

Dead before detection: addressing the effects of left truncation on survival estimation and ecological inference for neonates

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Summary

1. Neonate survival is a key life history trait, yet remains challenging to measure in wild populations because neonates can be difficult to capture at birth. Estimates of survival from neonates that are opportunistically captured might be inaccurate because some individuals die before sampling, resulting in data that are left truncated. The resulting overestimation of survival rates can further affect ecological inference through biased estimates of covariate effects in survival models, yet is not addressed in most studies of animal survival. Here, we quantify the effects of left truncation on survival estimates and subsequent ecological inference.

2. Vaginal implant transmitters (VITs) enable capture of ungulates at birth, yielding data without left truncation. The effects of left truncation on survival estimation were quantified using age-dependent survival models for VIT and opportunistically captured neonatal deer. Differences in daily survival rates (DSRs) and cumulative survival probability were calculated for the first 70 days of life. In addition, left truncation was simulated by removing fawns that died during the first 1 or 2 days of life from the VIT-caught sample, isolating the effect of left truncation.

3. Cumulative probability of survival during the first 70 days of life was overestimated by 7–23% for fawns caught opportunistically compared with those caught by VIT, depending on model design. Differences in DSRs were large at age 1 day, but had converged by age 30 days. Simulated left truncation resulted in overestimates of survival of up to 31%. Model selection and covariate coefficients were strongly affected by left truncation, producing spurious ecological inference, including changes to sign and/or magnitude of inferred effects of all covariates.

4. We recommend (i) every effort be made to capture neonates; (ii) consistent capture methods, using at least in part non-truncating techniques, be implemented across years and study areas; and (iii) exclusion of left-truncated data from survival estimates until DSRs converge with those calculated from non-truncated data. This work emphasizes the importance of accounting for left truncation in survival estimation for any species with strong age-dependent survival in order to prevent biased conclusions produced by sampling method rather than true ecological effects.

Key-words: age-dependent survival, truncated data, mark recapture, population ecology, survival analysis, wildlife, neonate

Introduction

Neonatal survival is a key ecological metric, driving the reproductive success of individuals and subsequent population change. For most vertebrates, the neonatal period immediately following birth of offspring or laying of eggs is the highest risk life history stage (Gaillard, Festa-Bianchet & Yoccoz 1998; MacNulty *et al.* 2009). Yet quantifying neonatal survival remains elusive for many species, largely due to challenges in early detection and capture of neonates (Pike *et al.* 2008; Silvy 2012) which is our focus, or the laying of eggs. This failure to detect truly neonatal individuals results in longitudinal survival

data that are left truncated, and inference is therefore based on the sample of individuals that have survived to be detected and captured (Tsai, Jewell & Wang 1987; Heisey & Patterson 2006).

Neonatal survival is typically estimated by closely monitoring marked adults during the reproductive period, using behavioural cues to detect reproduction, and then searching for offspring, nests or dens (White, Knowlton & Glazener 1972; Laurenson 1994; Safine & Lindberg 2008; Silvy 2012). Age of detected offspring or nests is then determined so that age-specific survival rates can be calculated, and survival outcomes monitored (Dinsmore, White & Knopf 2002). This approach introduces error into survival estimates both when offspring age is estimated using imperfect proxy measurements (Haskell *et al.* 2007) and when some neonates or nests die or fail before

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detection (i.e. left truncation, Fieberg & DelGiudice (2009). Although researchers can estimate the error in age determination of offspring or nests (Carstensen *et al.* 2009), estimation of or correction for the effects of left truncation is rarely attempted.

Increasingly, survival estimation is not the sole goal of research, but rather is a necessary component of subsequent analysis, such as modelling of ecological, genetic or behavioural drivers of survival. Left truncation can inflate estimates of neonatal survival and bias estimated effects of covariates (Fieberg & DelGiudice 2009; Berg & Gerard 2011; Yang & Aldrich 2012). When using left-truncated data for survival estimation, environmental or individual covariate values associated with these data are incomplete because they only come from individuals that have survived to be sampled, resulting in biased estimation of covariate effects (Bergeron, Asgharian & Wolfson 2008; Shen & Cook 2013). Accurate data on timing of mortality and effects of covariates are essential, and left truncation should therefore be a serious consideration in study design.

Progress has been made in incorporating individual heterogeneity into survival models in recent years and analytically accounting for many sources of variation in neonatal survival. From the Mayfield nest survival estimator (Mayfield 1961), which assumes a constant daily survival rate (DSR) throughout the nesting cycle in order to account for differing times of exposure to mortality risk, researchers have progressed to explicitly modelling the effects of nest age (Rotella, Dinsmore & Shaffer 2004) and variation in individual quality (Lindberg, Sedinger & Lebreton 2013). Such sophisticated survival models have also been applied to other vertebrate taxa in recent years (Keech *et al.* 2011; Halstead *et al.* 2012). Yet if low-quality individuals are removed disproportionately at very young ages, as is often the case in vertebrate populations, the data driving these models are left truncated and biased towards high-quality individuals. Therefore, none of these modelling solutions account for the sampling problems associated with left truncation.

Left truncation bias for neonates is primarily a sampling rather than a modelling problem. However, recent technological innovations present an opportunity to quantify the effect of left-truncated data on survival estimation and to develop approaches to successfully integrate truncated and non-truncated data into survival models. For instance, vaginal implant transmitters (VITs; Advanced Telemetry Systems, Isanti, MN, USA) have proven highly useful in the study of ungulate reproduction. VITs use a temperature-based switch linked to a VHF radiotransmitter to signal researchers when the transmitter is expelled during birth from the relatively warm body of a female ungulate into cooler air temperatures. In this way, VITs have allowed for the location of birth sites and neonates even for highly cryptic species such as white-tailed deer *Odocoileus virginianus* (Zimmerman) (Carstensen, Delgiudice & Sampson 2003; Swanson *et al.* 2008), mule deer *Odocoileus hemionus* (Rafinesque) Johnstone-yellin, Shipley & Myers 2006; Haskell *et al.* 2007; Bishop *et al.* 2011) and elk *Cervus elaphus* (Linnaeus) (Seward *et al.* 2005; Barbknecht *et al.* 2009).

Currently, VITs are seen by most researchers as a method to improve capture efficiency, rather than to increase accuracy of survival estimates by reducing left truncation (Carstensen, Delgiudice & Sampson 2003; Haskell *et al.* 2007). Indeed, most studies of neonate survival either do not use VITs or use a mixture of VITs and opportunistic captures across years and study areas without accounting for the effects of these two detection methods on survival estimation. Differences in estimates of offspring survival between VITs and opportunistic capture methods are likely, because newborn ungulates are highly cryptic in many species, becoming more active and detectable and less vulnerable to predation as they age (Gaillard, Festa-Bianchet & Yoccoz 1998; Van Moorter *et al.* 2009; Forrester & Wittmer 2013). To quantify the effect of left truncation on neonatal survival estimation and modelling of ecological covariates, we compared neonatal survival in a population of Sitka black-tailed deer (*Odocoileus hemionus sitkensis*, Merriam, 1898) sampled concurrently using both VIT and opportunistic capture methods.

Materials and methods

STUDY AREA

Our study area was located on central Prince of Wales Island, the largest island in the Alexander Archipelago of Southeast Alaska (Fig. 1). The regional ecosystem is a coastal temperate rain forest, and the watersheds within our study area, along with the majority of land in Southeast Alaska, are part of the Tongass National Forest. Precipitation, falling mostly as rain, averages 300 cm per year. Temperatures vary moderately annually, although deep snow (>50 cm) can accumulate during winter months. Habitat composition is naturally quite variable, including several types of old-growth forest, abundant riparian, estuarine and lacustrine environments, and muskeg heaths.

In addition, widespread clear-cut logging has produced single cohort, even-aged forest stands of differing successional stages throughout much of central Prince of Wales Island,

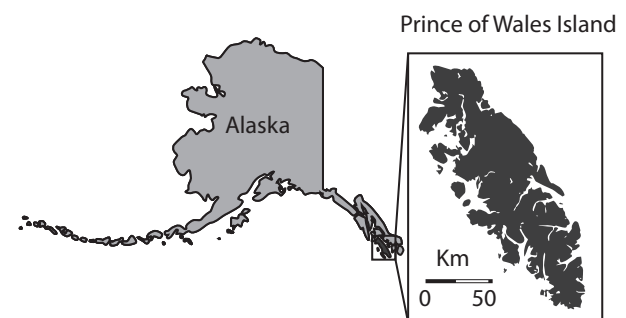


Fig. 1. The study area located on central Prince of Wales Island in Southeast Alaska. Study area consisted of three watersheds where substantial timber harvest has occurred and three watersheds where no significant timber harvest has occurred. Fawns were captured in 2011–2012, with and without VITs in approximately even numbers across these six study areas.

resulting in a patchwork distribution of altered and unaltered habitat in many watersheds (Alaback 1982; Alaback & Saunders 2013). We selected six watersheds in the central portion of Prince of Wales Island to examine survival of Sitka black-tailed deer, three of which were heavily harvested for timber and three that had no timber harvest within them.

DEER CAPTURE AND HANDLING

A total of 54 adult female deer were captured in April and May during 2010–2012. Each deer was fitted with a GPS collar with mortality sensor, measured to determine body size and condition and fitted with a VIT if pregnant. Pregnancy was assessed using a portable ultrasound machine (Sonosite Titan, Sonosite, Bothel, WA, USA). VITs had temperature switches triggered by expulsion at birth, producing a birth signal at temperatures below 35 °C. We monitored VITs twice daily, and ground searches for birth sites were initiated immediately upon detection of a VIT birth signal. If a VIT signal could not be detected (i.e. a female was outside of the VIT transmission range of *c.* 1 km), vehicle and aerial searches were conducted until the female was relocated. Birth sites found using VITs were confirmed based on presence of birth fluids, proximity of female and presence of fawns. If fawns were not found immediately at the birth site, a fawn search was initiated in the vicinity for at least 2 h, or until two fawns were detected.

In addition to fawn captures using VITs, we opportunistically captured neonatal fawns encountered along roads or otherwise encountered in the environment. Fawns were approached on foot and gently restrained in a mesh sack with eyes covered. Gloves were worn while handling fawns, and handling times were <10 min per fawn. Each fawn was fitted with an expandable radiocollar (VHF, or GPS with VHF; Advanced Telemetry Systems, Isanti, MN, USA) and measured to determine mass, chest girth, body length, hind foot length and new hoof growth. Radiocollar marking of fawns does not cause abandonment by mothers (Powell, DelGiudice & Sampson 2005). VHF signals from fawn collars were monitored 1–2 times per day from birth until August 1st and approximately twice per month through the first year of life. New hoof growth was not measured during 2010, and as a result, fawn survival analysis presented here includes only fawns captured during 2011–2012. Seventy-six fawns were captured opportunistically ($n = 40$ in 2011, $n = 36$ in 2012) and 31 from collared females fitted with VITs ($n = 15$ in 2011, $n = 16$ in 2012), for a total of 107 fawns during this 2-year period.

SURVIVAL ANALYSIS

Fawn ages and individual covariates

We estimated the age of opportunistically captured fawns using two different approaches that have been employed in previous studies. First, we used a published hoof growth equation for mule deer that uses new hoof growth (i.e. length of hoof above the cuticle line, which indicates growth of hoof since birth) as a proxy for age, based on a linear relationship

between age and hoof growth from sequential remeasurement of captive-raised (Robinette *et al.* 1973) or VIT-caught wild fawns (Haskell *et al.* 2007). New hoof growth is the most commonly used method for estimating age of opportunistically captured fawns (Lomas & Bender 2007; Grovenburg *et al.* 2011). However, the accuracy of estimates produced for very young fawns can be <50% (Sams *et al.* 1996; Carstensen *et al.* 2009), indicating that this metric may be too variable for use in neonatal-focused survival studies. We use this technique because it is ubiquitous in the literature and serves as a comparison with other age determination techniques. We used the hoof growth regression equation developed by Haskell *et al.* (2007) for determining age of mule deer fawns, as this is the only published equation based on wild, VIT-caught individuals of the study species.

Due to the fact that no hoof growth equation exists for the Sitka black-tailed deer subspecies, and because fawns caught opportunistically were thought to be quite young based on behavioural and morphological characteristics (Haugen & Speake 1958), we suspected that the accuracy of hoof growth equation might be too low given our study questions. Subsequently, we used an additional technique for age determination for comparison. We empirically developed a capture age window based on recaptures of VIT-caught fawns (i.e. fawns of known ages) and assigned the midpoint of this empirical capture window as the age of opportunistically captured fawns (Johnson, Barry & Bowyer 2004; Whiting *et al.* 2008). The oldest age at which recapture was successful was 10 days, which we used as a maximum age for fawns caught opportunistically. We then assigned the midpoint age of 5 days to all opportunistically captured fawns. We therefore had two different estimates of age at capture for fawns caught opportunistically, which in turn yielded two versions of the age-dependent individual covariates for survival analysis (i.e. birth date and birth mass). We calculated birth date by subtracting age at capture from capture date. Mass at birth was calculated based on an assumption of a linear relationship between mass and age, with age predicting mass through a daily mass gain (i.e. slope) of 0.195 kg/day (Anderson 1981).

Survival models

We examined the effect of left truncation (i.e. capture method) on fawn survival estimates using a set of nest-survival models with a logit link function in program MARK (White & Burnham 1999), which allowed us to consider effects of covariates that varied on a daily basis (e.g. fawn age) that might have a large effect on fawn survival. Analysis was carried out using the program Rmark (Laake 2013), implemented in the R statistical framework (R Development Core Team 2013). To account for potentially confounding individual covariates and explore effects of truncation on ecological inference, we included fawn sex, birth date, timber harvest regime of watershed, mass at capture and year into the full survival model. We also examined a set of survival models composed of combinations of the age-dependent covariates (fawn age, date of birth and mass at capture) because we specifically wanted to

quantify the effects of ageing techniques and left truncation on survival estimation.

The goal of our model development was to quantify the effect of left truncation on survival estimation and ecological inference and to isolate the effect of left truncation from that of age estimation technique. To do this, we ran a set of survival models across a range of left-truncation levels created using our VIT and opportunistically caught fawn data, with model structures that used VIT-only data (least truncation), separated these data, combined data with-group effect, and combined data without-group effect. We then simulated left truncation using VIT-only data to isolate the effect of left truncation from that of age estimation technique.

First, to create baseline survival models that contained no left truncation, we developed a set of nine models using data solely from VIT-caught fawns. Because all fawns within this data set were caught at birth, these models also were free from the effects of age determination techniques. We then quantified the effect of left truncation alone using simulations of left truncation. In the simulations, the VIT-only data were reduced systematically by first removing all fawns that died within the first day of life ($n = 7$), then those that died at 2 or fewer days old (an additional three fawns). We did not continue this simulation beyond 2 days, as our sample size would be too greatly diminished to support the full covariate model. To explore left truncation with empirical rather than simulated data, we compared the baseline VIT-only models to models using (a) fawns caught opportunistically (hereafter, opportunistic only), quantifying the specific effects of left-truncated data; (b) combined opportunistic and VIT-caught fawns without-group model structure (hereafter, combined without group), quantifying the effects of combining left truncated and untruncated data; and (c) combined VIT and opportunistic fawns with group structure (hereafter, combined with group), quantifying the effects of combining left truncated and untruncated data, but with appropriate model structure. For comparisons (b) and (c), which used fawns caught opportunistically, we developed two versions of each model based on our two age estimation techniques. Finally, we examined model rankings based on AICc scores (Burnham & Anderson 2002), as well as changes in beta coefficients of covariates in the full covariate model, for comparisons (a), (b) and (c).

The full covariate models were used to produce daily survival rates (DSRs) and cumulative survival probabilities for the neonatal period, across our comparisons and simulations. From each version of the full covariate model, we derived DSRs and cumulative survival probabilities for 1–69 days of age. DSRs were produced by varying the value of the age covariate from 1 to 69 days while holding other covariates at mean values, allowing us to project the effect of age from day 1 onwards even for opportunistically captured fawns (i.e. extrapolation of survival intercept from beta coefficient slope). Then, we calculated cumulative survival probabilities for each full model by multiplying DSR estimates for ages 1–69 days. Mean, standard errors and 95% confidence intervals for cumulative survival probabilities were estimated using 1000 non-parametric bootstrapped replicates of each model (Buckland

& Garthwaite 1991), implemented in the R package *Boot* (Cantey & Ripley 2013). For the combined with-group models, bootstrap resampling was implemented within VIT/opportunistic strata (Cantey & Ripley 2013).

Results

VIT SUCCESS RATES

Of the deer captured, 51 were determined to be pregnant at the time of capture and 49 were successfully fitted with VITs. Two other deer were pregnant but vaginal diameter was too small to accommodate the vaginoscope used in implanting the VITs. Of the 49 deployed VITs, 81% resulted in confirmed birth sites and 62% in captured fawns at the birth site, representing very high retention and fawn detection rates in comparison with other VIT-based studies (Bishop *et al.* 2011). In addition, 8% of females fitted with VITs expelled the devices before parturition, identified by VITs found at sites lacking the characteristics of birth sites.

SURVIVAL ANALYSIS

Fawn age and age-dependent covariate estimation

The mean value of measured new hoof growth for opportunistically captured fawns was 2.64 mm (SD = 1.51) and included 16 fawns for which no new hoof growth was observed (i.e. <24 h old), confirming that many fawns were quite young at capture. However, many of the age estimates produced by the hoof growth equation were higher than the 1–10 day-old plausible capture window from our field study (Mean = 10.4, SD = 3.77), with a minimum age estimate of 5.29 days. To generate more realistic age estimates, we subtracted 5.29 days of age from the distribution produced by the hoof growth equation, so that the youngest age estimates were 0 days, and all other ages were 5.29 days younger (Table 1). This adjustment produced a new mean age of 5.12 days (SD = 3.77). In contrast, the empirical capture window approach resulted in

Table 1. Differences in estimates of age-dependent covariates resulting from choice of age estimation technique and *P*-values of comparison of distributions from fawns caught at birth (i.e. VIT-caught fawns) using Welch's two-sample *t*-test. Techniques used were (i) hoof growth equation, from Haskell *et al.* (2007) and (ii) an empirically generated capture window, from this study

Variable	Age estimation technique	Mean	SE	<i>P</i> value
Age at capture (days)	Hoof growth equation	5.12	3.77	–
	Capture window	5.0	0.00	–
Mass at Birth (kg)	Hoof growth equation	2.18	0.66	0.001
	Capture window	2.17	0.78	0.003
	VIT (caught at birth)	2.57	0.47	–
Birth Date (Julian Date)	Hoof growth equation	160.33	10.21	0.799
	Capture window	160.44	9.80	0.835
	VIT (caught at birth)	160.90	10.31	–

uniform, 5-day-old fawn ages at birth, masking true variation in fawn age at capture but producing plausible fawn ages relative to the empirical capture window without the need for adjustment.

These differences in estimated age-at-capture between age determination techniques resulted in variation in derived, age-specific covariate values (i.e. mass at birth and birth date) for opportunistically captured fawns (Table 1). The fawn ages generated by the hoof growth equation and empirical capture window techniques both resulted in under-estimates of mean mass at birth relative to VIT-caught fawns, but generated a mean birth date equal to that of the VIT-caught fawns. This might indicate that the 0.195 kg/day rate of mass gain that we used to estimate mass at birth was too high for this very small subspecies of mule deer, but that fawn ages are likely fairly accurate.

Survival estimates

The varying levels of left truncation within the VIT-only data, opportunistic-only data, combined data without groups, combined data with groups and simulated-truncation data resulted in different DSRs and cumulative survival rates (Figs 2 and 3). The separated models based on opportunistic-only data produced estimates of DSRs and cumulative survival probability that were higher than those based on VIT-only data; Cumulative survival probabilities from opportunistic-only data were

0.40 (SE = 0.13) when the hoof growth regression equation was used and 0.44 (SE = 0.08) when the empirical capture window approach was used. In contrast, estimates of cumulative survival probability from VIT-only, untruncated data were 0.33 (SE = 0.13).

Combining opportunistic and VIT-caught fawn data without-group structure resulted in DSRs and cumulative survival probabilities that were slightly higher than those of the VIT-only model, resulting in cumulative survival estimates of 0.35 (SE = 0.19) using hoof growth regression-based age estimates and 0.36 (SE = 0.20) using the empirical capture window approach to age estimation.

As expected, when groups were used to control for VIT and opportunistic differences, opportunistically caught groups had higher cumulative survival probabilities than VIT-caught groups (Table 2), produced by large differences in DSR at 1 day of age that converged to no difference in DSR after approximately 30 days of age (Fig. 2). For the model that used age estimates from the hoof growth equation, across-group cumulative survival probability was 0.33 (SE = 0.06); DSRs for opportunistic groups relative to VIT groups were higher until approximately 24 days of age, producing cumulative survival probabilities of 0.40 (SE = 0.08) and 0.25 (SE = 0.11), respectively. When the empirical capture window was used to generate age estimates, across-group cumulative survival probability was 0.35 (SE = 0.07). DSRs converged at approximately 35 days of age (Fig. 2), with cumulative survival

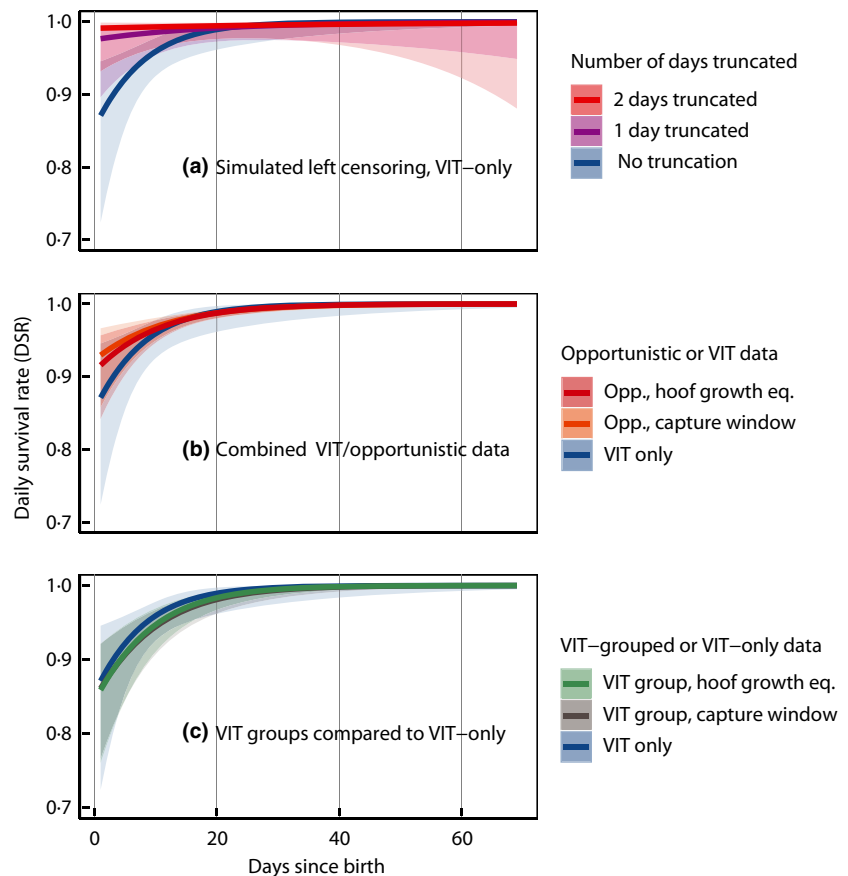


Fig. 2. Daily Survival Rates (DSRs) with means \pm 95% confidence intervals, for neonatal fawns from 1 to 70 days old. (a) Effects of simulated left censoring using VIT-caught fawns, excluding no fawns, fawns that died at <1 day old and fawns that died at <2 days old; (b) effects of maximum left censoring in our data set (only opportunistic individuals), compared with VIT-caught fawns; and (c) differences between estimates from VIT groups and VIT-only model. The full covariate model ($S \sim \text{Age} + \text{Mass} + \text{Birthdate} + \text{Sex} + \text{Timber} + \text{Year}$) was used to generate all estimates.

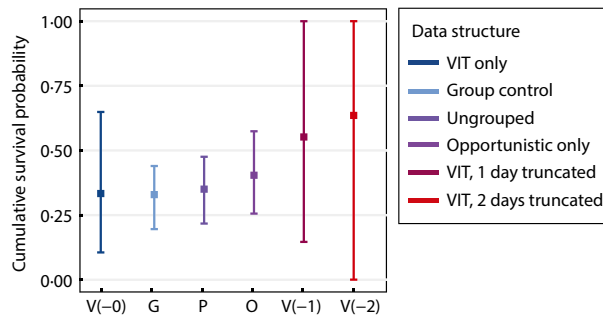


Fig. 3. Cumulative survival probabilities with means \pm 95% confidence intervals, for neonatal fawns from 1 to 70 days old. The gradient of left censoring effects is explored using both empirical and simulated data, from VIT with 0 days censored, to means of grouped VIT/opportunistic model, pooled model, opportunistic only model, VIT with 1 day censored and VIT with 2 days censored. Opportunistic fawn ages were generated from the Hoof growth equation (2007) age estimation equation. The full covariate model ($S \sim \text{Age} + \text{Mass} + \text{Birthdate} + \text{Sex} + \text{Timber} + \text{Year}$) was used to generate all estimates.

probabilities of 0.46 (SD = 0.09) and 0.23 (SD = 0.11) for the opportunistic and VIT groups, respectively.

Models that used simulated left-truncation data, through removal of VIT-only fawns that died in the 1st and 2nd days of life, resulted in cumulative survival probabilities that were progressively higher depending on level of truncation, and higher than for any other models. Removal of fawns that died during the first day of life resulted in an increase in cumulative survival probability to 0.55 (SE = 0.21), and removal of fawns that died during both the first and second days of life increased cumulative survival probability to 0.64 (SE = 0.28). These increases in cumulative survival were the result of increased DSRs at young ages (Fig. 2), resulting from an underestimation of the effect of age on survival (Table 3, Fig. 4).

Effects of truncation on model selection

Model selection based on AICc scores differed based on the level of left truncation in the data. The opportunistic-only and VIT-only models selected quite different top models (Table 4);

the top-ranked model based on the VIT-only model structure was the full covariate model, including effects of age, birth mass, birth date, sex, timber harvest and year, and no other models were within 2 AICc units when using VIT-only data. This model was not within 2 AICc units of the top-ranked model when using opportunistic-only data, based on either age estimation approach.

The combined VIT and opportunistic model structures, with or without groups, also disagreed with model rankings of the VIT-only model, instead selecting simpler models with fewer covariates than the full covariate model. The two versions of this model structure, based on age estimates from hoof growth regression and the empirical capture window, both yielded a top-ranked model that included age, birth mass and birth date as covariates (Table 4) and agreed on a joint model set within 2 AICc units of this best model. The combined, group-controlled model structure resulted in model rankings identical to that of the without-group structure. The simulations of left truncation resulted in a top-ranked model that included all covariates (i.e. the full model) for both levels of the simulated truncation (i.e. -1 and -2 days of mortality), although the simulation missing only 1 day of mortality selected two other models within 2 AICc units, whereas the simulation missing 2 days of mortality included only the full covariate model.

Effects of truncation on ecological inference

Model structure also strongly influenced the estimated effects of individual and environmental covariates (i.e. beta coefficients) in survival models. These alterations to coefficients included changes to both magnitude of coefficients, in which a small effect became a large effect or vice versa, and sign of coefficients, in which a positive effect on survival became a negative effect or vice versa.

Model structure therefore resulted in quite different ecological inference even when considering the full model, which included age, birth mass, birth date, sex, timber harvest regime and year covariates. In general, the more left truncation present in a given model structure, the greater the differences in coefficients between that model structure and the

Table 2. Left truncation in survival data produces differences in cumulative survival probability from 1 to 70 days of age, based on the model $S \sim \text{Age} + \text{Mass} + \text{Birthdate} + \text{Sex} + \text{Timber} + \text{Year}$ with mean values of covariates. A–E indicate level of truncation, from lowest to greatest. S(Both) indicates estimates from combined opportunistic and VIT data, and S(VIT) and S(Opp) indicate estimates based on VIT- or Opportunistic-only data

Model structure	Age estimation	S(Both)	SE	S(VIT)	SE	S(Opp)	SE
A. VIT only	–	–	–	0.33	0.13	–	–
B. Combined, with group	Hoof growth eq.	0.33	0.06	0.25	0.11	0.40	0.08
	Capture window	0.35	0.07	0.23	0.11	0.46	0.09
C. Combined, without group	Hoof growth eq.	0.35	0.07	–	–	–	–
	Capture window	0.36	0.08	–	–	–	–
D. Opportunistic only	Hoof growth eq.	–	–	–	–	0.40	0.09
	Capture window	–	–	–	–	0.44	0.08
E. Sim, -1 day	–	–	–	0.55	0.21	–	–
Sim, -2 day	–	–	–	0.64	0.28	–	–

Table 3. Comparison of Beta coefficients from the survival model, $S \sim \text{Age} + \text{Mass} + \text{Birthdate} + \text{Sex} + \text{Timber} + \text{Year}$, for varying levels of left truncation. A–E indicate level of truncation, from least to greatest

	Variable \pm SE					
	Age	Mass	Birthdate	Sex	Timber	Year
A. VIT-only	0.14 \pm 0.05	2.88 \pm 0.95	−0.02 \pm 0.04	−1.66 \pm 0.83	−0.16 \pm 0.67	1.73 \pm 0.69
B. Combined with groups						
Hoof growth equation	0.12 \pm 0.02	0.49 \pm 0.31	0.02 \pm 0.02	−0.06 \pm 0.32	0.42 \pm 0.34	0.50 \pm 0.34
Capture Window	0.11 \pm 0.02	0.31 \pm 0.69	0.02 \pm 0.02	−0.09 \pm 0.32	0.44 \pm 0.34	0.44 \pm 0.36
C. Combined without groups						
Hoof growth equation	0.13 \pm 0.02	0.37 \pm 0.26	0.03 \pm 0.02	−0.05 \pm 0.32	0.43 \pm 0.34	0.41 \pm 0.33
Capture Window	0.12 \pm 0.02	0.52 \pm 0.23	0.03 \pm 0.02	−0.04 \pm 0.31	0.44 \pm 0.34	0.39 \pm 0.35
D. Opportunistic-only						
Hoof growth equation	0.10 \pm 0.02	0.34 \pm 0.21	0.04 \pm 0.03	0.17 \pm 0.40	0.30 \pm 0.44	0.19 \pm 0.42
Capture Window	0.10 \pm 0.02	0.47 \pm 0.29	0.04 \pm 0.03	0.19 \pm 0.40	0.30 \pm 0.43	0.07 \pm 0.45
D. Simulated truncation						
−1 day mort	0.05 \pm 0.04	3.49 \pm 1.39	0.07 \pm 0.07	−1.58 \pm 1.08	1.05 \pm 0.88	0.33 \pm 0.77
−2 day mort	0.02 \pm 0.04	1.69 \pm 1.43	0.13 \pm 0.09	0.75 \pm 1.58	3.56 \pm 1.72	−0.05 \pm 0.89

non-truncated, VIT-only model structure (Fig. 4). Left truncation in the data progresses from no truncation in the VIT-only data, through the combined data with groups, combined data without groups, opportunistic-only data and finally simulated-truncation data.

Across this gradient of left truncation, the effect of age on survival consistently declined from a strongly positive effect in the VIT-only model, through diminishing positive effects in the with-group effect, combined and opportunistic-only models, to a marginally positive effect in the simulated-truncation models. The effect of birth date (i.e. being born at a later julian date) consistently increased from a slightly negative effect to a positive effect on survival through this same gradient of models. The effect of birth mass changed in a nonlinear fashion, declining from a strongly positive effect on survival in the VIT-only model to a weakly positive effect in the with-group effect and combined models and a neutral effect in the opportunistic-only model, then increasing to a strongly positive effect in the

simulated model structures. The effect of year declined steadily along the left-truncation gradient, from a strongly positive effect of the year 2012 over year 2011, to a neutral effect. The effect of sex changed in a nonlinear fashion, with a strong negative effect of male gender on survival for the VIT-only model changing to a neutral effect of male gender for grouped-controlled, combined and opportunistic-only structures, with a negative effect re-emerging for both simulated-truncation models. Timber harvest within a watershed had a marginally negative effect on survival in the VIT-only model, yet this effect steadily reversed through the truncation gradient, ending with a strongly positive effect on survival in the simulated-truncation models (Fig. 4).

Discussion

We found substantial differences in daily and cumulative survival estimates between fawns caught opportunistically and

Fig. 4. The effect of left censoring on coefficient magnitude and direction. Coefficients are shown for the full covariate model ($S \sim \text{Age} + \text{Mass} + \text{Birthdate} + \text{Sex} + \text{Timber} + \text{Year}$) across a gradient of left censoring in each panel, from no censoring using only VIT-caught fawns [V(−0)], through grouped (G), pooled (P) and opportunistic (O) models based on empirical VIT and opportunistic data, to simulations based on VIT-only fawns with left censoring [fawns that died at <1 day removed, V(−1), and <2 days removed, V(−2)].

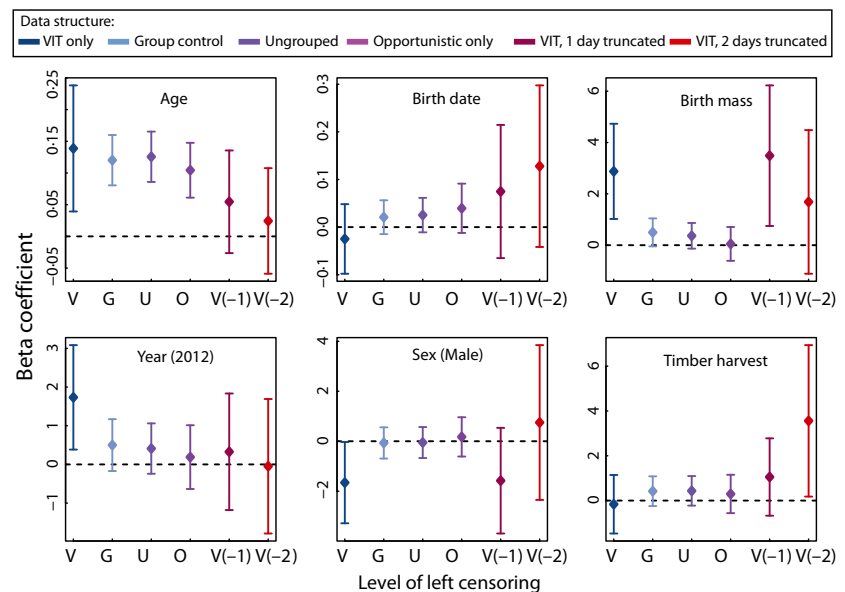


Table 4. Comparison of AICc-based model selection for varying levels of left truncation in survival data. A–E indicate level of truncation, from least to greatest. Only models ranked within 2 AICc units of the best model within a set are shown

Model structure	Parameters	ΔAICc
A. VIT only	$S \sim \text{Age} + \text{Mass} + \text{Birthdate} + \text{Sex} + \text{Timb.} + \text{Year}$	0
B. Combined, with groups	$S \sim \text{Age} + \text{Mass} + \text{Birthdate}$	0
	$S \sim \text{Age} + \text{Birthdate}$	0.79
	$S \sim \text{Age} + \text{Mass}$	1.02
C. Combined, without groups	$S \sim \text{Age} + \text{Mass} + \text{Birthdate}$	0
	$S \sim \text{Age} + \text{Birthdate}$	0.02
	$S \sim \text{Age} + \text{Mass}$	1.37
D. Opportunistic, only	$S \sim \text{Age} + \text{Birthdate}$	0
	$S \sim \text{Age}$	1.25
	$S \sim \text{Age} + \text{Mass} + \text{Birthdate}$	1.98
E. Simulated, –1 day mort	$S \sim \text{Age} + \text{Mass} + \text{Birthdate} + \text{Sex} + \text{Timb.} + \text{Year}$	0
	$S \sim \text{Age} + \text{Mass} + \text{Birthdate}$	0.98
	$S \sim \text{Age} + \text{Mass}$	1.07

VIT-caught fawns. Simulated left truncation of individuals that died at ages 1 and 2 days resulted in dramatic increases in DSRs and subsequently in cumulative survival compared with untruncated data, greater than differences found in our empirical data. This indicates that left truncation in data can bias survival estimates, even at low levels, if age has a large effect on survival. When we used only empirically left-truncated data, stemming from opportunistic capture of neonatal fawns, resulted in overestimates of DSRs up until approximately 30 days of age, the result was a positive bias in cumulative survival probabilities of 0.07–0.23 ($SD = 0.15, 0.14$) depending on which model design and age estimate was used.

Perhaps, even more significantly, ecological inference was heavily biased by left truncation, both during model selection based on AICc, and through large differences in beta coefficients of covariates. Using the untruncated VIT-only data, the full covariate model was the only model selected based on AICc score; In this model, there are strong positive effects on fawn survival of increasing age and birth mass, and increased survival in the year 2012. In contrast, male gender, increasing julian birth date and presence of timber harvest in a watershed had negative effects on fawn survival. Yet had we used a combination of truncated and untruncated data, a simpler top-ranked model would have been selected based on AICc, with age remaining as a covariate but with a diminished positive effect size, birth mass retaining only a marginally positive effect, increasing Julian julian birth date reversing coefficient sign with a positive effect on survival, and all other covariates excluded. The errors in ecological inference would be further magnified had we used only left-truncated data.

From the level of left truncation in our opportunistic-only data and simulations, which is by no means extreme or unrealistic in terms of real-world sampling age for neonatal animals, we would erroneously conclude that age had only a mild positive effect on survival, that increasing julian birth date positively rather than negatively effected survival, that year had no

effect at all and that timber harvest within a watershed produced a strongly positive rather than a negative effect on fawn survival. Conclusions reached from any of these levels of left truncation would not only be incorrect ecologically, but would likely negatively impact management of the species, for instance through the falsely positive effect of timber harvest on fawn survival in all models including left-truncated data.

The origins of these biases in coefficients and model selection could be the result of interactive effects with age. For example, timber harvest and birth date might strongly negatively influence survival of fawns during the first few days after birth but positively affect survival as they become older. Ultimately, left truncation is the product of individual survival outcomes early in life and is thus likely dependent on individual quality. Low-quality offspring are likely more susceptible to predation (Lindberg, Sedinger & Lebreton 2013; Reid *et al.* 2010), and a portion of them die before opportunistic sampling can occur. Low-quality offspring are likely the result of low-quality or inexperienced reproductive adults, which occupy poor birth site, nest, den or home-range habitat, or are unable to provide sufficient nourishment or protection to offspring (McLoughlin *et al.* 2006; Hamel *et al.* 2009). Here, we estimated that the effect of VIT-based captures (i.e. group effect) on survival was on average -0.55 ($SD = 0.39$) across our age determination techniques, which could be seen as a measure of the difference in frailty between the VIT and opportunistically caught groups. Several mechanisms could be responsible for this difference in frailty and bear further investigation. During this study, numerous females lost fawns at or shortly after birth, indicating that birth site and subsequent habitat selection by females may play a large role in determining fawn predation risk. Future work focusing on the underlying mechanisms through which individual heterogeneity produces differences in fitness could elucidate such processes. The effects of left truncation we document here have important implications for ecological studies of recruitment, survivorship and population dynamics, particularly those that employ capture–mark–recapture or known-fates estimation of survival that rely on opportunistic, uneven-aged sampling of organisms. Because we captured fawns using left-truncating and non-truncating methods concurrently and in the same geographic area, we were able to estimate the magnitude and persistence of survival differences resulting from left truncation of data; many studies do not have this luxury, yet assume survival is equivalent for animals caught with varying capture methods or that ecological conclusions are sound despite being based on truncated data. We emphasize the need to examine these assumptions empirically.

Survival rates are often the basis for demographic analysis and for making decisions about managing populations (Eberhardt, Blanchard & Knight 1994; Beissinger, Westphal & Westphal 1998; Servanty *et al.* 2011). If left truncation is present but not accounted for, results could be spurious and highly misleading for ecologists and managers. However, we suggest that truncated and non-truncated data can be successfully combined within survival models with minimal impact to survival estimation and inference, provided certain guidelines

are followed. Left truncation is fundamentally a sampling problem, and the level of left truncation before capture can occur will likely vary by study, by year and by species. Thus, it is key to acquire a subsample of study data from minimally truncated individuals, despite the higher costs of these data, for comparison with more truncated data. This allows for empirically based adjustments of the risk set at a given time, based on the convergence of age-dependent survival rates, with more truncated data only included once age-dependent survival rates have converged. Specifically, we recommend that (i) every effort is made to capture truly neonatal individuals for at least a portion of the sample; (ii) consistent capture methodology, consisting of either non-truncating or a balanced mixture of non-truncating and truncating techniques, is used across years and study areas; and (iii) left-truncated data should be excluded from age-dependent survival estimates until DSRs converge with those calculated from non-truncated data.

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Data accessibility

Data from this analysis are available at Dryad, doi: 10.5061/dryad.p1r40 (Gilbert *et al.* 2014). However, we will place a one-year embargo on the data, because it comprises an important part of the Ph.D. thesis of S. Gilbert and will be used in subsequent analyses.

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