 171 ±11.4kg and 145 ±17.8kg, the Ngorongoro wildebeest are approximately 184 ±11.8kg and 128 ±6.8kg, and the Kirawira wildebeest are the largest at 192 ±16.0kg and 145 ±9.5kg (Talbot and Talbot 1963; Watson 1967).

Figure 8. There are 4 resident sub-populations of wildebeest in Serengeti that are seasonally sympatric with the main migratory population (a). These 4 sub-populations occur in grasslands that receive more than 900 mm rain annually and are in proximity to water year round (see Table 2 for details). Furthermore, (b) the heterogeneity of grass nitrogen as estimated by the standard deviation suggests that resident wildebeest tend to occur in areas where resources vary at local scales. Darker cells indicate areas that have a mixture of nitrogen rich and nitrogen poor grass which means resident wildebeest can switch between low and high quality patches based on their seasonal availability without having to move large distances. Grass nitrogen in the south tends to be homogenously rich for a short period during the wet season, while it is homogeneously poor in the north. Therefore, grass quality varies in a similar fashion at multiple scales (i.e. locally and regionally) which supports 2 alternative foraging strategies in the Serengeti: grazers can either be resident and move locally at fine scales in specific areas, or migrate and move large distances at regional scales.

Differences between resident and migrant wildebeest

There are 4 key differences between the resident and migratory wildebeest populations in Serengeti. First, migratory wildebeest have a significantly smaller stature than individuals from the resident sub-populations in the ecosystem. The average male and female body sizes for Serengeti migrants are 160 ±13.4kg and 120 ±10.5kg, followed by the semi-migratory Masai Mara wildebeest which average 171 ±11.4kg and 145 ±17.8kg, the Ngorongoro wildebeest are approximately 184 ±11.8kg and 128 ±6.8kg, and the Kirawira wildebeest are the largest at 192 ±16.0kg and 145 ±9.5kg (Talbot and Talbot 1963; Watson 1967).
Second, the calving period for resident wildebeest tends to be earlier and less synchronous than migrants (Figure 9). Calving typically starts in November and can last until March depending on the sub-population (Watson 1967; Ndibalema 2009). The extended calving period means that resident wildebeest might be exposed to higher calf mortality due to predation.

Third, the sex ratio between resident and migratory populations differ. The male to female ratio in the Kirawira population is 0.26 as opposed to almost 1 in the migratory population (Ndibalema 2009; Mduma, Sinclair, and Hilborn 1999) suggesting there could be a substantial male-biased loss in resident herds. Carcass evidence does not suggest a male biased mortality, however this does not rule out the effects of poaching (Ndibalema 2009). Furthermore, there is no evidence that resident bulls join the migration even though their larger body size would give them a competitive advantage during the rut. The rut is usually over by the time the migration reaches the Kirawira area so it is unlikely that resident Kirawira males could be lured into the frenzy of the migrant rut and away from the resident population.

The fourth major difference that distinguishes resident wildebeest from migrants is the age of first reproduction. Watson (1967) found that resident wildebeest tend to reproduce

<table>
<thead>
<tr>
<th>Wildebeest sub-populations</th>
<th>Grass Nitrogen (%)</th>
<th>Rainfall (mm)</th>
<th>Distance to water (km)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ngorongoro</td>
<td>1.04 (0.12)</td>
<td>995 (42)</td>
<td>2.5 (1.4)</td>
</tr>
<tr>
<td>Kirawira</td>
<td>0.766 (0.07)</td>
<td>940 (39)</td>
<td>2.6 (1.4)</td>
</tr>
<tr>
<td>Masai-Mara</td>
<td>1.17 (0.12)</td>
<td>1042 (109)</td>
<td>4.6 (3.4)</td>
</tr>
<tr>
<td>Loliondo</td>
<td>1.08 (0.08)</td>
<td>873 (27)</td>
<td>15.1 (5.6)</td>
</tr>
<tr>
<td>Average across Serengeti ecosystem</td>
<td>1.04 (0.21)</td>
<td>805 (147)</td>
<td>20.1 (16.4)</td>
</tr>
</tbody>
</table>

Table 2. The average grass nitrogen content, annual rainfall and the average distance to water in the ranges of the 4 resident wildebeest populations in comparison to the average availability in the Serengeti ecosystem (i.e. that which is available to the migrant population). The data suggest that resident wildebeest only occur in areas that receive approximately 900mm or more of rainfall, and near permanent water. Values in brackets are standard deviations. Range distributions are estimated based on personal observations; Data for grass nitrogen, rainfall and distance to water as per (Hopcraft et al. submitted).
Why are wildebeest the most abundant herbivore in the Serengeti ecosystem?

earlier; between 50-75% of 2 year old resident females were pregnant while only 37% of 2 year old migrant females were pregnant. Early maturation in female wildebeest is a response to lower grazing competition and therefore more resources per individual (Mduma, Sinclair, and Hilborn 1999) which suggests resident wildebeest might not be regulated by food supply. Additionally, the resident bulls tend to participate in the rut earlier than their migrating counterparts (Watson 1967). If resident herds have fewer bulls, it is possible that the male competition during the rut may be less intense in resident herds than in migrant herds, which might allow resident bulls to mate while they are young. Less male competition might also explain why there is less breeding synchrony in resident herds, assuming the intense male-male competition during the rut explains the sharp leptokurtic peak in fertilization (Figure 4).

Population dynamics of resident versus migrant wildebeest

Population size and instantaneous growth rates

Table 3 summarizes the abundance of the main migratory population starting with the earliest crude guesstimates in 1956 up to the most recent estimates in 2006. The most striking pattern in the population abundance of the wildebeest in the Serengeti ecosystem is the dramatic increase in the migratory population following the large scale livestock rinderpest vaccination campaign surrounding the park in late 1950’s (Dobson 1995; Taylor and Watson 1967; Plowright and McCulloch 1967) (Figure 10). The abundance of the migratory wildebeest oscillates around 1.2 million animals. When the abundance is less than 1.2 million the recruitment rate is positive and the population grows, however when the population exceeds 1.2 million it tends to decline (Figure 11). The maximum rate of recruitment for the wildebeest population is approximately 10% per annum (Mduma, Sinclair, and Hilborn 1999) and occurred when the population was recovering from rinderpest (Figure 11).

In comparison, the largest resident population of wildebeest in the Serengeti is the Masai Mara population which varies around 40,000 animals (Figure 10). The Western Corridor
### Table 3. The population estimates for migratory wildebeest. References are 1 (Pearsall 1959); 2 (Swynnerton 1958); 3 (Grzimek and Grzimek 1960); 4 (Grzimek and Grzimek 1960); 5 (Talbot 1964); 6 (Talbot and Talbot 1963); 7 (Stewart 1962); 8 Estimate corrected by (Sinclair 1973); 9 (Watson 1967); 10 (Sinclair and Norton Griffiths 1982); 11 (Sinclair, Dublin, and Borner 1985); 12 (Conservation Information Monitoring Unit).

<table>
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<th>Year</th>
<th>Original</th>
<th>Accepted</th>
<th>Standard</th>
<th>Comment</th>
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<td>1956</td>
<td>10,100</td>
<td></td>
<td></td>
<td>Rough estimate based on ground transects</td>
</tr>
<tr>
<td>1957</td>
<td>19,000</td>
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<td></td>
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</tr>
<tr>
<td>1958</td>
<td>99,481</td>
<td></td>
<td></td>
<td>Census during exodus off plains; many animals missed in woodlands</td>
</tr>
<tr>
<td>1961</td>
<td>221,699</td>
<td>263,362</td>
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<tr>
<td>1963</td>
<td>32,000</td>
<td>35,612</td>
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<td>1965</td>
<td>381,875</td>
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</tr>
<tr>
<td>1966</td>
<td>334,425</td>
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<td>In woodlands</td>
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<td>1967</td>
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<td>2006</td>
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Why are wildebeest the most abundant herbivore in the Serengeti ecosystem?

about 10,000. The Loliondo herds are probably no more than 5,000 animals. The resident populations of wildebeest have essentially remained unchanged during the last 50 years, with the exception of the Masai-Mara population which has been reduced by 70%. The decline of the Masai Mara wildebeest population is primarily due to the expansion of mechanized agriculture on the Loita Plains in the late 1970’s which displaced wildebeest from the high quality grazing of their wet season calving grounds (Serneels and Lambin 2001; Ottichilo, de Leeuw, and Prins 2001).

Population regulation

What regulates the resident versus migrant populations of wildebeest in the Serengeti at very different abundances (Figure 10)? The migration essentially enables wildebeest to maximize their intake of seasonally available high quality grass, which means they can avoid being regulated by food quality (Hopcraft, Olff, and Sinclair 2010; Fryxell and Sinclair 1988). Furthermore, the super-abundance of animals in these herds reduces any single individual’s exposure to predation, and eliminates the role of top-down regulation via predation (Fryxell, Greever, and Sinclair 1988). Mduma (1999) comprehensively showed the abundance of dry season forage regulates the migratory population of wildebeest through adult and calf survival, as was suggested in earlier papers (Sinclair and Norton Griffiths 1982; Sinclair, Dublin, and Borner 1985). Although pregnancy rates show density dependence (i.e. a decline as the population increases), and neonatal mortality accounts for the greatest numerical loss, neither of these factors are key in population regulation (Mduma, Sinclair, and Hilborn 1999).
Section I: Background and Theory

Resident populations of wildebeest have not changed dramatically since the elimination of rinderpest in 1963 (with the exception of the Masai Mara) which suggests something in addition to disease regulates their abundance at low numbers. The recent decline of the Masai Mara population provides a convenient (but unfortunate) natural experiment which gives some valuable insights as to why resident wildebeest are less numerous than migrants. The expansion of industrialized agriculture excluded the wildebeest from their prime wet season grazing on their calving grounds and resulted in an overall reduction of the per capita availability of food. This semi-migrant population of wildebeest was forced to become more resident which made the Mara wildebeest closely dependent on rainfall during both wet and dry seasons (Serneels and Lambin 2001). The high abundance of predators in the Mara is supported by the large densities of resident prey (Ogutu and Dublin 2002), suggesting that the undernourished wildebeest population likely experienced greater predation which further compromised their survival. The Mara example illustrates how resident wildebeest are probably regulated at lower densities by predation as well as by seasonal shortages of adequate food (Fryxell, Greever, and Sinclair 1988).

Recruitment into the adult stage

The recruitment into the adult cohorts (i.e. beyond the age of 2) is largely dependent on the survivorship of the calves rather than either yearling survival or conception rates. Yearlings have a greater chance of survival than calves (Mduma, Sinclair, and Hilborn 1999), however there is a sex bias favoring females; yearling males tend to suffer greater mortality (Watson 1967) (Table 4 and Figure 12). Extreme food limitation during droughts, as occurred in 1993, can lead to increased rates of spontaneous abortion and fewer calves born than in normal years (Mduma, Sinclair, and Hilborn 1999), but under normal conditions the majority of conceptions are carried to term.

The first 6 weeks are the most critical time for resident and migrant wildebeest calves (Figure 13). As much as 20% of the calves can die if the grazing conditions are poor or widely spaced during the wet season (Watson 1967; Mduma, Sinclair, and Hilborn 1999). If the rain

Figure 11. The recruitment rate of migratory wildebeest as a function of population size suggests that the population is stable at approximately 1.2 million animals. Furthermore, the maximum rate of growth of the population is about 10% per annum (Mduma, Sinclair, and Hilborn 1999) (data from Table 3).
Why are wildebeest the most abundant herbivore in the Serengeti ecosystem?

Table 4. Life tables for male and female wildebeest. \( nx \) = number of wildebeest alive at age \( x \); \( dx \) = number of deaths at age \( x \); \( qx \) = per capita death rate, \( mx \) = age specific fecundity (number of female offspring produced at age \( x \)). Data from 1962-1965 (Watson 1967)

<table>
<thead>
<tr>
<th>Age</th>
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<th></th>
<th></th>
<th>Female</th>
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<tr>
<td></td>
<td>( nx )</td>
<td>( dx )</td>
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<td>840</td>
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<td>0.00</td>
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<td>1.00</td>
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</table>
failing on the short grass plains, cows will give birth in the woodlands. Females cannot sustain lactation in the woodlands because the grass is less nutritious (Murray 1995; Kreulen 1975). Furthermore, calves are exposed to more predators in the woodlands which leads to lower recruitment. The short grass plains provide very little cover for ambush predators such as lion (Hopcraft, Sinclair, and Packer 2005) which reduces the susceptibility of migrant wildebeest calves to predation, but not resident wildebeest calves. Furthermore, the synchronous parturition of migratory wildebeest swamps the predators with an abundance of prey resulting in relatively fewer attacks on calves than in resident herds.

As the grazing conditions decline during the transition from the wet season to dry season, migrant cows are forced to travel large distances in order to find adequate food and water which can result in many calves being severely weakened or abandoned. The severity of the transition and the spatial distribution of resources varies between years, and can cause increased mortality in calves around July (Mduma, Sinclair, and Hilborn 1999) (Figure 13). Because food and water are in close proximity in the ranges of resident wildebeest (Table 2 and Figure 8), the resident calves are not forced to travel large distances and therefore are probably not as susceptible to sudden environmental changes. Although the rut is very disruptive and many calves become temporarily separated from their mothers, this does not severely impact calf survival (Figure 13). At the time of weaning in September, calves are sufficiently robust that there is seldom a detectable mortality (Watson 1967), and is probably similar in both resident and migrant herds (with the exception of severe drought years).

Resident herds tend to calve less synchronously and therefore might be exposed to more predation (Ndibalema 2009), which might partially explain why there are fewer resident than migrant wildebeest. However, a comparison across multiple years suggests that there is no difference in calf survival at 4 months of age between the Western Corridor resident wildebeest
Why are wildebeest the most abundant herbivore in the Serengeti ecosystem?

Chapter 2

and migrant populations but large differences in yearling survival after their first dry season (Figure 14). Resident yearlings routinely suffer larger mortality than migrants, suggesting that recruitment for residents is determined more by predation (A. Sinclair, unpublished data). It is likely that survival of yearling migrants is determined by dry season forage (Mduma, Sinclair, and Hilborn 1999).

Causes of mortality

In 1964 when the migratory wildebeest population was 350,000 and growing, Watson estimated only 16% of the mortality could be attributed to density dependent causes. By 1994 when the population exceeded a million animals, Mduma estimated 75% of the mortality was caused by density dependent mortality such as undernutrition. For example, at the peak of the 1993 drought there were approximately 3,000 wildebeest dieing per day from starvation (Mduma, Sinclair, and Hilborn 1999).

A severe loss of body condition because of starvation can lead to increased predation or infection, especially during drought years. Females are more vulnerable to predation and starvation than males, and are most vulnerable at the end of the dry season, through the calving period and into peak lactation (October to June) (Sinclair and Arcese 1995). The nutritional content of the forage during the wet season is especially critical for females, and probably affect resident and migrant wildebeest similarly.

A comparison of predation rates between resident and migrant wildebeest suggests predation might partially account for the differences in abundances. Predation accounts for little of the overall mortality in the migratory population (between 2.5% to 5% per year). The most vulnerable cohort are calves, however adults in moderate or poor condition are more

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Figure 13. The percentage of calves in the adult population of migrant wildebeest over the year illustrates high calf mortality in the first 2 months post-partum, after which the survivorship is relatively constant (data from 1965 aerial surveys using vertical photos (Watson 1967) and corroborated by (Mduma, Sinclair, and Hilborn 1999)). Dark shading indicates wet season months, light shading represents dry season months.
likely to be killed than healthy individuals (i.e. those that are nutritionally compromised) (Mduma, Sinclair, and Hilborn 1999). Predation has a greater affect on resident populations because they do not move beyond the home ranges of resident predators and do not have the security afforded by large herds (Sinclair 1995).

### Disease

The most important disease to influence the abundance of both resident and migrant wildebeest in the Serengeti is rinderpest which was responsible for at least a 6 fold reduction in the population (assuming pre-rinderpest population was similar to the current population). This equated to approximately 85% mortality in the Serengeti population and was probably

![Figure 14. Ground transects of wildebeest herds suggest there are (a) no differences in the proportion of calves between resident and migrant populations indicating an equal recruitment rate. However, (b) there are relatively fewer yearlings in the resident herds which suggests they are exposed to greater mortality than migrants, probably because of predation (unpublished data from Sinclair, pers. comm.).](image)
very similar across Africa. There is no evidence infection rates differ between resident and migrant wildebeest, and therefore disease cannot account for the differences in their abundance.

**Summary: Suitable habitat and predation most likely limit the abundance of resident wildebeest**

In summary we return to our question: if wildebeest biology gives them a competitive advantage over their closest taxonomic relative, then why are resident wildebeest less numerous than migratory wildebeest? A comparison of the resident and migrant wildebeest ranges in Serengeti indicates that resident wildebeest only occur in areas where the local heterogeneity of grass quality and quantity occurs at fine scales, and where the annual rainfall exceeds 900mm with access to permanent water. There are only a few locations in the Serengeti where this is possible, which implies (a) resident wildebeest are limited by an availability of suitable habitat. Migrants escape local limitation by moving long distances between resource rich patches, thereby maximizing their access to high quality grazing. Additionally, migratory wildebeest move beyond the home ranges of resident predators which means the numerical response of predators is limited by the less numerous resident prey and not by the migrants. Resident wildebeest likely suffer greater predation because predators switch between migrant and resident prey (a Type II functional response). Therefore, migrants can (b) exhaust the local food supply without being regulated by it, as well as (c) un-couple themselves from any regulation by resident predators, which accounts for their greater abundance. In addition, the very high density of migratory wildebeest might increase male competition during the rut which could lead to greater breeding synchrony and better calf survival because of the advantages of predator swamping. Therefore, (d) a positive feed-back loop could enable migratory wildebeest and not resident wildebeest to become super-abundant.

However zebra, eland, Thomson’s gazelle and Grant’s gazelle also migrate in the Serengeti and yet their populations remain far less numerous than wildebeest (Figure 10). Therefore, migration alone cannot explain why wildebeest are the most abundant herbivore in Serengeti. In the next section we investigate why zebra (the next most numerous herbivore in Serengeti) are not as abundant as wildebeest.

**Why are migratory zebra not as abundant as migratory wildebeest?**

As we have seen up to this point, there are aspects of wildebeest biology such as grazing selection and birthing synchrony, which might give them a competitive advantage over other closely related taxa such as topi or Coke’s hartebeest. Additionally, by migrating, wildebeest reduce the limitations of food quality and avoid predator regulation which might otherwise cap their overall abundance in a similar fashion to the resident wildebeest populations. If the advantages of migration are so profound, then why are the other migratory species in the Serengeti not as abundant as wildebeest?

In this section we compare the migration of zebra in the Serengeti to that of wildebeest. A brief overview of zebra biology highlights the key digestive features that enable two species with similar body-sizes to specialize on different attributes of the grass. There have been several explanations proposed for drivers of the migration which we assess from the perspective of a generalist grazer like the zebra as opposed to more specialized grazer like the wildebeest. We conclude by summarizing the features of the Serengeti ecosystem that favor wildebeest migrations over zebra migrations.

**Zebra: Hind-gut fermenters versus ruminants**

Like wildebeest, zebra are obligate grazers consuming at least 90% C4 grasses (Tieszen and Imbamba 1980; Casebeer and Koss 1970; Codron et al. 2007), however their digestive systems are very different. Zebra are hind-gut fermenters, which mean the majority of
nutrient extraction occurs in a specialized section of the cecum and colon rather than in the rumen like wildebeest. Ruminants tend to be more efficient than hind-gut fermenters at extracting energy across a broader spectrum of moderate plant quality (Foose 1982; Duncan et al. 1990; Maloiy and Clemens 1991). Zebra and other hind-gut fermenters compensate for their less efficient digestion by consuming more grass biomass and processing it faster. The increased through-put of large amounts of grass means that hind-gut fermenters, like zebra, are better than wildebeest at extracting nutrients from poor quality plant material that tends to be fibrous and lignified. A comparison of diets illustrates that zebra consume proportionately more grass stems and sheaths than leaves and shoots, which are selected by wildebeest (Figure 1) (Bell 1970; Gwynne and Bell 1968).

The differences in digestive physiology between hind-gut fermenters and ruminants make it unlikely that zebra and wildebeest compete for the same attributes of the grass under normal grazing conditions, because zebra can tolerate lower quality food so long as there is sufficient biomass (Illius and Gordon 1992; Duncan 1992), while wildebeest are confined to better quality grasslands. Since equids can tolerate lower quality grass, they could have an “ecological refuge”, which could allow the two species to co-exist (Duncan et al. 1990; Bell 1971).

If grass biomass becomes limited but the quality remains high, such as on the short-grass plains of Serengeti, hindgut fermenters have difficulty acquiring sufficient quantities of food and are at competitive disadvantage to ruminants (Duncan et al. 1990). Therefore, although zebra can consume a wider range of plant material than wildebeest, they are probably more constrained by very strong depletions in food supply (rather than by food quality). Strong seasonal fluctuations of food supply during the Miocene probably favored the expansion of ruminants, which explains why many intermediate sized equids disappeared during this time, especially in North America (Janis, Gordon, and Illius 1994).

What is the extent of the wildebeest and zebra migration?

The digestive differences between ruminants and hindgut fermenters mean that zebra have less restricted foraging requirements than wildebeest and, therefore, the seasonal movements of zebra tend to be more diffuse. The patterns of wet season and dry season occurrence of radio collared zebra and wildebeest are different from each other as illustrated in Figure 15.

Up until the mid 1950’s there were various accounts of large herds of wildebeest and zebra seen around the ecosystem, however no one knew the extent of their movement. The first ecological surveys of the Serengeti ecosystem noted the different movement patterns between zebra and wildebeest and attributed these to differences in their grazing selection (Pearsall 1959; Darling 1960; Grzimek and Grzimek 1960), but it was not until 1957 that the true extent of the migration was studied. The earliest attempts to study the movement patterns of wildebeest used colored plastic collars, ear tags, paint, bleach and even hair clips to identify individuals. However, as one might imagine, re-locating marked animals in dense herds proved to be very difficult especially over large areas (Talbot and Talbot 1963; Grzimek and Grzimek 1960, 1960). Despite this, the early efforts by the Talbot’s in the Masai Mara and the Grzimek’s in Serengeti were instrumental in establishing the general movement of wildebeest which was used to realign the boundaries for the national park and should be credited for their foresight. The protection of the entire migratory route is without a doubt why the Serengeti is still one of the only herbivore migratory systems still persisting in the world (Harris et al. 2009).

Aerial surveys starting in 1962 lead to rough seasonal density maps that improved our understanding of wildebeest movement but left many questions unanswered (Watson 1967). This was followed by intensive monthly aerial surveys of multiple species for 39 months between September 1969 and August 1972 (M. Norton-Griffiths and A.R.E. Sinclair, pers.comm., and (Pennycuick 1975; Maddock 1979)). A more detailed analysis of wildebeest migration began with a radio collaring program between 1971 and 1973 which tracked 24 animals weekly.
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Figure 15. The seasonal distribution of radio collared wildebeest and zebra suggests that the zebra movement tends to be more diffuse than wildebeest. Wildebeest are constrained by food requirements and move in a coherent triangular pattern around the ecosystem. Zebra gain sufficient energy from lower quality grass provided there is sufficient biomass and move in dispersed linear north-south patterns.
from an aircraft for 21 consecutive months (Inglis 1976; Wilmshurst et al. 1999). More recently, the Frankfurt Zoological Society funded a GPS radio collaring program of 25 wildebeest and 17 zebra collared intermittently between 1999 to 2008 (Thirgood et al. 2004), which we present in the following sections.

**Distance of wildebeest and zebra migrations**

The straight line distance of the wildebeest migration from the southern plains to the Masai Mara via the western corridor and back again is about 650km, however the total distance a single animal walks is on average 1,550 km per year. The average daily step length for both wildebeest and zebra is remarkably similar; 4.25 km per day for both species. This concurs well with a 5km radius zone of perception for wildebeest (roughly 80km$^2$) that was estimated previously based on modeling historic data (Holdo, Holt, and Fryxell 2009).

The daily step length varies by season especially for wildebeest (Figure 16). Wildebeest tend to move their longest distances during the wet season directly after calving in February, as well as in the transition months from wet to dry season and visa versa (Inglis 1976; Hopcraft et al. in prep). These long movements are somewhat counter-intuitive as one might expect less movement during the wet season when resources are plentiful. However, the localized rain showers and shallow soils on the short grass plains result in fast greening and drying processes and, combined with the high energy requirements of lactating females, most likely accounts for large daily movements of wildebeest during the wet season. During the dry season the movement is less than 4km per day because food and water are accessible only in local areas around the Mara River. The daily movement of zebra shows a similar trend to wildebeest, however with much less variance (Figure 16).

The largest daily step recorded for a wildebeest (i.e. within a 24 hour period) was from a radio collared female who traveled 58 km from Seronera to Kirawira in May, 2000 (FZS, unpublished data) which is more than 3 times the previous estimates (Inglis 1976). The furthest distance covered by an individual wildebeest during a 9 month period from February to October 1999 was 1,518 km starting from the southern plains and ending in the Masai Mara. Therefore, the round trip for this individual would have exceeded 2,000km for the year had the radio collar not failed. For comparison, the longest recorded distance by an individual zebra during a 12 month period was 2,138 km in 2008. The largest daily step for a zebra was 33 km in February 2008 from Lemuta to Hidden Valley north of the Ndutu woodlands. In summary, travel distance for the two species is similar.

**Is the extent of the migration density dependent?**

The wildebeest population underwent a 10 fold increase in numbers between 1959 and 1977 because of the rinderpest vaccination campaign and, as a result, we might expect this sudden increase in density to force animals further afield in search of food and water. A comparison of the wet and dry season distributions of wildebeest during their recovery phase illustrates that the extent of their dry season range has shifted considerably (Figure 17). In 1958 when Fraser Darling surveyed the Masai Mara there was little evidence that the migration reached the Mara River. Darling noted the movement of resident wildebeest from Lemai to Loita plains but he has no accounts of large concentrations moving southward. He attributes earlier records of “hundreds of thousands of wildebeest occurring in the Masai Mara” in 1947 to a decline of the Mara population rather than to a separate south-bound Serengeti migratory population (Darling 1960).

Distribution maps created by Watson and M.I.M. Turner between 1962 to 1965 (as reported by (Pennycuick 1975; Watson 1967)) show the highest dry season densities of wildebeest occurred in the western corridor (specifically on the Ndabaka, Dutwa, Ndoha, Musabi, Kirawira and Nyasirori Plains in what is now the Serengeti National Park, and the Kawanga and Sibora Plains in what now is the Grumeti Reserve) (Figure 17a). The wildebeest population was
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Growing from 260,000 to 440,000 animals during this time. The distribution maps suggest there was some movement north to what is currently the Ikorongo Game Reserve and as far as the Wogakuria and Kogatende area. Earlier accounts also note the majority of the population moved westward from the plains with little northern movement (Grzimek and Grzimek 1960; Darling 1960; Pearsall 1959).

Between 1969 and 1972 the wildebeest population was growing from approximately 500,000 to 770,000 animals. During this time the wildebeest routinely occupied the Masai Mara, Lemai Wedge, and Wogakuria areas in the far north of the ecosystem during the dry season (Figure 17b) (M. Norton-Griffiths pers.comm. and Pennycuick, 1975 #655). There were occasional pockets of wildebeest remaining on the larger plains in the Western Corridor, but not in densities that are comparable to pre-1965. The small groups of wildebeest that persisted along the southeast edge of Maswa and the south-western woodlands during the dry season in 1962-65 as recorded by Watson (1967) no longer persisted by 1972 probably due to less forage being available. This large shift in dry season distribution of wildebeest was most likely a result of...
of less forage being available, especially since 1969 to 1970 were drier years compared to the previous period.

The most recent data from 25 GPS radio collared wildebeest between 1999 and 2007 suggest that the most commonly used locations in the dry season are almost exclusively around the Mara River and into the Masai Mara Reserve in Kenya (Figure 17c). The population has remained stable during this time at approximately 1.2 million which is substantially larger than the previous 2 periods. The area along the northwestern boundary from Ikorongo to Lemai and including Wogakuria poses an interesting and more recent trend in the distribution of the migration. These areas were once heavily used especially during the dry season between 1969 and 1972, however the wildebeest currently use this area less frequently than expected. This could be due to intensive poaching in the area (Hilborn et al.).

The wet season distributions remain relatively unchanged from 1962 to 2009, which supports previous findings that the dry season is the most critical time for wildebeest survival because this is when resources are most limited and wildebeest are forced to search further afield for sufficient resources. It was not until the population exceeded about 750,000 animals that the wildebeest migrated in a more cohesive fashion using the full extent of the Serengeti ecosystem.

The abundance of zebra in the Serengeti has remained stable since the early 1960’s (Figure 10) and there is no evidence that extent of the zebra migration changed during this period (Maddock 1979; Watson 1967). The stability of the zebra population during this time suggests that zebra are regulated by something other than food, because if food competition were important we would expect the zebra population to decline as the wildebeest population expanded. The zebra population is most likely regulated by predation especially on the juvenile age classes (Grange et al. 2004), and by migrating with the wildebeest, zebra could be diluting their exposure to predators. Therefore, migrating zebra do not gain the same advantages as migrating wildebeest in the Serengeti, which might partially explain why zebra are not as abundant as wildebeest.

**What drives the wildebeest and zebra migration?**

Before we can address the question of what drives the herbivore migrations in Serengeti, it might be prudent to first ask: why migrate? Grazing experiments have shown that solitary grazers gain energy faster than those living in groups, therefore a migratory system of super-abundant herds should be evolutionary unstable because of intra-specific competition (Fryxell 1995). However, there are multiple advantages to migrating: (i) individuals dilute their chances of being killed by a predator when they are in a herd, (ii) migration allows prey to seasonally escape predation because the predator population cannot respond numerically to an ephemeral prey base, and (iii) rotational grazing by herbivores can increase the quality of the grass (Fryxell 1995; Fryxell 1991; Fryxell, Greever, and Sinclair 1988; Braun 1973; McNaughton 1990; McNaughton et al. 1989). This general framework has lead to multiple explanations for drivers of migrations in Serengeti.

There is little doubt that the dynamics of the Serengeti ecosystem are rainfall dependent. Rainfall simultaneously determines both top-down and bottom-up processes by influencing predation rates as well as food quality and quantity (Hopcraft, Olff, and Sinclair 2010). Therefore, rainfall is the premise that underlies the following explanations of drivers of the migration since rainfall is intrinsically tied to everything else.

The strong rainfall gradient in Serengeti is matched by a counter gradient of soil nutrients which results in a clear shift in grass quality and abundance. The seasonal pulsing of high quality grass on the southern plains during the wet season attracts many grazer species (Holdo, Holt, and Fryxell 2009; Boone, Thirgood, and Hopcraft 2006; Kreulen 1975; McNaughton 1985; Wilmshurst et al. 1999). However, the shallow soils on the plains dry
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Figure 17. The extent of wildebeest distributions during the dry and wet season from (a) 1962 to 1965, (b) 1969 to 1973, and (c) 1999 to 2007. The dry season range has extended further north as the population increased from 260,000 animals to over 1.2 million suggesting the extent of the migration is density dependent. (Data from (Pennycuick 1975; Thirgood et al. 2004; Watson 1967) and FZS unpublished).
quickly which, in the absence of continued rain, forces wildebeest and zebra back into the greener long grass areas of the woodlands. During the core of the dry season, the only place with permanently flowing water is the Mara River where huge numbers of wildebeest concentrate for several months until the onset of the rains. If wildebeest and zebra were only responding to this seasonal rainfall driven gradient of food quality and abundance, we would expect the movement to be linear (i.e. directly up and down the rainfall gradient). However the true movement is more triangular (Figure 15). Therefore, there are probably additional factors that influence the movement of migrants.

There are several alternate explanations for the drivers of migrations in Serengeti based on seasonal gradients of food resources. Most of these drivers have equal benefits for both wildebeest and zebra, and do not provide explanations as to why migratory wildebeest are more abundant than migratory zebra. These drivers are all ultimately determined by rainfall and soil gradients. For instance, (1) there is a distinct gradient in the concentration of grass protein from the rich south-east plains to the poor northern woodlands (Braun 1973; Murray 1995; Kreulen 1975), so by moving to areas with the most recent growth on the southern plains, wildebeest and zebra are maximizing their total protein consumption. (2) By repeatedly grazing the same areas such as the short-grass plains, wildebeest and zebra induce the grasses to tiller which increase the abundance of high quality leaf material (compensatory vegetation production) (Augustine and McNaughton 2006; Braun 1973; Murray 1995; McNaughton 1976). Additionally, by frequently rotating between patches the grass has time to recover, which can ultimately support more migratory herbivores than resident herbivores (Fryxell 1995). (3) The concentration of calcium and phosphorous are optimal on the short grass plains but are only seasonally available to both zebra and wildebeest (McNaughton 1990; Murray 1995; Kreulen 1975). Physiological restrictions make it impossible for large herds of wildebeest and zebra remain in the north where calcium and phosphorous are low, and therefore necessitates the herds to move further afield in search of suitable calcium and phosphorous concentrations. (4) Grass sodium concentrations are highest in the short-grass plains and the Western Corridor (Hopcraft et al. submitted). Sodium is important especially for lactating females, which might partially explain why the migration tends to swing west making a triangular shape, before going north. (5) The timing of departure from the short-grass plains coincides with the increasing salinity in the ephemeral water holes (concentration of calcium carbonate) (Wolanski et al. 1999; Gereta and Wolanski 1998). However, the water salinity is related to rainfall which also determines the availability of forage, so it is not possible to separate the effects of water salinity as opposed to forage availability.

The advantages gained by moving onto the short grass plains in terms of reduced predation are probably greater for zebra than for wildebeest and provide some insights as to why zebra are not as abundant as wildebeest in Serengeti (Darling 1960; Fryxell and Sinclair 1988). There is little vegetative cover that conceals hunting predators on the short-grass plains which significantly reduces a predator's efficiency at catching prey (Hopcraft, Sinclair, and Packer 2005). As much as 59% to 74% of the mortality in the zebra population is due to predation (Sinclair and Norton Griffiths 1982), as opposed to less than 25% for wildebeest (Mduma, Sinclair, and Hilborn 1999). This is supported by studies of radio collared lions (Packer, pers. comm.) which show that lions kill zebra more often than expected; zebra compose about 18% of kills where as we expect them to be about 8% based on their abundance in the ecosystem (by comparison, wildebeest compose 25% of lion kills but based on their abundance we would expect this to be about 60%) (Hopcraft 2002). Furthermore, equids spend up to 15hrs/day grazing because of the lower digestive efficiency associated with hind-gut fermentation (ruminants spend about 8 hours/day grazing). Therefore zebra often continue grazing into the night and might be more exposed to predation (Duncan et al. 1990). As a result, the reduced predation risk on the short grass plains could be very beneficial for zebra. Evidence suggests that zebra movement on the plains is determined by predation risks more than wildebeest, which supports this hypothesis (Hopcraft et al. in prep). The reduced
**Box 1: Threats to the Serengeti Wildebeest**

There are several current issues threatening the wildebeest population which could lead to its collapse and cause permanent changes in the dynamics of the Serengeti ecosystem.

1) Less predictable rainfall patterns as a result of global warming could result in drying and greening processes that occur out of phase across the ecosystem. If wildebeest cannot reliably track the changes in grass quality (Holdo, Holt, and Fryxell 2009), this could result if greater rates of starvation and could reduce the population below its current carrying capacity.

2) Uncontrolled deforestation in the Mau Forests and large scale irrigation schemes are causing the Mara River to have less water volume and become more ephemeral (Gereta, Mwangomo, and Wolanski 2009). The drying of the Mara River, which is the only permanent source of water in the ecosystem, would lead to a collapse of the wildebeest population.

3) Plans for a national high-way across the northern Serengeti would bisect the migratory path of wildebeest and potentially block animals from reaching their dry season refuge in the Masai Mara. If wildebeest are blocked from accessing water and grazing during the dry season, the population would collapse.

4) Increasing human density on the perimeter of the ecosystem are turning soft boundaries and buffer areas into hard boundaries. Fencing the national park would restrict the migration and could lead to a collapse of the population. Furthermore, fences give the false impression of agricultural security on the edge of the national park and could lead to increased human-wildlife conflicts.

5) Exposure to diseases such as anthrax or rinderpest (via livestock) could potentially reduce the wildebeest population, similar to the rinderpest epidemic in the early 1900’s.

6) Any increase in the amount of illegal hunting would lead to further declines in the population. Current estimates indicate 40-60,000 wildebeest are poached every year, which equates to 3-5% of the population and accounts for about a third to a half of the total mortality.

7) The provision of artificial watering points (i.e. boreholes) could result in overgrazing which could lead to erosion and an overall decline in productivity. Furthermore, permanent water tends to induce migratory species to move less, which increases the prey base for predators, and results in unsustainable predation rates on resident drought-tolerant species (Owen-Smith and Mills 2008).

exposure to predation on the short grass plains is most advantageous to wildebeest during the calving season, because neonates are especially vulnerable to predators. Selecting the safest areas would significantly reduce a calf’s exposure to predation and could increase the chances of survival.

**Summary: Migration alone cannot explain the super-abundance of wildebeest**

Migration enables animals to maximize access to high quality forage without exhausting the local supply. However, if migration allows animals to capitalize on resources then we should expect zebra to be as plentiful as wildebeest in Serengeti, but they are not. Zebra are at least 6 times less abundant than wildebeest. Given zebra are a generalist grazer
and better at digesting low quality grass than wildebeest, we might even expect zebra abundance to be greater than wildebeest (i.e. opposite to what we find). In fact, the seasonal movement and distribution of zebra is less constrained than wildebeest probably because of their generalist diet (Hopcraft et al. in prep). However, wildebeest are more efficient at digesting cellulose than zebra, especially when they can access moderate to high quality grass which is common in Serengeti. Despite this, the overall abundance of wildebeest is regulated by the amount of dry season food (Mduma, Sinclair, and Hilborn 1999), while evidence suggests that the zebra population is regulated by predation especially on the juvenile age classes (Grange et al. 2004). The less efficient digestive system and the high impact of predation partially explains why zebra are not as abundant as wildebeest, and provides some valuable clues as to why wildebeest are super-abundant in Serengeti ecosystem particularly.

**CONCLUSION: WHY ARE WILDEBEEST NUMERICALLY DOMINANT IN THE SERENGETI ECOSYSTEM?**

To conclude, we return to our original question; why are wildebeest so abundant in Serengeti? There are specific aspects of wildebeest biology which are unique and give them a competitive advantage over other species, and which partially explains their abundance. These biological attributes include; synchronous birth of precocial calves which coincides with seasonal abundance of food and swamps the predator community, and a strong selection for high quality mat-forming grasses on which they have the highest intake rates. However, these factors alone do not explain wildebeest abundance because we should expect to see similar densities of wildebeest in other ecosystem which is not the case. The Serengeti ecosystem has a unique counter-gradient of soil fertility and rainfall which creates exceptionally large areas of high quality grasses (more than 3,500 km²). Furthermore, this nutritional gradient in the grass occurs at a scale which is accessible to migratory wildebeest. Therefore, specific aspects of wildebeest diet and reproduction, combined with their capacity to move long distances in an ecosystem with a predictable nutrient gradient enables migrant wildebeest to escape regulation by predation or food quality, and this combination enables wildebeest to dominate the ecosystem beyond the capacity of any other competitor species. In addition, the large densities of wildebeest in Serengeti might facilitate themselves in a positive feed-back loop by keeping large areas heavily grazed which further stimulates increased production and protein concentration in the grass.

Wildebeest are super-abundant in Serengeti because the ecosystem closely matches their requirements. This general conclusion can be applied to other migratory systems, which share key commonalities: (1) refuge areas for migrating animals during times of stress, (2) ephemeral and unusually high resources which means animals are better off moving than remaining resident, and (3) the areas are connected allowing animals to freely move between patches. In Serengeti, this occurs for wildebeest, but not for buffalo, impala, or topi because their resources are not spread out in such a way that matches their requirements. However, in the Boma-Jonglei system of southern Sudan, kob (about the size of impala) and tiang (a race of topi) dominate the system and also migrate, but wildebeest do not. The resources in the Boma-Jonglei system are distributed in such a way that that matches the requirements of kob and tiang in a similar fashion that makes the Serengeti ecosystem very well suited for wildebeest. If any of these attributes were slightly different in the Serengeti, the system might favor zebra, topi, or Coke’s hartebeest which are dominant migrants in other systems.

It is clear that the Serengeti would have completely different dynamics if not for wildebeest, and reciprocally, wildebeest would not be so abundant if not for the unique features of the Serengeti. Therefore the two are inextricably intertwined, making the Serengeti synonymous with epic herds of migrating wildebeest.
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SECTION I: Background and Theory.


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