

FREQUENCY AND CORRELATES OF BIRTH-SITE FIDELITY IN PRONGHORNS (*ANTILOCAPRA AMERICANA*)

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Although a variety of species exhibit birth-site fidelity, examples from ungulate species are rare. We recorded birth-site locations of pronghorns (*Antilocapra americana*) at the National Bison Range in northwestern Montana during 2000–2004 and found that 82% of females changed locations from the previous year. Females that exhibited birth-site fidelity had successfully weaned more fawns and were less likely to have experienced a fawn mortality event in the previous year than females that changed birth sites. Females that weaned a single fawn or weaned 0 fawns were equally likely to change birth sites. There was a year effect on distribution of birth sites as well as on birth-site fidelity. Dry range conditions in 2003 after multiple years of low precipitation may have caused more females to move their birth sites to areas of greater forage availability. The low observed frequency of birth-site fidelity may be a result of high fawn mortality rates at the National Bison Range. Success in the previous year appears to be one of the environmental cues that pronghorn females use to select a birth site.

Key words: *Antilocapra americana*, birth site, neonatal mortality, pronghorn, site fidelity, ungulates

In many mammals, neonatal mortality is high, and the survival of young contributes to the main source of variation in female fitness (Byers 1997a; Clutton-Brock 1991; Gaillard et al. 2000). Especially in mobile mammals, a potentially important contributor to infant survival is the mother's choice of a birth site. Mothers may be highly mobile before they give birth, but afterward they are confined to the birth-site area by the limited mobility of the infant. Thus, to the extent that potential birth sites differ in level of neonatal mortality risk, the behavioral rules that females use to choose birth sites become important targets of selection. One behavioral rule that might identify sites with lower than average neonatal mortality risk would be to show birth-site fidelity after a year when offspring survived and to choose a new birth site after a year when offspring died.

The most general form of site fidelity, or the tendency to return to a previously occupied area, has been reported in at least 3 phyla (Switzer 1993). Fidelity to a specific birth site is common, particularly in nesting birds (Beletsky and Orians 1991; Hepp and Kennamer 1992; see Greenwood [1980] for review), but few examples are known in ungulates. Walther

(1965) categorized ungulate species as hiders or followers according to spatial characteristics of mother–young interactions after birth. Birth-site selection may be more critical in hider species than in follower species because hider neonates typically stay in a restricted area after birth until the period of hiding ends (Lent 1974; Walther 1965).

Birth-site fidelity was reported in several studies of hider species (e.g., white-tailed deer [*Odocoileus virginianus*]—Nixon et al. 1992; Ozoga et al. 1982; and moose [*Alces alces*]—Baskin 1987; Testa et al. 2000; Welch et al. 2000). Einarsen (1948) suggested that pronghorns (*Antilocapra americana*) return to traditional fawning areas unless dry conditions prompt females to move to areas of better forage quality. Autenrieth (1976) disagreed, but did not examine birth-site fidelity at the level of individual females.

A variety of factors may affect a female's birth-site selection. Variation in forage quality could lead individuals to select sites with the high resource levels necessary during late gestation and lactation. Alternatively, females might choose to reduce predation risk to offspring by selecting sites with lower predator concentrations or sites with increased defensibility or ability to effectively conceal a neonate. Female ungulates with dependent young may make trade-offs between forage availability and reduced predation risk, so choice of birth site may similarly reflect a balance between multiple factors (Berger 1991; Bergerud 1985; Bowyer et al. 1999; Rachlow and Bowyer 1998; Schwede et al. 1993). Instead of, or in addition

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to, directly assessing current environmental factors, females may use their own reproductive success at a particular location as an estimator of birth-site quality. Multiple studies have reported correlations between reproductive success and subsequent birth-site fidelity, primarily in birds (Freer 1979; Hepp and Kenamer 1992; Payne and Payne 1993; Switzer 1997). Evidence for such a decision rule in ungulates is mixed. Moose move subsequent birth sites further from previous sites after loss of their calves (Testa et al. 2000; Welch et al. 2000). In contrast, choice of lambing location by bighorn sheep (*Ovis canadensis*) does not appear to be influenced by lamb mortality at a previous site (Hass 1989). One possibility for this difference is that unlike moose, sheep neonates are followers (Geist 1971; Lent 1974) and thus are less confined to the birth site.

Pronghorns at the National Bison Range (NBR) in Moiese, Montana, appear to be highly variable in their choice of birth-site locations, and individual females may exhibit birth-site fidelity during some years and not during other years. Females do not defend territories, and they range across the entire refuge throughout the year. We investigated whether pronghorn females practiced birth-site fidelity and with what frequency, and what factors might be associated with fidelity to a particular birth site. Because twinning rates at the NBR are virtually 100% (Byers 1997a), we could compare the effects of weaning 0, 1, or 2 fawns on a female's subsequent birth-site fidelity, and consider separately the effects of individual fawn survival and mortality events. We used observational data to examine whether the number of fawns weaned, maternal age, or precipitation in the previous year predicted birth-site fidelity, testing the hypothesis that females use a win-stay, lose-switch tactic when choosing a birth site.

MATERIALS AND METHODS

Study site.—We collected birth-site and fawn-survivorship data as part of a long-term population study of pronghorns at the NBR, a 7,504-ha National Wildlife Refuge located in northwestern Montana (47°20'N, 114°15'W). The NBR is bounded by a 2.5-m perimeter fence that prevents migration of ungulates. Pronghorn habitat at the NBR is characterized by rolling hills dominated by Palouse prairie, a shortgrass plant community with abundant forbs. Pronghorns range over the entire refuge throughout the year, and are able to cross under internal fences.

During the years of this study (2000–2004) the pronghorn population ranged from 50 to 120 individuals. All pronghorns on the NBR were individually identifiable, either through colored and numbered ear tags, or by individual horn and pelage characteristics. Although the NBR population is essentially closed, there is no evidence of inbreeding depression (Byers 1997a). All females at the NBR conceive at 18 months, with twinning rates of nearly 100%, and birth weights and postnatal growth rates are greater than those recorded in captive pronghorns (Byers 1997a). From 1981 to 2004 we observed 2 mal-formed, stillborn fawns and approximately 3 fawns that became listless and disoriented in the week after birth out of approximately 300 observed births and 2,400 observed neonates. All other mortalities involved the abrupt disappearance of a vigorous fawn, consistent with death caused by a predator. Byers (1997b) reported a close correlation between the yearly number of management removals of coyotes from the NBR in spring and the yearly percentage of fawns that survived to

weaning. During 1981–1996, annual fawn mortality varied from 52% to 99%; these values are higher than those recorded in most other pronghorn populations (Byers 1997b). We defined fawn mortality as death before October of the 1st year of life, which typically coincides with the end of the weaning period. Known predators of pronghorn fawns on the NBR include coyotes (*Canis latrans*) and golden eagles (*Aquila chrysaetos*—Byers 1997a). Byers (1997a) gives a more complete description of the study site and population. Because July–October precipitation is likely the main source of variation in yearly energy budgets of ungulates at the NBR (Byers and Hogg 1995), we obtained precipitation data for those months collected by the National Oceanic and Atmospheric Administration weather station in St. Ignatius, Montana (47°18'N, 114°05'W).

Behavior of mothers.—Females occur in social groups except when individuals become solitary shortly before giving birth. Each female seeks an isolated location and remains there until giving birth. She then stays in that area until the fawns die or, if 1 or both fawns survive, for approximately the next 20 days until the fawns become large enough to move into a nursery group (Byers 1997a). Pronghorns are classic hider species, with young fawns spending the majority of time lying motionless. After birth and after every nursing session, the mother leads the fawns some distance and then stands while the fawns select a new hiding place. Typically, the mother and fawns remain in a circumscribed area for the first 10 days, with an average distance between fawn beds of 103 m (range 0–400 m—Byers and Byers 1983). However, mothers occasionally move a single remaining fawn as far as 1 km after predation of the other fawn (Byers 1997a). Because the area occupied by mother and neonates is not static and may change considerably over several days, we use the term “birth site” to refer to the restricted area occupied by a mother and fawns during the first 10 days after birth.

Data collection.—Each spring, in preparation for the capture and ear-tagging of fawns, we surveyed females daily and assessed their pregnancy status. We recorded a birth-site location when we observed a female in labor or when we captured a fawn within 3 days of its birth. We obtained fawn ages either by observing the mother in labor, or by estimating age in days from behavioral criteria, condition of pelage, and from presence and degree of desiccation of the umbilicus (Von Gunten 1978). There was no evidence that females moved fawns in response to human capture, and, in all study years, nearly all females experienced human capture of their fawns. For each female, the location where we 1st observed her fawns was marked on a map of the NBR showing all refuge roads, internal fences, drainages, as well as most peaks and ridges. Map scale was 1:51000 and with the use of these landmarks allowed mapping of the birth site to within 200 m. Later, we entered each location into ArcView GIS version 3.2 (ESRI, Redlands, California) and calculated distances between successive birth sites using the Animal Movement extension (Hooge et al. 1999). Because we located consecutive birth sites in more than 1 instance for some females, these individuals were represented in multiple years. We classified birth-site fidelity when a female used a birth site < 1 km from the site used in the previous year. Welch et al. (2000) described moose returning to calve at sites < 1 km distant in subsequent years as highly site-faithful. Additionally, previous observation of pronghorns at the NBR suggests that, although it is possible, it is unusual for females to move with young fawns more than 1 km in the first 3 days postpartum (Byers 1997a). To investigate whether birth sites were distributed across the NBR in a similar manner annually, we divided the NBR into quadrants and compared the proportions of birth sites located within each area across all years (Fig. 1). During the autumn rut we conducted daily surveys of the population and recorded the individual identity of all living fawns. All aspects of our research were

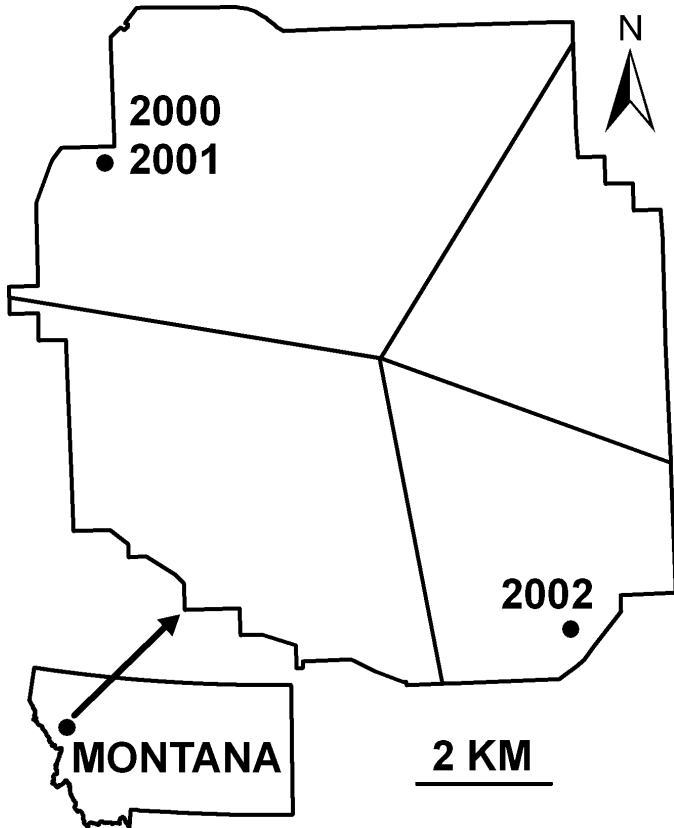


FIG. 1.—Boundary outline of the National Bison Range Wildlife Refuge showing quadrants used for comparison of birth-site distribution across years. Black circles identify the birth sites used by female A in 3 consecutive years and dates next to each circle indicate the year of use. This female exhibited birth-site fidelity during 2000–2001, but not during 2001–2002.

approved by the Institutional Animal Care and Use Committee at the University of Idaho and followed guidelines established by the American Society of Mammalogists (Animal Care and Use Committee 1998).

Statistical analyses.—We performed 2-tailed Wilcoxon rank sum tests to compare mean number of fawns weaned, fawn mortality, fawn survival, maternal age, and July–October precipitation between instances when a female stayed at the same birth site and when a female changed birth sites in the subsequent year.

To distinguish between females that weaned a single fawn and those that weaned twins, we created the variable Fawn Mortality, where $Fawn\ Mortality_{(twins\ weaned)} = 0$ and $Fawn\ Mortality_{(1\ or\ 0\ fawns\ weaned)} = 1$. Similarly, we created the variable Fawn Survival, where $Fawn\ Survival_{(0\ fawns\ weaned)} = 0$ and $Fawn\ Survival_{(1\ or\ 2\ fawns\ weaned)} = 1$. We performed bivariate logistic regressions with fidelity as the binary dependent variable and either number of fawns weaned in the previous year (0, 1, or 2), Fawn Mortality, Fawn Survival, July–October precipitation, maternal age, or birth year as the independent variable. Because birth year was categorical, we coded dummy variables for use in logistic regression. We also performed multiple logistic regression with a stepwise selection procedure, which initially considered number of fawns weaned in the previous year, July–October precipitation, maternal age, and birth year as independent variables, and used significance levels of 0.1 for entry into the model and 0.05 to stay. We calculated Hosmer–Lemeshow statistics to test goodness-of-fit for

TABLE 1.—Observed frequency of birth-site fidelity in a subsequent year by pronghorn females on the National Bison Range Wildlife Refuge, Montana, during 2000–2003.

| Year ^a | n | Females returning | | Females changing | |
|-------------------|----|-------------------|------------|------------------|------------|
| | | Number | Percentage | Number | Percentage |
| 2000 | 20 | 4 | 20 | 16 | 80 |
| 2001 | 29 | 5 | 17 | 24 | 83 |
| 2002 | 35 | 4 | 11 | 31 | 89 |
| 2003 | 10 | 4 | 40 | 6 | 60 |
| Total | 94 | 17 | 18 | 77 | 82 |

^a No association was found between fidelity and year ($\chi^2 = 4.35, P = 0.23$).

all logistic regressions and only accepted models with significance levels > 0.1 , indicating no significant deviation from a logistic fit.

We performed chi-square tests to compare the proportion of females that stayed and changed birth sites across years and to compare distribution of birth sites within 4 areas of the NBR across years. Probability values that were ≤ 0.05 were considered significant. We present values as means $\pm SE$. We performed all statistical analyses using SAS/STAT version 9.1 (SAS Institute Inc. 2002).

RESULTS

We collected birth-site location, October fawn survival, and birth-site location in the subsequent year in 94 instances, representing 59 different females during the 2000–2004 fawning seasons (Table 1). Total fawn mortality for the population averaged 0.87 ± 0.03 (range 0.77–0.92) during the years of this study. In all years, number of females that changed birth sites between years was greater than number of females that gave birth in the same site in 2 successive years. The proportions of females that either stayed or changed birth sites did not differ across all years (Table 1). Females were variable with respect to birth-site fidelity, with distances between consecutive birth sites ranging from < 100 m to > 10 km. We recorded birth-site locations in > 2 years for 26 females, and of these 7 exhibited the same fidelity tactic each year (always stayed or always changed), and 19 exhibited both tactics across years (sometimes stayed and sometimes changed).

Females that used the same birth site in the subsequent year had lower values of Fawn Mortality in the previous year than those that changed birth sites ($Z = -2.49, P = 0.01$), indicating that females that lost 1 or both fawns were more likely to give birth in a different location in the following year. The 2 groups of females did not differ significantly with respect to number of fawns weaned in the previous year, Fawn Survival, maternal age, or July–October precipitation (all $P > 0.1$; Table 2). Bivariate logistic regressions with birth-site fidelity and each independent variable indicated that fidelity was negatively correlated with Fawn Mortality ($\chi^2 = 4.67, P = 0.03$), and weakly correlated with number of fawns weaned ($\chi^2 = 3.52, P = 0.06$). Birth year, maternal age, July–October precipitation, and Fawn Survival were not correlated with fidelity (all $P > 0.1$).

The multiple logistic regression model resulting from a stepwise selection procedure found that birth-site fidelity was

TABLE 2.—Fawn survival variables, maternal age, and summer precipitation in year 1 for females that used the same birth site (stayed) or used a different birth site (changed) in year 2 during 2000–2003. Sample sizes are reported as number of females, including some multiple-year records from a few individual females.

| | Stayed | | Changed | |
|--------------------------------------|----------|------------------|----------|------------------|
| | <i>n</i> | $\bar{X} \pm SE$ | <i>n</i> | $\bar{X} \pm SE$ |
| Number of fawns weaned (0, 1, or 2) | 17 | 0.65 \pm 0.24 | 77 | 0.34 \pm 0.30 |
| Fawn Mortality (0 or 1) ^a | 17 | 0.82 \pm 0.10 | 77 | 0.97 \pm 0.18 |
| Fawn Survival (0 or 1) | 17 | 0.47 \pm 0.13 | 77 | 0.31 \pm 0.05 |
| Maternal age (years) | 15 | 3.73 \pm 0.38 | 66 | 4.38 \pm 0.22 |
| July–October precipitation (cm) | 17 | 9.33 \pm 0.89 | 77 | 9.51 \pm 0.36 |

^a A significant difference was found between groups ($Z = -2.49$, $P = 0.01$).

significantly predicted by number of fawns weaned ($\chi^2 = 6.91$, $P < 0.01$) and the birth year dummy variable comparing 2000 to 2003 ($\chi^2 = 7.72$, $P < 0.01$). Maternal age and July–October precipitation did not meet the significance level of $P \leq 0.1$ needed for model entry.

We found a significant year effect on the overall distribution of birth sites among the 4 regions of the NBR. Because of dry conditions in 2003, females were in extremely poor condition and after a large winter die-off, unusually few gave birth in 2004 (Byers et al. 2005). Performing a chi-square analysis including the 10 birth sites recorded in 2004 resulted in expected cell counts of < 5 , so we also performed the chi-square analysis without the 2004 sample. Both methods showed significant association between year and distribution of birth sites ($\chi^2 = 30.98$, $P < 0.01$ for all years; $\chi^2 = 21.65$, $P = 0.01$ for 2000–2003 only).

DISCUSSION

Female pronghorns exhibited low levels of birth-site fidelity overall, with 18% returning each year to the same birth site they used the previous year and 82% moving to a new birth site. This was slightly lower than the 25% of moose that used sites < 1 km apart in subsequent years (Welch et al. 2000). Although the overall proportion of females choosing to stay or move did not change each year, the identity of females practicing each tactic did change. Some females kept the same tactic, whereas other females used different tactics over consecutive years. The number of fawns weaned was positively correlated with subsequent birth-site fidelity, and more specifically, any fawn mortality was negatively correlated with fidelity. A fawn survival event in itself did not affect the likelihood of subsequent birth-site fidelity.

Most arguments for the selection of birth sites in ungulates invoke trade-offs between nutritional requirements of the mother and the need to lower predation risks (Berger 1991; Rachlow and Bowyer 1998). Patterns of fidelity in pronghorns might result from females tracking habitat parameters that vary annually. This is supported by our finding that females did not distribute their birth sites equally across the NBR each year, perhaps due in part to females taking advantage of temporal variation in forage quality or predation risk. Although NBR

pronghorns appear to maintain a high nutritional plane with maximal reproductive output (Byers 1997a), annual changes in habitat quality may result from variation in precipitation as well as distribution of American bison (*Bison bison*). The NBR maintains a bison herd of about 400–500 individuals that is rotated periodically between 5 internal rangeland units to minimize potential for overgrazing. Unfortunately, we did not have sufficiently detailed data on bison distribution to test for a possible effect on pronghorn birth-site selection. In a multiple regression model, year was a factor in predicting birth-site fidelity, specifically the dummy variable comparison between the years 2000 and 2003. This was not surprising, given the poor condition of females and the unusual adult mortality in 2003. These results likely reflect the dry range conditions in 2003 after multiple years of low July–October precipitation, which may have resulted in the high frequency (89%) of females that changed birth sites in 2004, possibly to areas of higher forage quality.

Although environmental variables such as forage availability and bison distribution can affect habitat quality, females may be choosing birth sites based on assessment of predation risk. Fawn mortality on the NBR is largely due to predation, and previous work has shown significant increases in recruitment after spring coyote removals (Byers 1997b; Corneli et al. 1984). We did not survey predators during our study, but predator concentration in itself is not the only factor affecting predation risk to fawns. The characteristics of a particular birth site may alter predation risk, with certain locations such as ridgetops allowing better detection of predators and defense of fawns (Byers 1997a). Indeed, we observed that some birth sites were used repeatedly by pronghorn females each year, although not necessarily the same individuals.

Switzer (1993) argued that animals adopting a “win–stay, lose–switch” decision rule will remain on the previous territory if the previous outcome was good and will change territories if the previous outcome was bad, regardless of the quality of alternate territories. However, as predictability decreases, previous outcome becomes less relevant to subsequent settlement, and the rule does not perform well in predictable habitats if a higher-quality option is available (Switzer 1993). Changes in predator distribution and concentration may cause a female to leave a previously successful birth site. The NBR may support an unnaturally elevated concentration of predators during fawning season because the external boundary fence restricts the movement of pronghorns but not of coyotes, who are able to dig under the fence. The high numbers of ungulate young born each spring, including white-tailed deer, mule deer (*Odocoileus hemionus*), elk (*Cervus elaphus*), and bighorn sheep, likely provide a significant enticement for coyotes, even those that may spend the rest of the year off the refuge (Byers 1997a). Increased dispersal of birth sites has been suggested as a strategy to avoid predators (Berger 1991; Bergerud et al. 1984), and random distribution of birth sites within suitable habitat may be a strategy to reduce the information available for predators to focus their hunting on previous birth-site areas (Bowyer et al. 1999). Because pronghorns at the NBR are unable to disperse past the refuge boundaries, behaving

unpredictably at the level of the landscape may be a tactic to reduce fawn mortality.

Although fawn mortality events were negatively correlated with fidelity (i.e., mothers that raised twins were more likely to exhibit birth-site fidelity), 2 of 5 mothers with surviving twins changed birth sites in the subsequent year. In 2002, we observed an adult coyote on the ridge where one such female gave birth and coyote pups actively using a den on the far side of the ridge approximately 1 km from her birth site. This female successfully raised twins in 2002 but changed birth sites in 2003. This might have been a reflection of her experience with coyotes in that area, and, although she successfully weaned twins, she chose a distant location in the following year to avoid an area where she had experienced high coyote activity in the previous year.

Whether site changes by females that successfully raised twins indicate change in environmental conditions or simply represent a random stay-move female site-fidelity strategy is unclear. Testa et al. (2000) reported that female moose moved greater distances between consecutive birth sites after calf mortality than did females with surviving calves, but only distinguished between females with 1 or 2 calves and females with no calves. Because NBR pronghorns have twins each year, we were able to partition between effects of 0, 1, or 2 fawn mortality events. Pronghorn females appeared to be sensitive to any fawn mortality events, and were equally likely to change birth site in the subsequent year if 1 or both fawns died. Our findings illustrate the complexity of birth-site selection and fidelity in pronghorns and suggest the need for further study of other populations. Of particular interest is whether pronghorns subjected to lower levels of fawn mortality would exhibit higher frequencies of birth-site fidelity.

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