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Are opportunistic captures of neonate ungulates biasing relative estimates of litter size?

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Abstract

The capture of neonate ungulates allows for the collection of valuable ecological data, including estimates of litter size. However, varied methods used to capture neonate ungulates can result in sampling biases. Our objective was to determine if opportunistic captures of neonate ungulates (i.e., locating neonates by visually scanning for adult females displaying postpartum behaviors) bias relative estimates of litter size and investigate potential causes if a bias does exist. We analyzed data from 161 litters of mule deer (*Odocoileus hemionus*) sampled using three different capture methods during 2019–2021 in Utah, USA. Estimates of litter size derived from opportunistic captures were smaller than estimates derived from movement-based captures or captures completed with the aid of vaginal implant transmitters (VITs). Age at capture was inversely related to estimates of litter size and likely influenced the detection bias associated with opportunistic captures. Neonates captured opportunistically were not older than neonates captured using movement-based methods, but were older than neonates captured with the aid of VITs. Distance between neonates from the same litter did not influence estimates of litter size. Researchers should be aware of the biases associated with different capture methods and use caution when interpreting data among multiple capture methods. Estimates of litter size derived from opportunistic captures should not be compared to estimates of litter size derived from alternative capture methods without accounting for the detection bias we observed.

Keywords: Capture methods, Litter size, Mule deer, Neonates, *Odocoileus hemionus*, Sampling bias, Ungulates, Utah, Vaginal implant transmitters

Background

Multiple methods have been utilized to locate neonate ungulates and improve the likelihood of capture. Neonates can be captured opportunistically, without prior knowledge of a specific parturition event, by searching potential parturition sites or observing postpartum behaviors by adult females [1–6]. Opportunistic captures can also be performed using aerial/terrestrial vehicles,

audio recordings, spotlights, thermal sensors, or trained animals [7–12]. Alternatively, neonate ungulates can be captured with prior knowledge of a specific parturition event. Parturient ungulates often display characteristic movement patterns, so targeted captures can occur by monitoring the movement of adult females with tracking collars [13–15]. Targeted captures can also occur with the aid of vaginal implant transmitters (VITs), a radio transmitter expelled at parturition that signals the occurrence of a parturition event [16–18]. Capturing neonate ungulates allows for the collection of valuable ecological data, including early-life survival, cause-specific mortality,

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morphometry, movement, parturition date/location, and sex ratio.

Notably, the variety of methods utilized to capture neonate ungulates has led to concerns of sampling biases. For example, age at capture tends to be higher for neonates captured using opportunistic methods than for neonates captured with the aid of VITs [19, 20]. Opportunistic captures are also more likely than VIT-aided captures to miss early-life mortalities, biasing estimates of survival and cause-specific mortality [18, 21–23]. Moreover, opportunistic captures may not be randomly distributed, resulting in biased distributions of parturition events favoring researcher access [16, 24, 25]. An additional, untested bias when capturing neonate ungulates may be skewed estimates of litter size. This knowledge gap is problematic considering litter size is frequently estimated during early-life capture events [26–31]. While estimates of litter size derived from early-life capture events are likely prone to detection failure, relative estimates can still be utilized to make comparisons among years, sites, and age classes.

Litter size has major implications for individual fitness and population dynamics in species with variable litter sizes. For example, litter size within a species tends to be positively related to the total body mass or relative body fat of female ungulates [32–35]. Following parturition, female ungulates with larger litters incur greater lactation costs and have reduced fat reserves compared to conspecifics with smaller litters [36–38]. The implications of litter size also extend to neonate ungulates. Neonates in larger litters tend to have lower rates of survival than conspecifics in smaller litters [27–29]. Neonate mass within a species is also inversely related to litter size [33, 39, 40]. At the population level, rates of recruitment may increase with larger litter sizes [27]. Despite the potential ecological implications of litter size, the potential biases associated with method of capture when estimating litter size of ungulates are unknown.

Our objective was to determine if opportunistic captures of neonate ungulates bias relative estimates of litter size and investigate potential causes if a bias does exist. We used captures of neonate mule deer (*Odocoileus hemionus*) and three capture methods (opportunistic, movement-based, and VIT-aided) as an initial case study. Because opportunistic methods tend to capture older individuals than alternative methods and bias estimates of survival, we hypothesized that opportunistic captures would also bias relative estimates of litter size [18–23]. We predicted that estimates of litter size derived from opportunistic captures would be smaller than estimates of litter size derived from movement-based or VIT-aided captures. We also hypothesized that age at capture and distance between neonates from the same litter would

be linked to estimates of litter size and capture method. Likelihood of capture tends to decrease as neonates age, and neonates from the same litter often bed separately once moved from the parturition site [41–44]. Thus, we predicted that new hoof growth (a proxy for age) would be inversely related to litter size and would be greater for litters associated with opportunistic captures than for litters associated with movement-based or VIT-aided captures. Further, we predicted that distance between neonates from the same litter would be inversely related to new hoof growth and would be greater for litters associated with opportunistic captures than for litters associated with movement-based or VIT-aided captures.

Methods

Study area

We performed this study in the Book Cliffs (39.5°, −109.3°) and the Cache (41.7°, −111.5°) management units of Utah, USA (Fig. 1). Elevations in the Book Cliffs spanned from approximately 1675 m to 2590 m, average annual precipitation was 22.9 cm, and average annual temperature was 10.3 °C (averages from 1981 to 2010) [45]. Terrain in the Book Cliffs consisted of cliff faces,
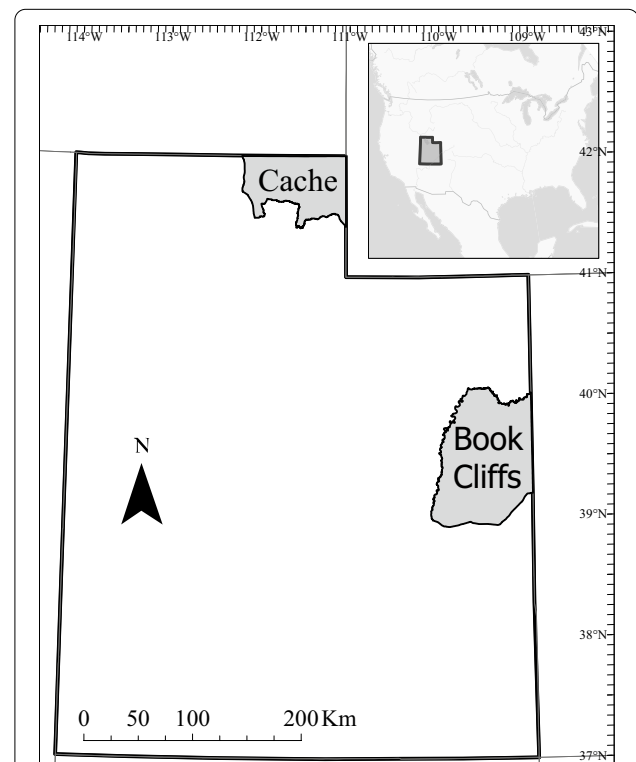
Fig. 1 Study areas (shaded and labeled) associated with captures of neonate mule deer during 2019–2021 in Utah, USA. A total of 128 neonates were captured in the Book Cliffs management unit and 110 neonates were captured in the Cache management unit

ridges, valleys, and flatlands over an area of proximately 9300 km^2. The vegetation community in the Book Cliffs varied from a sagebrush steppe (*Artemisia* spp.) to a pine–juniper woodland (*Pinus monophyla–Juniperus oteosperma*). Elevations in the Cache spanned from approximately 1300 m to 3040 m, average annual precipitation was 43.4 cm, and average annual temperature was 5.1 °C (averages from 1981 to 2010) [45]. Terrain in the Cache consisted of ridges and valleys over an area of approximately 4000 km^2. The vegetation community in the Cache varied from a sagebrush steppe to a pine–aspen woodland (*Pseudotsuga menziesii–Populus tremuloides*). Predators of mule deer in the Book Cliffs and Cache included black bears (*Ursus americanus*), bobcats (*Lynx rufus*), coyotes (*Canis latrans*), and mountain lions (*Puma concolor*).

Adult captures
An independent capture company (Helicopter Wildlife Services, Austin, TX, USA or Quicksilver Air Inc., Peyton, CO, USA) captured adult (i.e., ≥ 2 years old) female mule deer via helicopter net-gunning during February–March of 2019–2021 [46, 47]. Following capture, the capture company hobbled and blindfolded animals to minimize stress and transported animals to a nearby processing site. At the processing site, we fitted animals with a tracking collar (G5-2DH, 595g, Advanced Telemetry Systems, Isanti, MN, USA) which included global positioning system (GPS) technology that recorded coordinates every 2 h. Collars were also equipped with a very high frequency (VHF) transmitter. In addition, we checked the pregnancy status of animals via transabdominal ultrasonography [16, 48]. If an animal was pregnant, we inserted a VIT (M3930U, 23g, Advanced Telemetry Systems) using a vaginoscope [16, 24]. All VITs included light and temperature sensors to detect expulsion, and a VHF transmitter. An ultra high frequency (UHF) link between each collar and VIT allowed for near-instant notification of VIT expulsion, sent via email [49].

Neonate captures
We captured neonate mule deer during May–July of 2019–2021 using 3 capture methods: opportunistic, movement-based, and VIT-aided. To perform opportunistic captures, we visually scanned potential mule deer habitat for adult females [50, 51]. If females displayed typical postpartum behaviors (e.g., increased vigilance, reluctance to flee, social isolation, or vocalizations) or physical characteristics (e.g., enlarged udder or sunken flanks), we continued monitoring the female for evidence of neonates [50–52]. Upon observation of a neonate, we proceeded directly to the neonate's location. If we did not

observe a neonate, we systematically searched the area surrounding the female's location.

To perform movement-based captures, we monitored movement patterns of adult females with tracking collars, but without a VIT [43, 53]. If females displayed movement patterns indicative of parturition (e.g., a sudden, lengthy movement followed by a sustained reduction and localization of movement), we systematically searched the area surrounding the female's most recent coordinates [43, 54, 55]. The sample of collared females without a VIT included animals that previously expelled a VIT (and were incorporated into the study during a previous year) and animals that were not pregnant at the time of capture (but became pregnant during a subsequent year).

To perform VIT-aided captures, we systematically searched the area surrounding expelled VITs [16, 52, 56]. Generally, we waited more than 3 h after VIT expulsion before initiating a search to allow for female–neonate bonding to occur [56–58]. Wait times varied based on accessibility of parturition sites and the number of parturition events that occurred on the same day. If neonates were not located near the parturition site, we searched the female's most recent coordinates.

Data collection
Following capture of a neonate, we blindfolded the animal and completed processing while wearing nitrile gloves. We recorded GPS coordinates of the capture location and fitted each neonate with an expandable tracking collar (M4230BU, 125g, Advanced Telemetry Systems). We also recorded new hoof growth—the distance from the hairline to the distal edge of the growth ring on a front hoof [59–61]. Processing time was typically < 10 min. If a lone neonate was found, we began searching the surrounding area for additional neonates from the same litter. All similar-sized neonates located in the same search area during the same search period were assumed to be from the same litter. We confirmed the validity of this assumption using a UHF link between neonate collars and adult collars worn by mothers associated with movement-based or VIT-aided captures. We received notification via email if collared mothers and their offspring were in close proximity, which indicated that mother–offspring relationships were correctly identified. Although the mother–offspring relationships of neonates without a collared mother could not be confirmed post-capture, we assumed that our mother–offspring identification was consistent among capture methods. We estimated litter size based on the number of neonates located during our search, even if neonates fled before capture could occur. If it became too dark to locate neonates, we postponed searches until the next day.

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Data analysis

To determine if opportunistic captures biased estimates of litter size, and why any bias may have occurred, we analyzed capture data and estimates of litter size using 2 logistic regression models and 3 linear regression models. We did not combine models into a multivariate regression framework because explanatory variables showed evidence of correlation [62, 63]. When creating models that examined the relationship of age at capture, we used new hoof growth as a proxy for age at capture. New hoof growth is linearly related to the age of neonate mule deer and has been used to estimate age when exact birth dates are not known [21, 30, 33, 64]. However, established equations to estimate age can produce ages that vary by more than 11 days [57, 60]. Similar equations established for white-tailed deer (*Odocoileus virginianus*) can produce estimated ages that are accurate (i.e., within 1–3 days of the true age) <50% of the time [61]. Thus, we did not convert new hoof growth measurements to an estimated age at capture to avoid cases of pseudo-accuracy.

We used a mixed-effects logistic regression to examine the relationship between capture method and litter size (coded as litter size of $1 = 0$, litter size of $2 = 1$). We also used a mixed-effects logistic regression to examine the relationship between mean new hoof growth per litter (henceforth shortened to "new hoof growth") and litter size. We used a mixed-effects linear regression to examine the relationship between capture method and new hoof growth. We also used a mixed-effects linear regression to examine the relationship between new hoof growth and distance between neonates from the same litter. Finally, we used a mixed-effects linear regression to examine the relationship between capture method and distance between neonates from the same litter. To limit confounding variables that might influence hoof growth measurements and/or distances between neonates from the same litter, we censored neonates that were found underdeveloped/stillborn ($n = 12$), predated prior to our arrival ($n = 2$), or captured on a different date than neonates from the same litter ($n = 2$). In addition, we censored neonates that fled before data could be collected ($n = 3$). In all models, we included management unit and year as random effects and confirmed that relevant assumptions were met [62, 63]. We analyzed data using the lme4 package in Program R version 4.0.2 and used an α-value of 0.05 in all interpretations [65, 66].
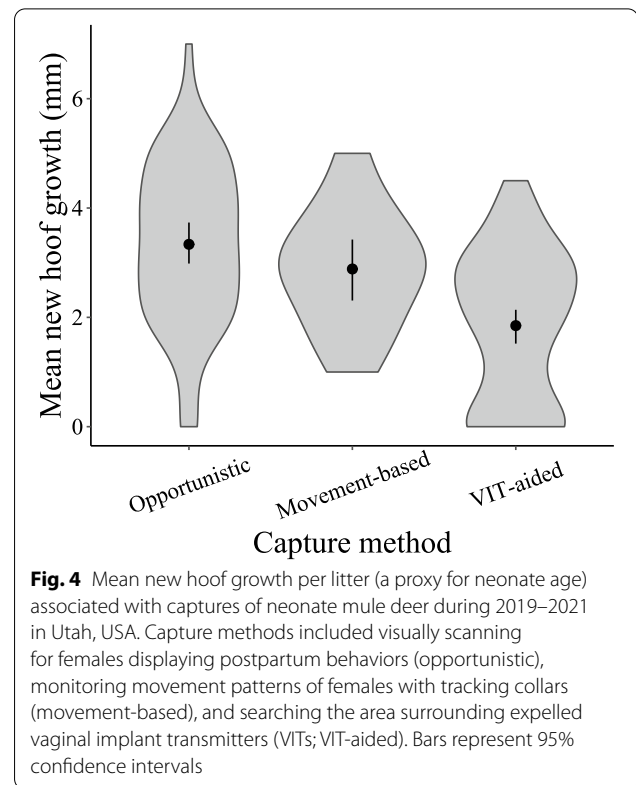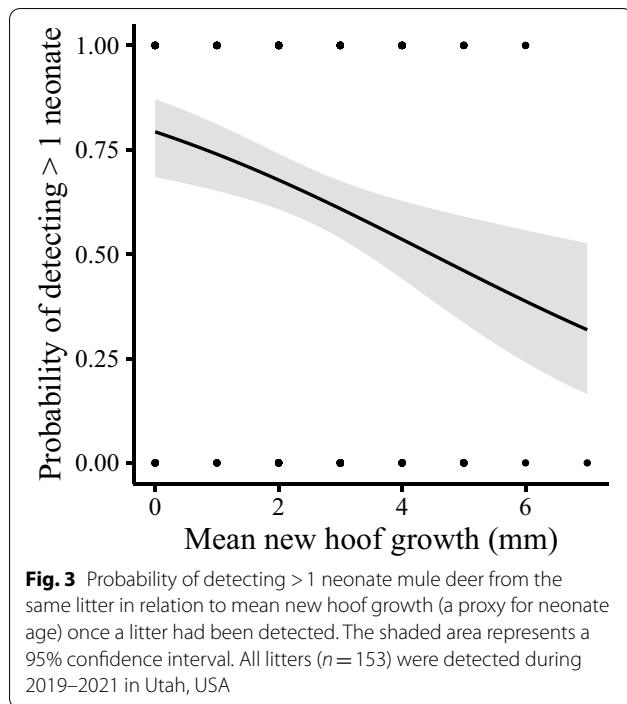
Results

We analyzed data from 161 litters (238 neonates) of mule deer captured over a period of 3 years. Of the litters we analyzed, 90 litters (128 neonates) were associated with the Book Cliffs management unit and 71 litters (110 neonates) were associated with the Cache management unit. We located 64 litters using opportunistic methods, 14 litters using movement-based methods, and 83 litters using VIT-aided methods. Based on our estimates of litter size, 84 litters (52.2%) comprised 1 neonate and 77 litters (47.8%) comprised 2 neonates. We did not find evidence of any litters comprising more than 2 neonates. Mean ($\pm$ SE) litter size derived from captures on the Book Cliffs (1.4 $\pm$ 0.1) and the Cache (1.5 $\pm$ 0.1) were not different ($P = 0.11$). There was no evidence that any mother–offspring relationships were incorrectly identified.

Estimates of litter size derived from opportunistic captures were smaller than estimates of litter size derived from movement-based ($\beta = 1.3$, OR $= 3.7$, 95% CI $= 1.1$–12.7, SE $= 0.6$, $z_{11} = 2.1$, $P = 0.03$) or VIT-aided captures ($\beta = 1.5$, OR $= 4.6$, 95% CI $= 2.2$–9.6, SE $= 0.4$, $z_{80} = 4.2$, $P \leq 0.001$). Estimates of mean ($\pm$ SE) litter size derived from opportunistic captures, movement-based captures, and VIT-aided captures were 1.3 $\pm$ 0.1 neonates, 1.6 $\pm$ 0.1 neonates, and 1.6 $\pm$ 0.1 neonates, respectively (Fig. 2). There was an inverse relationship between new hoof growth and estimated litter size ($\beta = -0.3$, SE $= 0.1$, $z_{152} = -2.0$, $P = 0.04$; Fig. 3). New hoof growth associated with opportunistic captures was not different than new hoof growth associated with movement-based captures ($\beta = -0.3$, SE $= 0.4$, $t_{10} = -0.7$, $P = 0.46$, $R^2 m = 0.1$,
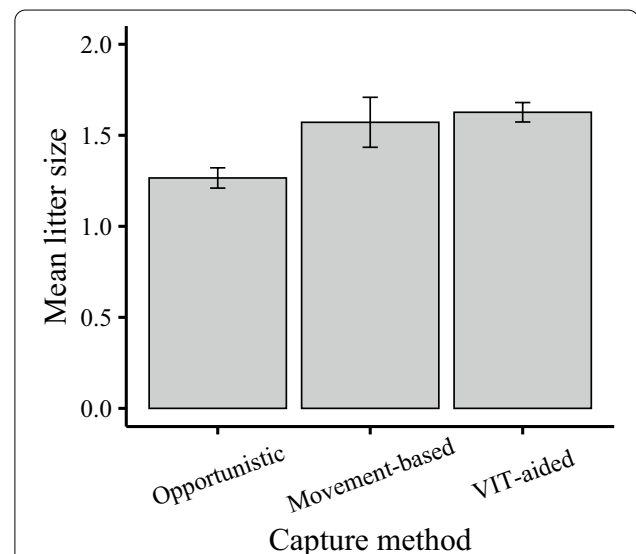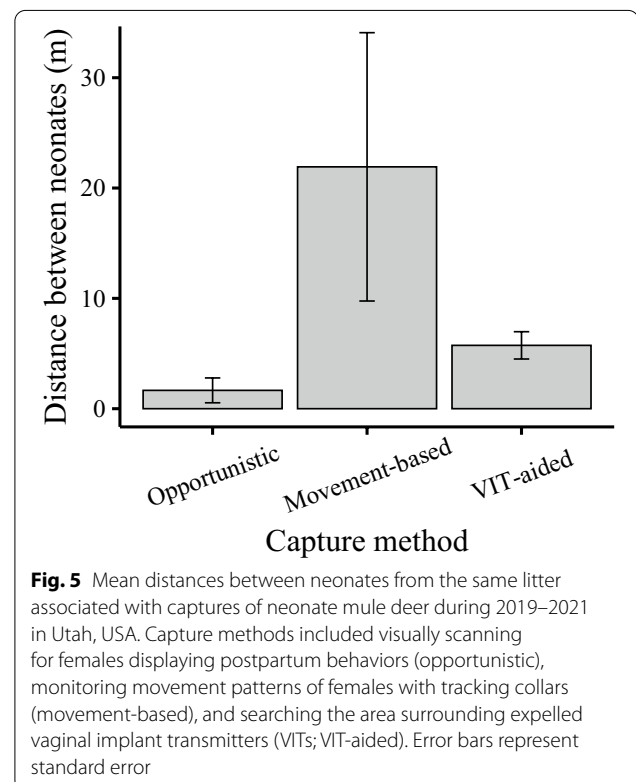

Fig. 2 Estimates of mean litter size derived from captures of neonate mule deer during 2019–2021 in Utah, USA. Capture methods included visually scanning for females displaying postpartum behaviors (opportunistic), monitoring movement patterns of females with tracking collars (movement-based), and searching the area surrounding expelled vaginal implant transmitters (VITs; VIT-aided). Error bars represent standard error

Fig. 3 Probability of detecting > 1 neonate mule deer from the same litter in relation to mean new hoof growth (a proxy for neonate age) once a litter had been detected. The shaded area represents a 95% confidence interval. All litters ($n = 153$) were detected during 2019–2021 in Utah, USA

Fig. 4 Mean new hoof growth per litter (a proxy for neonate age) associated with captures of neonate mule deer during 2019–2021 in Utah, USA. Capture methods included visually scanning for females displaying postpartum behaviors (opportunistic), monitoring movement patterns of females with tracking collars (movement-based), and searching the area surrounding expelled vaginal implant transmitters (VITs; VIT-aided). Bars represent 95% confidence intervals

$R^2c = 0.3$), but was greater than new hoof growth associated with VIT-aided captures ($\beta = -1.1$, SE $= 0.3$, $t_{73} = -4.0$, $P \leq 0.001$, $R^2m = 0.1$, $R^2c = 0.3$). New hoof growth means ($\pm$ SE) associated with opportunistic captures, movement-based captures, and VIT-aided captures were 3.3 ± 0.2 mm, 2.9 ± 0.3 mm, and 1.8 ± 0.2 mm, respectively (Fig. 4). There was no relationship between new hoof growth and distance between neonates from the same litter ($\beta = 2.2$, SE $= 1.3$, $t_{64} = 1.7$, $P = 0.10$). Distances between neonates from the same litter associated with opportunistic captures were shorter than distances associated with movement-based captures ($\beta = 1.4$, SE $= 0.6$, $t_5 = 2.4$, $P = 0.02$, $R^2m = 0.1$, $R^2c = 0.2$), but were not different than distances associated with VIT-aided captures ($\beta = 0.9$, SE $= 0.5$, $t_{43} = 1.9$, $P = 0.06$, $R^2m = 0.1$, $R^2c = 0.2$). Mean ($\pm$ SE) distance between neonates from the same litter associated with opportunistic captures, movement-based captures, and VIT-aided captures was 1.7 ± 1.1 m, 21.9 ± 12.2 m, and 5.7 ± 1.2 m, respectively (Fig. 5).

Discussion

Our results indicate that estimates of litter size derived from opportunistic captures were smaller than estimates of litter size derived from movement-based or VIT-aided captures. Interpretations of estimates of litter size derived from opportunistic captures should not be made without accounting for this bias. While all capture methods likely had some level of detection failure when

Fig. 5 Mean distances between neonates from the same litter associated with captures of neonate mule deer during 2019–2021 in Utah, USA. Capture methods included visually scanning for females displaying postpartum behaviors (opportunistic), monitoring movement patterns of females with tracking collars (movement-based), and searching the area surrounding expelled vaginal implant transmitters (VITs; VIT-aided). Error bars represent standard error

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estimating litter size, opportunistic captures appear to increase the likelihood of detection failure. The only in utero evaluation of mule deer litter size that has occurred in Utah (as far as we are aware) reported a mean litter size of 1.8 for adults ≥ 2 years old [67]. Our estimates of mean litter size derived from movement-based and VIT-aided captures were closer to the previous estimate than our estimate of mean litter size derived from opportunistic captures ($x = 1.6$, 1.6, and 1.3, respectively). Sampling biases associated with opportunistic captures are well recorded, especially when compared to VIT-aided captures [18–23]. Potential sampling biases using movement-based captures, however, are poorly understood. While our study provides one example of movement-based methods minimizing bias when capturing neonate ungulates, our sample size for litters associated with movement-based captures was relatively small ($n = 14$). We present interpretations of our results associated with movement-based captures not as concrete conclusions, but as potential patterns to inspire future research [68]. Movement-based captures may be utilized more often as fine-scale movement data increases in availability and statistical analyses to detect parturition improve [43, 53].

Our investigation into why estimates of litter size were smaller for opportunistic captures revealed that age at capture was an influential factor. As new hoof growth (which served as a proxy for age at capture) increased, the probability of detecting >1 neonate from the same litter decreased. This inverse relationship between age at capture and probability of detection was likely due to a combination of increased neonate mobility and the occurrence of mortality events. The likelihood of capturing neonate mule deer decreases when searches are initiated ≥ 4 days post-parturition, and mean age at capture using opportunistic methods generally ranges between 3 and 7 days [21, 43, 51, 69]. In addition, the age difference between neonates captured using VITs and neonates captured opportunistically is large to enough to result in differential estimates of survival [18, 21–23]. Researchers should keep in mind species-specific precocity and risk of early-life mortality when attempting to estimate litter sizes from other ungulates. Interestingly, new hoof growths associated with opportunistic and movement-based captures did not differ despite opportunistic and movement-based captures producing different estimates of litter size. This result suggests age at capture is not the only factor that influences estimates of litter size, and an additional difference in capture methodology may have even greater influence. An increased awareness of the recent locations of female ungulates may allow for movement-based captures to more effectively locate neonates from the same litter, but more work is required to confirm this suspicion.

We did not find strong evidence supporting the idea that differences in distance between neonates from the same litter resulted in opportunistic captures biasing estimates of litter size. Age at capture was not linked to distance between neonates from the same litter. Distances between neonates from the same litter associated with opportunistic captures were shorter than distances associated with movement-based captures, but were not different than distances associated with VIT-aided captures. However, the increased detection bias associated with opportunistic captures may have influenced our results. Female ungulates often separate neonates soon after parturition [41, 42, 50, 70]. Distance of separation varies, but can be more than 400 m for mule deer [70]. Thus, when performing opportunistic captures we may have failed to detect multiple neonates from the same litter unless neonates were close together. While we attempted to exercise equal effort in all searches, sampling protocols that dictated a standardized search distance may have helped to minimize sampling bias [51, 52]. A relatively standardized search distance for movement-based captures (the area surrounding the female's most recent coordinates) may have resulted in movement-based captures having greater distances between neonates from the same litter.

Conclusions

Capturing neonate mule deer using opportunistic methods results in smaller (and likely less accurate) estimates of litter size compared to movement-based and VIT-aided captures. An increased age at capture appears to be one of the primary reasons why this detection bias exists. As litter size continues to be utilized as an indicator of individual fitness and population trends, researchers should be aware of the biases of using different methods to capture neonate ungulates. We suggest using movement-based or VIT-aided captures to ensure minimal bias when estimating litter size during early-life capture events.

Author contributions
BM, RL, and KH conceived the study design and acquired funding. All authors contributed to data collection. MT, BM, RL, and TH analyzed and interpreted data. MT drafted the manuscript with substantial revisions from all authors. All agreed to be accountable for the accuracy and integrity of the manuscript. All authors read and approved the final manuscript.

Declarations

Ethics approval and consent to participate
All methods were approved by the Institutional Animal Care and Use Committee at Brigham Young University (protocol 19-0202) and followed guidelines from the American Society of Mammalogists [71].

Consent for publication
Not applicable.

Competing interests
The authors declare that they have no competing interests.

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