


# Season of birth affects juvenile survival of giraffe

Derek Edward Lee<sup>1,2</sup>  · Monica Louise Bond<sup>2</sup> · Douglas Thomas Bolger<sup>3</sup>

Received: 15 August 2016 / Accepted: 12 January 2017 / Published online: 27 February 2017  
© The Society of Population Ecology and Springer Japan 2017

**Abstract** Variation in timing of reproduction and subsequent juvenile survival often plays an important role in population dynamics of temperate and boreal ungulates. Tropical ungulates often give birth year round, but survival effects of birth season for tropical ungulate species are unknown. We used a population of giraffe in the Tarangire Ecosystem of northern Tanzania, East Africa to determine whether calf survival varied by season of birth. Variation in juvenile survival according to season of birth was significant, with calves born during the dry season experiencing the highest survival probability. Phenological match may confer a juvenile survival advantage to offspring born during the dry season from greater accumulated maternal energy reserves in mothers who conceive in the long rainy season, high-protein browse in the late dry-early short rainy seasons supplementing maternal and calf resources, reduced predation due to decreased stalking cover, or some combination of these. Asynchrony is believed to be the ancestral state of all ungulates, and this investigation has illustrated how seasonal variation in vegetation can affect juvenile survival and may play a role in the evolution of synchronous births.

**Keywords** Giraffe · Juvenile survival · Match-mismatch · Population dynamics · Reproduction · Reproductive timing

## Introduction

Variation in juvenile survival plays an important role in population dynamics of ungulates (Coulson et al. 1997; Gaillard et al. 2000; Petorelli et al. 2005). In populations of large herbivores, juvenile survival is often more sensitive to environmental variation than adult survival (Gaillard et al. 2000; Eberhardt 2002; Gaillard and Yoccoz 2003, for reviews), and often explains a large part of the variance in parents' lifetime reproductive success (Clutton-Brock et al. 1988) or population growth rates (Raithel et al. 2007). An important factor affecting juvenile survival can be timing of reproduction (Festa-Bianchet 1988; Aanes and Andersen 1996), and juvenile survival of herbivores can be regulated by bottom-up or top-down selective forces (Estes 1966; Ims 1990; Cote and Festa-Bianchet 2001).

Mammalian herbivores in temperate regions generally give birth synchronously (also called seasonality, or birth pulse reproduction) during a short period that coincides with the spring flush of nitrogen-rich plant growth (Asdell 1964; Bunnell 1982; Bronson 1985), and births outside spring and summer seasons are typically not viable due to extreme winter cold (Stearns 1992; Langvatn et al. 2004). Survival rates of northern-latitude ungulate newborns that are born early or late in the spring, thus outside the regionally synchronous birth pulse, are reduced for many species (Sugden 1961; Sadleir 1969; Dauphine and McClure 1974; Bunnell 1980; Clutton-Brock et al. 1983; Santiago-Moreno et al. 2006). However, other studies have found no effect on juvenile survival from birthdates outside the local birth pulse (Fairbanks 1993; Bowyer et al. 1998; Smith and Anderson 1998; Cote and Festa-Binachet 2001; Buu-veibaatar et al. 2013).

In tropical regions, births are thermally viable in all seasons due to mild year-round temperatures, thus

✉ Derek Edward Lee  
derek@wildnatureinstitute.org

<sup>1</sup> Department of Biological Sciences, Dartmouth College,  
Hanover NH 03755, USA

<sup>2</sup> Wild Nature Institute, PO Box 165, Hanover NH 03755, USA

<sup>3</sup> Environmental Studies Program, Dartmouth College,  
Hanover NH 03755, USA

asynchronous (also called non-seasonal, or birth flow) reproduction is common (Owen-Smith and Ogutu 2013). As in temperate zones, tropical latitudes also exhibit clear seasonal peaks in herbivore food supply and quality determined by the onset of seasonal rainfall (Rutherford 1980; Ogutu et al. 2007; Wittemyer et al. 2007). Where resources are seasonally variable, we could expect juvenile survival effects due to season of birth (Findlay and Cooke 1982; O'Donoghue and Boutin 1995). Several studies have examined birth timing of African ungulates (Sinclair et al. 2000; Ryan et al. 2007; Zerbe et al. 2012; Owen-Smith and Ogutu 2013), but none to date have examined the fitness consequences of reproductive timing, as has been done for northern species. Because juvenile survival is often the demographic parameter of greatest influence on realized population growth rates (Gaillard et al. 2000), understanding selective pressures on juvenile survival is important (Smith and Anderson 1998; Barber-Meyer et al. 2008).

We used a population of wild giraffes (*Giraffa camelopardalis* Linnaeus) in the Tarangire Ecosystem (TE) of northern Tanzania, East Africa (3.7°S, 36.0°E; Lee et al. 2016a) to quantify juvenile survival effects of birth season. Giraffes give birth year-round at all latitudes (Dagg 2014), with births generally evenly distributed in every month throughout the year and no clear seasonal birth pulse near the equator <3° latitude (Foster and Dagg 1972; Leuthold and Leuthold 1975; Sinclair et al. 2000; but see; Ogutu et al. 2014). Birth pulses are difficult to determine for wild giraffes based on calf counts because significant mortality can occur between birth and detection of the newborn, leading to variation in apparent reproduction (Lee and Strauss 2016; Lee et al. 2016b), therefore we did not attempt to detect or describe a birth pulse.

Regardless of whether or not a birth pulse is present, phenological match, or reproduction that coincides with the season of maximum forage quality can increase juvenile survival (Pianka 1976; Kennish 1997; Langvatn et al. 2004). Protein is a limiting nutrient for herbivores inhabiting semiarid regions, and therefore hypothetically may mediate some degree of seasonal juvenile survival in giraffes (Bell 1971; Sinclair 1975). Browse quality in the TE has not been measured, but in the nearby and similar Serengeti ecosystem, protein concentration is highest and browse most abundant during the late dry and early short rains seasons (October–December) when *Acacia* and other woody plants are growing rapidly (Pellew 1980, 1983, 1984a). Protein concentration in *Acacia* trees peaks at the end of the dry season (October), when *Acacia* trees flush with new growth in anticipation of the coming short rains. Protein concentration in all non-*Acacia* woody plants is highest during the early growing season at the beginning of the short rains (November–December). Protein concentration declines in all woody plants as

total green biomass increases during the long rains (Pellew 1980, 1983). Observed birth interval of giraffes is  $20.5 \pm 2$  months (Foster and Dagg 1972; Pellew 1983; Hall-Martin and Skinner 1978; Bercovitch and Berry 2009; Strauss et al. 2015), so individual females exhibiting the mean birth interval between sequential births would be out of synchrony with the phenological match period of elevated protein concentration during many of their reproductive attempts.

We used individual-based data collected as encounter histories constructed from seasonal photographic capture-mark-recapture (PCMR) data for wild Masai giraffes (*G. c. tippelskirchii*) in the TE to estimate variation in juvenile survival during the first year of life according to season of birth. We examined data from 449 calves born during three precipitation seasons over 3 years, looking for evidence of variation in juvenile (1st year after birth) survival. We also estimated seasonal variation in apparent reproduction rates (calves per adult female) during the interval before each survey as an index of mortality of neonatal giraffes during the period between birth and first observation. To examine whether and how phenological match could affect the evolution of reproductive synchrony, we examined the consequences of seasonal variation in calf survival by calculating mean lifetime reproductive success of adult female giraffes who delay reproduction to have all their calves during seasonal vegetation phenological match, relative to females who reproduce as often as possible, regardless of season.

## Methods

### Study system

Giraffes are large (830–1000 kg), long-lived, iteroparous, non-migratory, non-territorial, browsing ruminants that eat leaves, twigs, and fruits of many species of woody vegetation (Dagg and Foster 1976; Pellew 1984b; Dagg 2014). Their main natural predators are African lions (*Panthera leo* Linnaeus) and spotted hyenas (*Crocuta crocuta* Erxleben; Dagg and Foster 1976; Dagg 2014). Female giraffes attain sexual maturity at approximately 5 years of age and may breed up to age 20 (Dagg and Foster 1976; Dagg 2014). Giraffes have a gestation length of  $448 \pm 5$  days (mean  $\pm$  SD), resume estrous cycling  $103 \pm 46$  days after giving birth (even while still lactating), and cycle every 15 days for  $68 \pm 87$  days before their next pregnancy (del Castillo et al. 2005). Young typically are weaned at 9 months of age, and are independent at 14 months (Langman 1977).

The TE is a tropical savanna-woodland ecosystem in the eastern branch of the Great Rift Valley that encompasses roughly 30,000 km<sup>2</sup> (Lamprey 1964; Borner 1985; Prins 1987), with a giraffe density of approximately 0.16 km<sup>-2</sup>

(TAWIRI 2011). Density dependence is likely not an issue in this system as the population has been declining since 1986 (TAWIRI 2011), most likely due to poaching (Strauss et al. 2015; Lee et al. 2016a). Lion density is  $0.10 \text{ km}^{-2}$  (Lee et al. 2016a). The TE has three precipitation seasons with average monthly rainfall of: short rains (October–January)=63 mm, long rains (February–May)=100 mm, dry (June–September)=1 mm. Mean total annual rainfall was 650 mm for years 1980–2009, range=312–1398 mm (Foley and Faust 2010).

Our study area in the TE included 5 distinct sites: Tarangire National Park, Lake Manyara National Park, Manyara Ranch Conservancy, Lolkisale Game Controlled Area, and Mto wa Mbu Game Controlled Area. The two national parks had stricter enforcement of anti-poaching laws and no permanent settlements, Manyara Ranch was a private ranch/wildlife conservancy with some anti-poaching activity and a moderate density of pastoralists and livestock but no permanent settlements, and the two Game Controlled Areas had few anti-poaching activities, high density of pastoralists and livestock, agriculture and permanent human settlements, and wildlife harvesting via subsistence and trophy hunting, although hunting of giraffe was legally prohibited (Borner 1985; Gamassa 1995; Nelson et al. 2010).

## Data collection

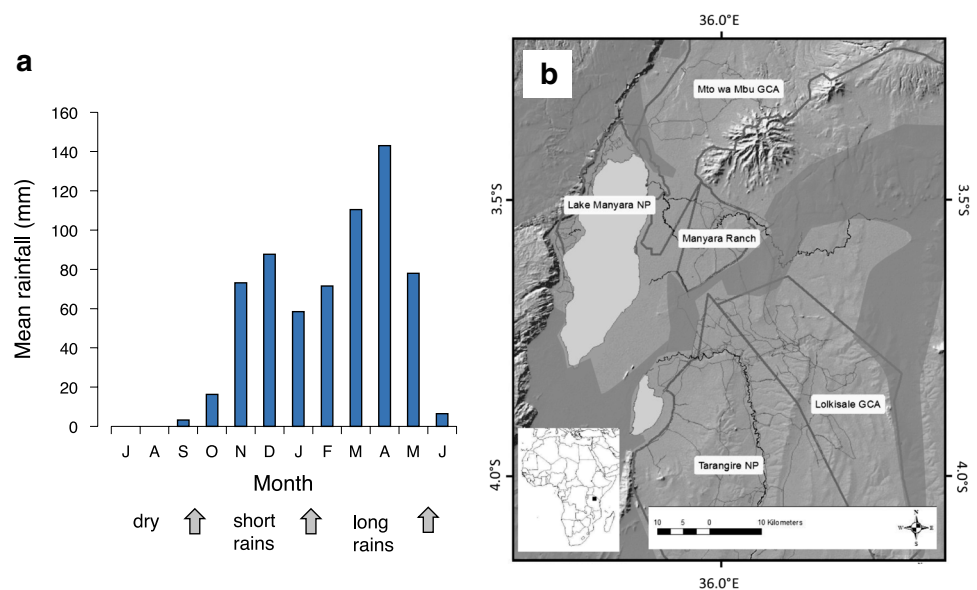
Between January 2012 and October 2014, we conducted systematic road (dirt track) transect sampling by driving a 625-km network of fixed-route transects in the study area collecting photographic capture-mark-recapture (PCMR) data during the same periods every year near the end of each precipitation season (Fig. 1). We used a robust design

sampling framework (Pollock 1982), with 3 occasions per year wherein each sampling occasion was composed of 2 sampling events (Fig. 2). During each sampling event we surveyed all dirt track transects in the study area once (3 occasions per year  $\times$  2 events per occasion  $\times$  3 years = 18 total sampling events). Sampling events lasted 7–10 days, time between sampling events was 2–5 days, and intervals between sampling occasions were approximately 3.6 months (but intervals for parameter estimation were 4 months, the period between end dates for each sampling occasion).

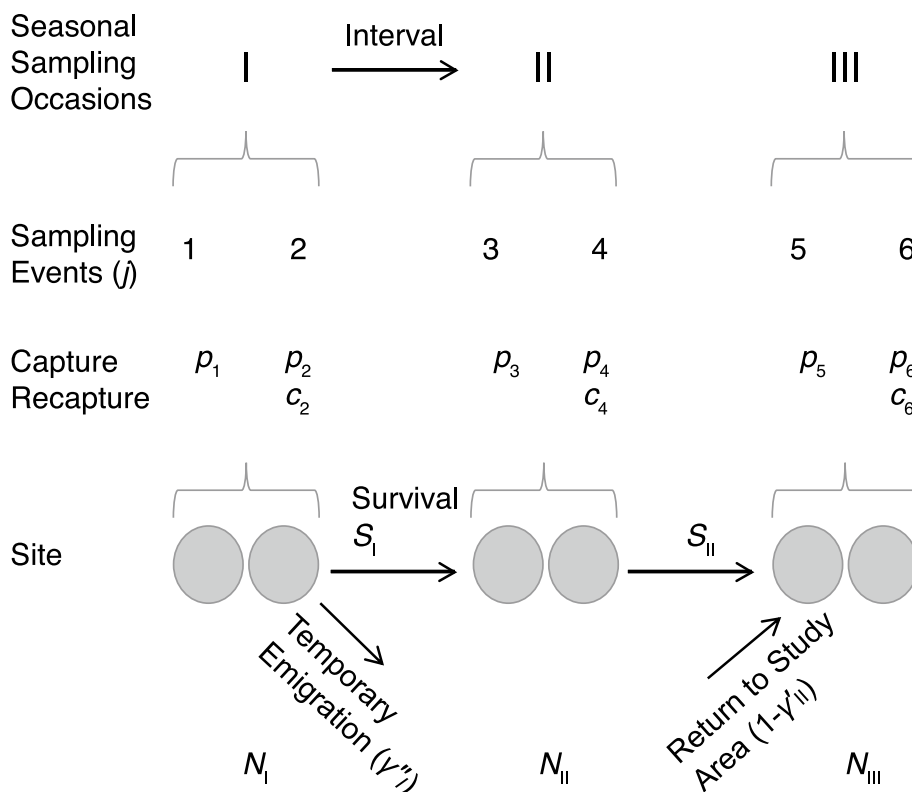
Transect density throughout the study area was high relative to giraffe home-range size (approximately  $90 \text{ km}^2$  mean female home range). Driving speed was maintained between 15 and 20 kph on all transects, and all survey teams included the same 2 dedicated observers and a driver. Each track segment was sampled only 1 time in a given event. We systematically shifted the order and direction in which sites and track transects were sampled similar to a Latin Square design to reduce sampling biases.

During PCMR sampling events, the entire study area was surveyed and a sample of individuals were encountered and either “marked” or “recaptured” by slowly approaching and photographing the animal’s right side (Canon 40D and Rebel T2i cameras with Canon Ultrasonic IS 100–400 mm lens, Canon USA, Inc., One Canon Park, Melville, New York, 11747). We photographed and later identified individual giraffes using their unique and unchanging coat patterns (Foster 1966). We attempted to photograph every giraffe encountered for individual identification, and recorded sex (male, female), GPS location, and age class. We categorized giraffes into 4 age classes: newborn calf (0–3 months old), older calf (4–11 months old), subadult

**Fig. 1** **a** sampling occasions (arrows) relative to monthly rainfall and precipitation seasons. **b** Thick gray lines delineate the 5 sites sampled. Shaded areas are land use dominated by agriculture, and thin lines are tracks driven during surveys. Rainfall data from Foley and Faust (2010)



**Fig. 2** Diagram of Pollock’s (1982) Robust Design statistical model and associated parameters during one calendar year. Each circle represents a sampling event during which all road transects in the study area are driven once. Parameter subscripts refer to the relevant event, occasion, or interval



(1–3 years old for females, 1–6 years old for males), or adult (>3 years for females, >6 years for males) using a suite of physical characteristics, including body shape, relative length of the neck and legs, ossicone characteristics (Strauss et al. 2015), and height (Lee et al. 2016a). We only utilized data from newborn calf-age animals born in the 4-month interval before each survey.

We matched giraffe identification images using WildID ([http://software.dartmouth.edu/Macintosh/Academic/WildID\\_1.0.0.zip](http://software.dartmouth.edu/Macintosh/Academic/WildID_1.0.0.zip)), a computer program that matched a large test dataset of giraffe images collected using our protocols with a very low false rejection rate (0.007) and 0.0 false acceptance rate (Bolger et al. 2012). Based on matching results we created individual encounter histories for all animals for analysis. We assigned an individual to 1 of the 5 sites for the entire study according to where the majority of encounters occurred. When no majority was present, we assigned the animal to the first observed location.

**Calf survival analysis**

Throughout model ranking and selection procedures for calf survival, we ranked models using  $qAIC_c$ , and we used model  $qAIC_c$  Weights ( $W$ ) and likelihood ratio tests as the metrics for the strength of evidence supporting a given model as the best description of the data (Burnham

and Anderson 2002). Due to model selection uncertainty, we present model-averaged parameter values and based all inferences on these model-averaged values (Burnham and Anderson 2002). We considered covariates to be statistically significant if the 85% confidence interval of the beta coefficient did not include zero (Arnold 2010). We tested goodness-of-fit in encounter history data using U-CARE (Choquet et al. 2009), and we found evidence for lack of fit ( $\chi^2_{62} = 97, P=0.006$ ), but we felt this was largely due to lack of age effects in the goodness-of-fit tested model, whereas age effects were included in our model selection and estimation. Additionally, because the computed  $\hat{c}$  adjustment was <3 ( $\hat{c} = 1.5$ ) we did not apply a variance inflation factor (Burnham and Anderson 2002; Choquet et al. 2009).

We modeled and estimated parameters using Pollock’s (1982) robust design statistical models in program MARK 7.1 (White and Burnham 1999). We modeled and estimated probabilities of capture ( $p$ ), recapture ( $c$ ), survival ( $S$ ), and temporary emigration parameters ( $\gamma'$  and  $\gamma''$ ). We began with our most-parameterized model, which included survival as a linear effect of calf age, varied categorically by site, by birth season, and by season, and with site and sampling event specific effects in all other parameters:  $\{S(\text{age} + \text{site} + \text{birth season} + \text{season}) \gamma'(\text{age} + \text{site} \times \text{event}) \gamma''(\text{age} + \text{site} \times \text{event}) p(\text{site} \times \text{event}) c(\text{site} \times \text{event})\}$ . In young

ungulates, survival generally increases with age (Gaillard et al. 2000) and may also differ by sex (Clutton-Brock et al. 1985). Preliminary analyses indicated that age, but not sex, was a significant factor in juvenile giraffe survival.

We began by ranking competing models with reduced temporal complexity of detectability parameters ( $p$  and  $c$ ), and temporary emigration parameters ( $\gamma'$  and  $\gamma''$ ). Once the most parsimonious form of detectability and temporary emigration parameters was obtained, we ranked 6 additional models of survival with site, birth season, and seasonal effects (Table 1). During survival model selection, we kept detectability and temporary emigration parameters in their most parsimonious form, and included age effects on survival throughout. The *site* effect modeled survival as site-specific in all 5 sites. *Season* modeled survival different in each of the 3 seasons (short rains, long rains, and dry). *Birth season* is a cohort-like intercept effect where all calves born in a given season (short rains, long rains, or dry) have similar survival probabilities throughout their juvenile year of life. We also ranked a *constant* model with no effects of site, season, or birth season. We computed calf survival to 1 year old as the product of model-averaged estimates of seasonal survival during the first three seasons of life.

### Apparent reproduction

Apparent reproduction is a compound parameter composed of true reproductive rate of adult females, and survival of neonates between birth and first observation during our surveys.

**Table 1** Selection results for seasonal models of survival of 449 neonatal giraffes in the Tarangire Ecosystem, Tanzania 2012–2014. The *site* effect modeled survival different in all 5 sites

| Model Number | Survival Model               | $\Delta\text{qAIC}_c$ | $W$  | $k$ |
|--------------|------------------------------|-----------------------|------|-----|
| 1            | Birth Season                 | 0                     | 0.34 | 96  |
| 2            | Birth Season + Site          | 1.21                  | 0.19 | 100 |
| 3            | Season + Birth Season        | 1.31                  | 0.17 | 98  |
| 4            | Constant                     | 1.49                  | 0.16 | 94  |
| 5            | Season + Birth Season + Site | 3.01                  | 0.07 | 102 |
| 6            | Season + Site                | 5.48                  | 0.02 | 100 |
| 7            | Season                       | 5.56                  | 0.02 | 96  |

*Season* modeled survival different in each of the 3 seasons (short rains, long rains, and dry) across years. *Birth season* is a cohort-like effect where all calves born in a given season (short rains, long rains, or dry) have similar survival probabilities throughout their lives. The *constant* model has no effects of site, season or birth season. All models included the additional effect of *age* in survival and temporary emigration parameters, and *site* and *time* effects in detectability in the form  $\{S(\text{age} + \dots) \gamma' = \gamma'' (\text{age}) p = c(\text{site} + \text{sampling event} + \text{season})\}$

We estimated site- and season-specific apparent reproduction rates as the ratio of newborn calves per adult female, using logistic models applied to PCMR data with the number of observed newborn calves as the number of successes, and the site-specific  $\hat{N}$  of adult females from Lee et al. (2016a) as the number of trials. We used program R (R Core Development Team 2013) to model and estimate apparent reproduction rates using generalized linear models with a logistic distribution. We ranked 4 basic models for seasonality of apparent reproduction (Table 2) following model selection methods as described for survival above. Because seasonality was the focus of this paper, we computed weighted average estimates of seasonal apparent reproduction among all sites, with site-specific proportion of adult female population as the weighting factor.

The raw data ratio of adult females to calves as an index of reproductive rate is biased unless variation in the probability of detection is accounted for, along with calf mortality between birth and the first observation of the calf during surveys (Nichols 1992; Bonenfant et al. 2005). Therefore, we corrected our raw calf counts for detectability during each survey by dividing the count by site- and season-specific capture probabilities during that survey. We also corrected calf counts for mortality between birth and our survey by dividing the detectability-corrected count by the square root of site- and season-specific survival estimates for calves estimated for the appropriate interval (Caswell 2001). Thus,  $\text{corrected calf count} = \text{raw count} / p_j / \sqrt{S_i}$  where  $p$  is capture probability and  $S$  is survival (both  $p$  and  $S$  are site- and season-specific). In this manner, we attempted to make our calf counts at each site in each survey unbiased by imperfect detectability during surveys, and also unbiased by background mortality of neonates between birth and our survey.

Because we accounted for known site–season estimates of background mortality between birth and survey, we attributed most of the unexplained variation in apparent reproduction rate to mortality of neonatal giraffes

**Table 2** Selection results for seasonal models of apparent reproduction of giraffes (newborn calves/adult female) in the Tarangire Ecosystem, Tanzania 2012–2014

| Model number | Reproduction model   | $\Delta\text{qAIC}_c$ | $W$  | $k$ |
|--------------|----------------------|-----------------------|------|-----|
| 1            | Season $\times$ Site | 0                     | 1.00 | 15  |
| 2            | Season + Site        | 29.0                  | 0    | 7   |
| 3            | Season               | 49.1                  | 0    | 3   |
| 4            | Constant             | 75.9                  | 0    | 1   |

The *site* effect modeled reproduction as site-specific in all 5 sites. *Season* modeled reproduction different in each of the 3 seasons (short rains, long rains, and dry) across years

in addition to the background mortality rate during the period immediately postbirth, before they were available to be detected by our surveys, thus providing evidence of seasonal neonatal survival effects. There are no data on true adult female calving rate or breeding propensity from the TE, but previously documented calving rates show extremely low spatiotemporal variability ( $CV=0.07$ ) relative to estimates of reproductive success ( $CV=0.39$ ; Lee and Strauss 2016). Thus, we assumed calving rate was relatively constant and variation in apparent reproduction was primarily due to neonatal mortality. However, some seasonal variation in calving rate could still be present, with a possible small birth pulse that is mediated by rainfall-triggered primary productivity affecting estrous timing (Dagg 2014; Dagg and Foster 1976; Hall-Martin et al. 1975; Sinclair et al. 2000).

### Consequences of phenological match-mismatch

We examined the consequences of phenological match by computing mean lifetime reproductive success (LRS) according to 2 schedules of intercalf intervals (ICI). LRS was number of calves surviving to age 1 year. The 2 ICI schedules were ‘phenological mismatch’ for mothers who reproduced according to the mean intercalf interval ( $ICI=20$  months), and ‘phenological match’ mothers who delay reproduction to give birth to every calf during the dry season ( $ICI=24$  months). We assumed mothers in both reproductive schedules lived 10 years as reproductive adults and both gave birth to their first calf in September (during the dry season). Calves survived to age 1 year according to the birth-season-specific estimated probabilities of survival (see Results). We also used these calculations to determine what level of calf survival was required to make  $LRS_{ICI_{24}} > LRS_{ICI_{20}}$ .

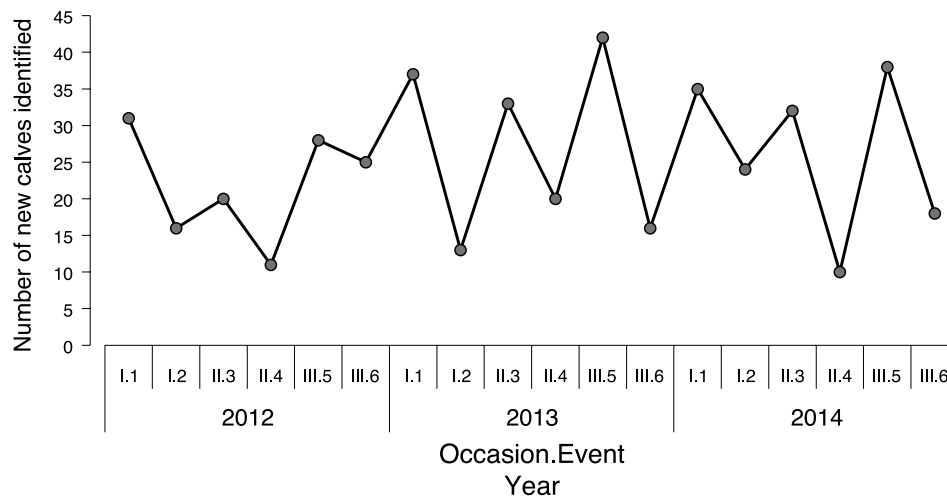
## Results

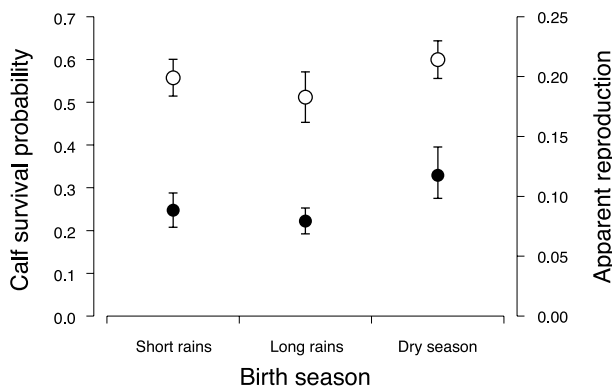
We analyzed encounter histories for 449 individually identified neonatal calves (Fig. 3), with an effective sample size of 1167. Capture and recapture rates ( $0.40 \pm 0.11$ ) were adequate for robust survival estimation. The most parsimonious form of detectability and temporary emigration parameters was:  $\{\gamma' = \gamma''(\text{age}), p = c(\text{site} \times \text{event})\}$ . Survival model selection is given in Table 1.

Survival modeling indicated significant variation in giraffe calf survival associated with birth season (Fig. 4), as the birth season model explained the data significantly better than the constant model (Table 1; likelihood ratio test  $\chi^2_1 = 6.24$ ,  $P=0.044$ ). Calves born during the dry season had a significantly higher probability of surviving to 1 year of age [ $0.60 \pm SE 0.04$ ; dry season  $\beta=0.766$ , 85% CI (0.287, 1.067)], relative to calves born during the long rains ( $0.51 \pm 0.06$ ). Calves born during the short rains had a slightly higher probability of survival ( $0.56 \pm 0.04$ ) relative to the long rains, but the effect was not statistically significant [short rains  $\beta=0.292$ , 85% CI (-0.052, 0.636)]. The season-of-birth survival effect we detected was a cohort-like effect that was independent of the among-season variation in survival which was ranked above the constant model, but was not significant (Table 1).

Seasonal variation in apparent reproduction was significant (Tables 2, 3), with greatest apparent reproduction during the dry season ( $0.120 \pm 0.021$ ), lowest mean apparent reproduction in the long rains ( $c/AF=0.079 \pm 0.011$ ), and apparent reproduction in the short rains ( $0.088 \pm 0.014$ ) slightly higher than in the long rains. The pattern of seasonal variation in apparent reproduction was in synchrony with the seasonal pattern of juvenile survival (Fig. 4).

**Fig. 3** Number of newly identified newborn giraffe calves (0–3 months old) during each sampling event. Sampling events are back-to-back sampling efforts within seasonal sampling occasions that occur three times per year near the end of each precipitation season. Data are from the Tarangire Ecosystem, Tanzania 2012–2014





**Fig. 4** Estimates ( $\pm$ SE) of giraffe calf 1st-year survival according to season of birth (open circles), and seasonal apparent reproduction (filled circles) in the Tarangire Ecosystem, Tanzania 2012–2014

Match-mismatch calculations using observed birth-season-specific survival rates indicated the ICI<sub>20</sub> phenological mismatch mothers had six calves equally distributed among precipitation seasons, while ICI<sub>24</sub> phenological match mothers had five calves all in the dry season. ICI<sub>20</sub> phenological mismatch mothers thus had higher LRS than ICI<sub>24</sub> phenological match mothers (LRS: ICI<sub>20</sub> = 3.34; ICI<sub>24</sub> = 3.00). Survival of calves born in the

dry season had to be increased to 0.67 (12% higher than the observed) for LRS ICI<sub>24</sub> to exceed LRS ICI<sub>20</sub>.

### Discussion

We found evidence that giraffe calves born during the dry season had a higher survival probability relative to calves born in other seasons. In tropical and subtropical areas, large mammal birth timing is likely controlled by nutritionally mediated conceptions (Hall-Martin et al. 1975; Wittemyer et al. 2007; Owen-Smith and Ogotu 2013), but this study is the first to indicate that there is a fitness advantage due to season of birth affecting calf survival. The seasonal patterns in calf survival and apparent reproduction both indicated that seasonal vegetation phenological match conferred survival benefits to offspring born in the dry season.

Giraffes and other large ungulates are generally considered ‘capital breeders,’ because they rely mostly on accumulated body reserves to satisfy the energy needs of reproduction, relative to ‘income breeders’ that meet their energy needs for reproduction by short-term acquisition (Stearns 1992; Jönsson 1997). Such patterns of resource allocation are fundamental to life history theory and tradeoffs (Roff 1992; Stearns 1992), as well as how species are expected to respond to phenological match-mismatch in the face of climate change (Kerby and Post 2013). Our data suggest that phenological match confers a juvenile survival advantage to offspring born during the dry season due to: (1) greater accumulated maternal energy reserves in mothers who conceive at the end of the long rainy season (greater capital); (2) higher protein concentration of available browse during the late dry-early short rains supplementing mother and calf energy budgets (greater income); (3) lower predation during the dry season due to reduced stalking cover for predators; or a combination of these factors.

Adult female giraffes in northern Tanzania are most likely in optimal body condition during the long rains after several months of high-quality food availability, particularly if the preceding years’ precipitation was below average (Pellew 1984b), thus potentially conferring a nutritional or developmental advantage to resultant offspring that are born in the dry season. Several studies have demonstrated a correlation between rainfall, animal condition, or resource availability during the time of conception with the timing of ungulate births (Estes 1976; Post et al. 2003; Moe et al. 2007; Ryan et al. 2007; Ogotu et al. 2014). Conception in giraffes is also dependent on maternal condition, and is likely regulated by browse biomass in a manner similar to that documented for African elephants (*Loxodonta africana* Blumenbach) such that giraffe mothers who give birth in the dry season have accumulated greater energy capital at conception relative to those that give birth in other seasons

**Table 3** Model coefficients from top model of apparent reproduction of giraffes (newborn calves/adult female) in the Tarangire Ecosystem, Tanzania 2012–2014

| Model term                     | Coefficient | SE    | z value | P value |
|--------------------------------|-------------|-------|---------|---------|
| Intercept                      | −2.266      | 0.199 |         |         |
| Season long rains              | −0.847      | 0.356 | −2.38   | 0.018   |
| Season short rains             | 0.560       | 0.252 | 2.22    | 0.027   |
| Site LMNP                      | −0.219      | 0.327 | −0.67   | 0.504   |
| Site MRC                       | 0.746       | 0.220 | 3.40    | 0.001   |
| Site MGCA                      | −0.624      | 0.381 | −1.64   | 0.101   |
| Site TNP                       | 0.192       | 0.215 | 0.89    | 0.372   |
| Season long rains × Site LMNP  | 1.119       | 0.497 | 2.25    | 0.024   |
| Season short rains × Site LMNP | −0.500      | 0.442 | −1.13   | 0.259   |
| Season long rains × Site MRC   | 0.176       | 0.388 | 0.45    | 0.651   |
| Season Short Rains × Site MRC  | −1.304      | 0.298 | −4.37   | 0.00001 |
| Season long rains × Site MGCA  | 1.435       | 0.541 | 2.65    | 0.008   |
| Season short rains × Site MGCA | 0.182       | 0.471 | 0.39    | 0.699   |
| Season Long Rains × Site TNP   | 0.372       | 0.379 | 0.98    | 0.326   |
| Season short rains × Site TNP  | −1.054      | 0.285 | −3.70   | 0.0002  |

Reference categories were Season Dry and Site LGCA

(Hall-Martin et al. 1975; Wittemyer et al. 2007; Owen-Smith and Ogutu 2013).

Giraffes are particularly adept at acquiring and mobilizing resources for reproduction, as evidenced by the fact that they can be simultaneously pregnant with a developing fetus and lactating for a rapidly growing dependent calf for an average of 4 months (Langman 1977; del Castillo et al. 2005; Dagg 2014). Giraffe mothers may be supplementing their capital breeding strategy with an income strategy during the late dry-early wet season that takes advantage of high protein browse, and that may explain the survival advantage of calves born in the dry season (Pellew 1984a). Giraffe calves never suckle from females other than their mother, but they do begin to browse and ruminate at 3–4 months of age (Pratt and Anderson 1979). Calves born during the dry season are thus able to begin their browsing on the abundant and nutritious young shoots of diverse plant species available during the subsequent early short rains (Pellew 1980, 1983), and that may also confer a survival advantage.

Predation is often the main source of juvenile mortality for ungulates (Linnell et al. 1995), and spatio-temporal variation in giraffe calf survival due to predation pressure has been documented (Lee et al. 2016b). We believe predation may also be a component of the seasonal variation in juvenile giraffe mortality we observed. We expect seasonal predation rates are likely lower in the dry season because lions are the predominant predators on giraffes (Dagg 2014), and lions generally take prey according to accessibility (Hopcraft et al. 2005). During the dry season grass and herbaceous stalking cover is at a minimum, potentially reducing lion predation on giraffe calves in that season. Accelerated growth rates of calves born during phenological match may also reduce the period when calves are most vulnerable to predation. Future work will quantify growth rates of calves born in different seasons to determine whether browse quality plays a role in calf growth as well.

### Match-mismatch

Interbirth interval is one of the most variable aspects of a female giraffe's lifetime fitness. The coefficient of variation in interbirth interval is 25% in captive, and 27% in wild giraffe, and is largely determined by length of time between parturition and conception (Bercovitch et al. 2004; Bercovitch and Berry 2009). Giraffe have a mean 20-month intercalving interval, so subsequent births are one season earlier than the previous birth, and mothers who delay conception would reduce their lifetime reproductive output. On the other hand, females whose previous calf was born during the dry season may benefit from delaying estrous in order to synchronize their next pregnancy with the dry season calf survival peak. The large potential for individual

variation in time between parturition and estrous suggests that some giraffe may be delaying estrous to achieve phenological match between their calf's birth and the dry season juvenile survival peak.

Our observed variation in survival of giraffe calves born in the dry season is theoretically sufficient to confer some LRS advantage to mothers who delay birth timing. However, our LRS calculations indicated that mothers who delay estrous to give birth to every calf during the dry season ( $ICI_{24}$ ) will have lower lifetime reproductive success than mothers who reproduce according to the mean reproductive schedule ( $ICI_{20}$ ), if birth-season-specific calf survival is the mean estimated value. If survival of calves born during the dry season was increased to 0.67, then mothers delaying to achieve phenological match would achieve higher lifetime reproductive success. Additionally, if adult female giraffes suffer any costs of reproduction,  $ICI_{24}$  mothers that delay might also benefit from achieving the same LRS with 1 fewer birth during their lifetime relative to  $ICI_{20}$  mothers. This demonstrates that variation in calf survival by birth season may be exerting selection pressure for increased seasonality of reproduction, but current survival differences are not sufficient to select for females that delay conception to synchronize subsequent births with the season of greatest calf survival.

Any period of extended drought that reduces maternal condition such that many adult females are unable to breed until the drought ends could result in a synchronous return to condition and estrous with a subsequent synchronous birth pulse. This effect, coupled with seasonal variation in neonate and calf survival biasing calf counts, may explain the small birth pulses reported from calf counts in the Serengeti (Sinclair et al. 2000) and Masai Mara (Ogutu et al. 2014). An extensive evaluation of pregnancy rates from hormone assays for wild giraffes would clarify the issue of birth timing and apparent birth pulses.

Rainfall-mediated seasonal changes in vegetation may increase birth synchrony in the TE via environmental control, and also through adaptive effects on juvenile survival. We suggest some mothers conceive during the long rainy season, which results in increased survival of their calves due to the greater accumulated maternal capital energy reserves; income from the high-protein browse supplementing the mother during the lactation period, or supplementing the calf during initial browsing; reduced exposure of the calf to predation; or some combination of these effects. This implies that seasonal variation in vegetation quality and quantity underlies the observed pattern in seasonal giraffe calf survival. Asynchronous reproduction is believed to be the ancestral state of ruminants, and this investigation has illustrated how seasonal variation in vegetation may have played a role in the evolution of synchronous births.



**Acknowledgements** This research was carried out with permission from the Tanzania Commission for Science and Technology (COSTECH), Tanzania National Parks (TANAPA), the Tanzania Wildlife Research Institute (TAWIRI), African Wildlife Foundation, Manyara Ranch Conservancy, and the villages of Selela, Lolkisale, and Emboret, under COSTECH permits 2011-106-NA-90-172, 2012-175-ER-90-172, and 2013-103-ER-90-172. We are extremely grateful to J. Keyyu, V. Kakenge, A. Mwakatobe, and K. Oola at TAWIRI; F. Olekashe at MRC, J. Salehe at African Wildlife Foundation, and I. Lejora, D. Njau, S. Quolli from TANAPA. Financial support was provided by Dartmouth College Graduate Studies, Fulbright U.S. Scholar Program, Sacramento Zoo, Safari West, Columbus Zoo, Cincinnati Zoo, Tulsa Zoo, Dartmouth College Cramer Fund, and the Explorer's Club.

## References

- Aanes R, Andersen R (1996) The effects of sex, time of birth, and habitat on the vulnerability of roe deer fawns to red fox predation. *Can J Zool* 74:1857–1865
- Arnold TW (2010) Uninformative parameters and model selection using Akaike's Information Criterion. *J Wildl Manage* 74:1175–1178
- Asdell SA (1964) Patterns of mammalian reproduction. Cornell University Press, Ithaca
- Barber-Meyer SM, Mech LD, White PJ (2008) Elk calf survival and mortality following wolf restoration to Yellowstone National Park. *Wildl Monogr* 169:1–30
- Bell RHV (1971) A grazing ecosystem in the Serengeti. *Sci Am* 225:86–93
- Bercovitch FB, Berry PSM (2009) Reproductive life history of Thornicroft's giraffe in Zambia. *Afr J Ecol* 48:535–538
- Bercovitch FB, Bashaw MJ, Penny CG, Rieches RG (2004) Maternal investment in captive giraffes. *J Mammal* 85:428–431
- Bolger DT, Morrison TA, Vance B, Lee D, Farid H (2012) A computer-assisted system for photographic mark-recapture analysis. *Methods Ecol Evol* 3:812–822
- Bonenfant C, Gaillard J-M, Klein F, Hamann J-L (2005) Can we use the young:female ratio to infer ungulate population dynamics? An empirical test using red deer *Cervus elaphus* as a model. *J Appl Ecol* 42:361–370
- Borner M (1985) The increasing isolation of Tarangire National Park. *Oryx* 19:91–96
- Bowyer RT, van Ballenberghe V, Kie JG (1998) Timing and synchrony of parturition in Alaskan moose: long-term versus proximal effects of climate. *J Mammal* 79:1332–1344
- Bronson FH (1985) Mammalian reproduction—an ecological perspective. *Biol Repro* 32:1–26
- Bunnell FL (1980) Factors controlling lambing period of Dall's sheep. *Can J Zool* 58:1027–1031
- Bunnell FL (1982) The lambing period of mountain sheep: synthesis, hypotheses, and tests. *Can J Zool* 60:1–14
- Burnham KP, Anderson DR (2002) Model selection and multi-model inference: a practical information-theoretical approach. Springer-Verlag, New York
- Buuveibaatar B, Young JE, Berger J, Fine AE, Lkhagvasuren B, Zahler P, Fuller TK (2013) Factors affecting survival and cause-specific mortality of saiga calves in Mongolia. *J Mammal* 94:127–136
- Caswell H (2001) Matrix population models. Sinauer, Sunderland
- Choquet R, Lebreton J-D, Gimenez O, Reboulet A-M, Pradel R (2009) U-CARE: Utilities for performing goodness of fit tests and manipulating CAPTURE-RECAPTURE data. *Ecography* 32:1071–1074
- Clutton-Brock TH, Guinness FE, Albon SD (1983) The costs of reproduction to Red deer hinds. *J Anim Ecol* 52:367–383
- Clutton-Brock TH, Major M, Guinness FE (1985) Population regulation in male and female red deer. *J Anim Ecol* 54:831–846
- Clutton-Brock TH, Albon SD, Guinness FE (1988) Reproductive success in male and female red deer. In: Clutton-Brock TH (ed) Reproductive success: studies of individual variation in contrasting breeding systems. Chicago University Press, Chicago, pp 325–343
- Cote SD, Festa-Bianchet M (2001) Birthdate, mass and survival in mountain goat kids: effects of maternal characteristics and forage quality. *Oecologia* 127:230–238
- Coulson T, Albon SD, Guinness FE, Pemberton J, Clutton-Brock TH (1997) Population substructure, local density, and calf winter survival in red deer. *Ecology* 78:852–863
- Dagg AI (2014) Giraffe biology, behavior and conservation. Cambridge University Press, New York
- Dagg AI, Foster JB (1976) The giraffe: Its biology, behavior, and ecology. Van Nostrand Reinhold, New York
- Dauphine TC, McClure RL (1974) Synchronous mating in Canadian barren-ground caribou. *J Wildl Manage* 38:54–66
- del Castillo SM, Bashaw MJ, Patton ML, Rieches RR, Bercovitch FB (2005) (*Giraffa camelopardalis*) reproductive condition and the impact of endocrine status on daily time budgets. *Gen Comp Endocr* 141:271–281
- Eberhardt LL (2002) A paradigm for population analysis of long-lived vertebrates. *Ecology* 83:2841–2854
- Estes RD (1976) The significance of breeding synchrony in the wildebeest. *E Afr Wildl J* 14:135–152
- Fairbanks WS (1993) Birthdate, birthweight, and survival in pronghorn fawns. *J Mammal* 74:129–135
- Festa-Bianchet M (1988) Birthdate and survival in bighorn lambs (*Ovis canadensis*). *J Zool* 214:653–661
- Findlay CS, Cooke F (1982) Synchrony in the lesser snow goose (*Anser caerulescens caerulescens*). II the adaptive value of reproductive synchrony. *Evolution* 36:786–799
- Foley CAH, Faust LJ (2010) Rapid population growth in an elephant *Loxodonta africana* population recovering from poaching in Tarangire National Park, Tanzania. *Oryx* 44:205–212
- Foster JB (1966) The giraffe of Nairobi National Park: home range, sex ratios, the herd, and food. *Afr J Ecol* 4:139–148
- Foster JB, Dagg AI (1972) Notes on the biology of the giraffe. *Afr J Ecol* 10:1–16
- Gaillard JM, Yoccoz NG (2003) Temporal variation in survival of mammals: a case of environmental canalization? *Ecology* 84:3294–3306
- Gaillard JM, Festa-Bianchet M, Yoccoz NG, Loison A, Toigo C (2000) Temporal variation in fitness components and population dynamics of large herbivores. *Annu Rev Ecol Syst* 31:367–393
- Gamassa DGM (1995) Blockade of wildlife migration corridors by agricultural development in Northern Tanzania. In: Bisonette J, Krausman P (eds) Integrating People and Wildlife for a Sustainable Future. The Wildlife Society, Bethesda, pp 609–613
- Hall-Martin AJ, Skinner JD, Van Dyke JM (1975) Reproduction in the giraffe in relation to some environmental factors. *E Afr Wildl J* 13:237–248
- Hopcraft JG, Sinclair ARE, Packer C (2005) Planning for success: Serengeti lions seek prey accessibility rather than abundance. *J Anim Ecol* 74:559–566
- Ims RA (1990) On the adaptive value of reproductive synchrony as a predator swamping strategy. *Am Nat* 136:485–498
- Jönsson KI (1997) Capital and income breeding as alternative tactics of resource use in reproduction. *Oikos* 78:57–66

- Kennish R (1997) Seasonal patterns of food availability: Influences on the reproductive output and body condition of the herbivorous crab *Grapsus albolineatus*. *Oecologia* 109:209–218
- Kerby J, Post E (2013) Capital and income breeding traits differentiate trophic match–mismatch dynamics in large herbivores. *Philos T Roy Soc Lon B* 368:20120484
- Lamprey H (1964) Estimation of the large mammal densities, biomass, and energy exchange in the Tarangire Game Reserve and the Maasai Steppe in Tanzania. *E Afr Wildl J* 1:3–92
- Langman VA (1977) Cow–calf relationships in giraffe (*Giraffa camelopardalis giraffe*). *Z Tierpsychol* 43:264–286
- Langvatn R, Mysterud A, Stenseth NC, Yoccoz NG (2004) Timing and synchrony of ovulation in red deer constrained by short northern summers. *Am Nat* 163:763–772
- Lee DE, Strauss MKL (2016) Giraffe demography and population ecology. Reference module in earth systems and environmental sciences. Elsevier, Amsterdam. Available via ScienceDirect. [10.1016/B978-0-12-409548-9.09721-9](https://doi.org/10.1016/B978-0-12-409548-9.09721-9). Accessed 3 Dec 2016
- Lee DE, Bond ML, Kissui BM, Kiwango YA, Bolger DT (2016a) Spatial variation in giraffe demography: a test of two paradigms. *J Mammal* 97:1015–1025
- Lee DE, Kissui BM, Kiwango YA, Bond ML (2016b) Migratory herds of wildebeests and zebras indirectly affect calf survival of giraffes. *Ecol Evol*. doi:[10.1002/ece3.2561](https://doi.org/10.1002/ece3.2561)
- Leuthold W, Leuthold BM (1975) Temporal patterns of reproduction in ungulates of Tsavo East National Park, Kenya. *Afr J Ecol* 13:159–169
- Linnell JDC, Aanes R, Andersen R (1995) Who killed Bambi? The role of predation in the neonatal mortality of temperate ungulates. *Wildl Biol* 1:209–223
- Moe SR, Rutina LP, du Toit JT (2007) Trade–off between resource seasonality and predation risk explains reproductive chronology in impala. *J Zool* 273:237–243
- Nelson F, Foley C, Foley LS, Leposo A, Loure E, Peterson D, Peterson M, Peterson T, Sachedina H, Williams A (2010) Payments for ecosystem services as a framework for community–based conservation in northern Tanzania. *Conserv Biol* 24:78–85
- Nichols JD (1992) Capture–recapture models: using marked animals to study population dynamics. *Bioscience* 42:94–102
- O'Donoghue M, Boutin S (1995) Does reproductive synchrony affect juvenile survival rates of northern mammals? *Oikos* 74:115–121
- Ogutu JO, Piepho H-P, Dublin HT, Bhola N, Reid RS (2007) El Niño–Southern Oscillation, rainfall, temperature and Normalized Difference Vegetation Index fluctuations in the Mara–Serengeti ecosystem. *Afr J Ecol* 46:132–143
- Ogutu JO, Piepho H-P, Dublin HT (2014) Reproductive seasonality in African ungulates in relation to rainfall. *Wildl Res* 41:323–342
- Owen-Smith N, Ogutu JO (2013) Controls over reproductive phenology among ungulates: allometry and tropical–temperate contrasts. *Ecography* 36:256–263
- Pellew RA (1980) The production and consumption of *Acacia* browse and its potential for animal protein production. International symposium on browse in Africa (Addis Ababa, 1980). International Livestock Centre for Africa, Addis Ababa
- Pellew RA (1983) The giraffe and its food resource in the Serengeti. I. Composition, biomass and production of available browse. *Afr J Ecol* 21:241–267
- Pellew RA (1984a) The feeding ecology of a selective browser, the giraffe (*Giraffa camelopardalis tippelskirchi*). *J Zool* 202:57–81
- Pellew RA (1984b) Food consumption and energy budgets of the giraffe. *J Appl Ecol* 21:141–159
- Petorelli N, Gaillard JM, Yoccoz NG, Duncan DM, Maillard D, Delorme D, Van Laere G, Toigo C (2005) The response of fawn survival to changes in habitat quality varies according to cohort: quality and spatial scale. *J Anim Ecol* 74:972–981
- Pianka ER (1976) Natural selection of optimal reproductive tactics. *Am Zool* 4:775–784
- Pollock KH (1982) A capture–recapture design robust to unequal probability of capture. *J Wildl Manage* 46:752–757
- Post E, Boving PS, Pedersen C, MacArthur MA (2003) Synchrony between caribou calving and plant phenology in depredated and non–depredated populations. *Can J Zool* 81:1709–1714
- Pratt DM, Anderson VH (1979) Giraffe cow–calf relationships and social development of the calf in the Serengeti. *Z Tierpsychol* 51:233–251
- Prins HHT (1987) Nature conservation as an integral part of optimal land use in East Africa: the case of the Masai Ecosystem of northern Tanzania. *Biol Conserv* 40:141–161
- R Core Development Team (2013) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna
- Raithel JD, Kauffman MJ, Pletscher DH (2007) Impact of spatial and temporal variation in calf survival on the growth of elk populations. *J Wildl Manage* 71:795–803
- Roff DA (1992) The evolution of life histories. Theory and analysis. Chapman and Hall, New York
- Rutherford MC (1980) Annual plant production – precipitation relations in arid and semi–arid regions. *S Afr J Sci* 76:53–56
- Ryan SJ, Knechtel CU, Getz WM (2007) Ecological cues, gestation length, and birth timing in African buffalo (*Syncerus caffer*). *Behav Ecol* 18:635–644
- Sadleir RMFS (1969) The ecology of reproduction in wild and domesticated mammals. Methuen, London
- Santiago-Moreno J, Gomez-Brunet A, Toledano-Díaz A, Picazo R, Gonzalez-Bulnes A, Lopez-Sebastian A (2006) Seasonal endocrine changes and breeding activity in Mediterranean wild ruminants. *Repro Dom Anim* 41:72–81
- Sinclair ARE (1975) The resource limitation of trophic levels in tropical grassland ecosystems. *J Anim Ecol* 44:497–520
- Sinclair ARE, Mduma SAR, Arcese P (2000) What determines phenology and synchrony of ungulate breeding in Serengeti? *Ecology* 81:2100–2111
- Smith BL, Anderson SH (1998) Juvenile survival and population regulation of the Jackson elk herd. *J Wildl Manage* 62:1036–1045
- Stearns SC (1992) The evolution of life histories. Oxford University Press, Oxford
- Strauss MKL, Kilewo M, Rentsch D, Packer C (2015) Food supply and poaching limit giraffe abundance in the Serengeti. *Popul Ecol* 57:505–516
- Sugden LG (1961) The California bighorn in British Columbia with particular reference to the Churn Creek herd. British Columbia Department of Recreation and Conservation, Victoria
- TAWIRI (2011) Aerial survey in the Tarangire–Manyara ecosystem. Tanzania Wildlife Research Institute, Conservation Information and Monitoring Unit, Arusha
- White GC, Burnham KP (1999) Program MARK: survival estimation from populations of marked animals. *Bird Study* 46(Supplement):120–138
- Wittemyer G, Rasmussen HB, Douglas-Hamilton I (2007) Breeding phenology in relation to NDVI variability in free–ranging African elephant. *Ecography* 30:42–50
- Zerbe P, Clauss M, Codron D, Lackey LB, Rensch E, Streich JW, Hatt J-M, Muller DWH (2012) Reproductive seasonality in captive wild ruminants: implications for biogeographical adaptation, photoperiod control, and life history. *Biol Rev* 87:965–990