Habitat selection and survival of pronghorn fawns at the Carrizo Plain National Monument, California

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On the Carrizo Plain National Monument (CPNM), California, little is known about survival rates and habitat characteristics of pronghorn fawns (Antilocapra americana). A marked decline in pronghorn numbers on the CPNM (from approximately 200 to <30 individuals from 1989 to 2011) prompted a study of fawn habitat use and fawn survival from 2009 to 2011. Only 45 fawns were born during this period. We attached GPS collars to 44% of these fawns (<5 days-of-age). We then used the locations of collared fawns to develop two separate binary logistic regression models to explore the best combination of micro- and macrohabitat-scale environmental variables for predicting (1) fawn habitat selection and (2) fawn survival. Model results for habitat selection showed that fawn locations were associated with increased concealment at close distances (5 m and 50 m) and decreased concealment at far distances (100 m). Fawn locations were on lower sloped terrain and closer to available drinking water and saltbush (Atriplex spp.). Model results for fawn survival showed that increased survival time was associated with higher sloped terrain, proximity to available drinking water and saltbush, and increased distance from high-use roads. Collectively, these results demonstrate that fawn habitat selection is scale-dependent and likely influenced by the combined spatio-temporal needs of both females and their young. The results of this study can be used to inform critical management actions on the CPNM.

Key words: Antilocapra americana, California, Carrizo Plain, fawn, habitat, offspring, pronghorn, recruitment, selection, survival

Pronghorn (Antilocapra americana) in California’s San Joaquin Valley were once abundant, representing one of the highest densities in the country prior to the 1800s (Newberry
1855, cited in Yoakum 2004b; Pyshora 1977). By the 1940s however, overhunting, disease, competition from livestock, and conversion of native grasslands to croplands and non-native plant assemblages had triggered a demographic collapse and pronghorn became extirpated from the region (CDFG 1982, Koch and Yoakum 2002). As part of an effort to reintroduce the species to portions of its historic range, the California Department of Fish and Game (now Wildlife; CDFW) translocated over 200 individuals in 1987, 1988, and 1990 from northeastern California to areas within and surrounding what is now the Carrizo Plain National Monument (CPNM). Initially, the translocated population increased but, following a period of prolonged drought, numbers began to fluctuate and eventually declined (Koch and Yoakum 2002, Sommer 2012). By 2012, it was estimated that fewer than 30 individuals occupied the CPNM. Small, isolated populations such as this are of particular concern to resource managers because of increased vulnerability to localized extinction.

Extinction risk is amplified for low-density populations if annual rates of recruitment are not sufficient to overcome the compounding effects associated with demographic or environmental stochasticity (Courchamp et al. 2008). For pronghorn, annual reproductive output (the number of offspring produced per adult female per year) is typically consistent, but survival of juveniles is far lower and more variable than survival of adults (Vriend and Barrett 1978, Gaillard et al. 2000, Eberhardt 2002), causing high annual variation in recruitment (Kohlman 2004). For pronghorn fawns <45 days-of-age, predation is commonly cited as a primary mortality factor (Byers 1997b, O’Gara and Shaw 2004). However, the effect of predation on recruitment has been shown to covary with habitat quality, whereby predation of fawns is high when environmental conditions are poor (Kohlman 2004). Marginal or sub-marginal habitats tend to produce costs to fitness, such as low offspring survival, which cause population size to become unstable or to decline (Vriend and Barrett 1978). On the CPNM, prior research indicated that habitat conditions for pronghorn are moderate to poor due, in particular, to low shrub cover (Longshore and Lowrey 2008).

Pronghorn fawns exhibit hiding behavior to avoid detection by predators (Byers 1997b, Yoakum 2004a). It is generally understood that fawns select individual bed-sites within a larger fawning area pre-selected by adult females (Yoakum 2004a). While the success of fawn hiding behavior is dependent upon the availability of vegetative and topographic concealment (Alldredge et al. 1991, Canon and Bryant 1997), adult females require open, relatively flat landscapes (<10% slope) with low vegetation height for long-range visibility and detection of predators (Ockenfels and Wennerlund 1994), as well as high-quality forage conditions during lactation (Yoakum 2004c). Accordingly, contrasting habitat requirements for fawns and females must be met simultaneously and at different spatial scales. At the micro-habitat scale, selection is based on the hiding requirements of fawns. At the macro-habitat scale, selection is dependent on the visibility and dietary requirements of females balanced with the needs of their offspring.

Pronghorn on the CPNM are at risk of extirpation and adequate rates of recruitment are necessary to prevent further decline. A conservation strategy that aims to reverse that downward trend requires site-specific knowledge of the factors influencing fawn survival, information that has been largely unavailable for this population. Here, we use Global Positioning System (GPS) collars to investigate how pronghorn fawns on the CPNM select specific environmental features at variable spatial scales, and how that selection influences fawn survival. Results from this study can be used to inform management actions on the CPNM and surrounding region.
Materials and Methods

Study area.—The Carrizo Plain National Monument is located within the coast range in southeastern San Luis Obispo County, California (Goodwin Education Center: 35° 11’ 24” N, 119° 51’ 48” W). The monument contains one of the largest remnants of the San Joaquin Valley grassland ecosystem (Schiffman 2000), encompassing 102,639 hectares co-managed by CDFW, Bureau of Land Management (BLM) and The Nature Conservancy (TNC). Topography within the monument is primarily a broad plain bordered by two mountain ranges: the Temblor Range along the northeast border and the Caliente Range along the southwest border. Elevation along the valley floor averages 615 m, and the highest elevation is Caliente Peak (1,556 m). Annual precipitation occurs primarily between December and April and can be highly variable among years (\( \bar{x} = 24.56 \) cm, \( SE = 2.31 \) cm). During this study, annual precipitation was 17.58 cm in 2009, 48.39 cm in 2010 and 23.52 cm in 2011. Runoff from rainfall sustains the ephemeral Soda Lake, a shallow, alkali terminal lake in the center of the valley floor (Penrod et al. 2010). Mean minimum daily temperature ranges between 5°C and 24°C.

Historically, the area was used for dry-land wheat farming. While most farming activities have ceased, some livestock grazing continues. Due to past agricultural practices, much of the grassland habitat on the CPNM is now dominated by non-native annual grasses, notably brome (Bromus spp.) and wild oats (Avena spp.). Alkali sink vegetation, including spiny saltbush (Atriplex spinifera) and iodine bush (Allenrolfea occidentalis), is found at the lowest elevations. Juniper-oak, cismontane woodland, and cismontane juniper woodland and scrub are found in the higher elevations. For a more detailed description of vegetation on the CPNM refer to Stout et al. (2013).

Fawn capture and monitoring.—Fawns were captured using methods described by O’Gara et al. (2004) and Gregg et al. (2001) in accordance with safe handling guidelines (Sikes et al. 2011). Pronghorn fawns (\( \leq 5 \) days-of-age) were outfitted with GPS collars each year during April and May of 2009–2011. Collars were designed to be lightweight (\( \leq 120 \) g), to expand comfortably as fawns developed in size (i.e., the use of Velcro in place of traditional threaded stitching), and to detach at approximately 90 days-of-age (i.e., neck circumference = 30 cm; O’Gara 2004). For fawns whose birth was not observed, birth date was estimated by behavioral criteria, condition of pelage, hoof and dental development, and desiccation of the umbilical cord (see O’Gara et al. 2004).

All pronghorn fawns known to occur on the CPNM (both collared and uncollared) were monitored daily. Individual collared fawns were identified by their unique VHF telemetry signal. The propensity of neonatal siblings to bed together allowed for observation of uncollared fawns when siblings were collared. We further used individual pelage characteristics of the mother (Byers 1997a) and location of the general fawning area as identifying characteristics for uncollared fawns. Fawns that lived >90 days were considered to have been recruited into the population based on abundant evidence that 95% of fawn mortality takes place at <18 days-of-age (Gregg et al. 2001). Results for survival rates were compared to 18 other studies conducted within 10 different states as reported by O’Gara and Shaw (2004). Deceased fawns were recovered as quickly as possible to determine whether death was due to predation and, if so, to identify the species of predator according to the criteria of O’Gara and Shaw (2004). Carcasses found to be in good condition (i.e., fresh and intact) were transported to the CDFW Wildlife Investigations Laboratory for necropsy.
Statistical analyses.—Location information from collared individuals was used to develop a fawn habitat selection model and a fawn survival model. We used a combination of biotic and abiotic environmental parameters within an Akaike Information Criterion (AIC) modified for small sample size (AICc) and logistic regression framework to predict habitat selection and survival (Hosmer and Lemeshow 2000, Burnham and Anderson 2002). We selected model parameters based on a comprehensive review by Yoakum (2004a) that listed critical criteria for fawning areas including vegetation height and type, physiography (Einarsen 1948), availability of nutritious forage (Ellis 1970), vegetative cover (Autenrieth 1984), lack of fences (O’Gara et al. 1986), proximity to available water (Ockenfels et al. 1992), and minimal anthropogenic disturbance (U.S. Fish and Wildlife Service 1994). The log-likelihood estimates from each of the alternative logistic regression models were used to rank the set of candidate models. We eliminated models with ΔAICc of >2, and used Akaike weights (wi) and evidence ratios to assess the relative strength of evidence for each remaining model (Burnham and Anderson 2002). Statistical analyses were performed using SigmaPlot 12.3 and Geographical Information System (GIS) analyses were conducted using ArcMap 10.1 (ESRI, Inc. Redlands, California).

For the fawn habitat selection model, we compared the relationship of collared fawn locations and random locations to a suite of micro- and macrohabitat explanatory variables. We considered microhabitat characteristics to be located within a spatial scale small enough to elicit a response by individual fawns. Microhabitat was defined exclusively as the area within a 100-m radius of a fawn and included measurements of vegetation height and composition (i.e., forb, grass, shrub, bare ground), as well as adult and fawn visibility, at 70 fawn locations and 61 random locations. Measurements were made at each location and along four equidistant transects at distances of 5 m, 10 m, 20 m, 30 m, 40 m, 50 m, and 100 m. Transects were oriented by randomly selecting an aspect for one transect and then distributing the remaining three transects by a separation of 90 degrees (modified from Canon and Bryant 1997). Visibility was defined as the proportion of a 1-m measuring stick (located at the center of each plot) visible from each of the measured locations at the height of a fawn (0.5 m) and an adult (1 m).

Macrohabitat characteristics were defined as landscape-scale features that could potentially influence female habitat selection but not necessarily fawn habitat selection. Macrohabitat predictors were measured with a GIS at 30-meter resolution and included percent slope of terrain (vertical distance/horizontal distance) and linear distances to water, fences, saltbush (Atriplex spp.), high-use primary roads (Soda Lake Rd., Panorama Rd., Selby Rd., and Elkhorn Rd.), and all roads (i.e., high-use primary roads and low-use roads combined). Open drinking water for pronghorn on the CPNM is found primarily at man-made water sources (e.g., water troughs). We located all known water sources using a data layer provided by CDFW and then inventoried each of them for the availability of water (i.e., active or inactive). We did not consider Soda Lake or ephemeral drainages as sources of water for pronghorn. Human activity on the CPNM occurs primarily along roads, which we used as the best available measure of anthropogenic disturbance. Data layers for saltbush, roads and fences were provided by the BLM.

For the fawn survival model we compared the relationship between locations of collared fawns ≤17 and >17 days-of-age and a suite of macrohabitat features including linear distances to water, fences, saltbush, high-use primary roads, and all roads combined (i.e., high-use primary roads and low-use roads), as well as the slope of terrain. We did not include microhabitat features (i.e., vegetation height and type, or visibility) in the fawn
survival model and, instead, used a subset of covariates to increase parsimony and prevent overfitting the model. We predicted fawns >17 days-of-age would have a higher expectancy for survival than fawns ≤17 days of age, and that habitat selection by fawns in these two groups would vary, based on information from Gregg et al. (2001) that the majority (95%) of fawn mortalities take place among fawns ≤17 days-of-age, as well as corresponding evidence from our survival data (see Results).

**Results**

*Fawn productivity and survival.*—In total, 45 pronghorn fawns were known to have been born on the CPNM during three seasons from 2009 to 2011. The number of fawns recruited out of the total born each season was 3 of 22 (14%) in 2009, 5 of 12 (42%) in 2010, and 4 of 11 (36%) in 2011. Collars were attached to 20 of 45 fawns (44%; 7 males and 13 females) born during the study (13 fawns in 2009, 4 fawns in 2010, 3 fawns in 2011). Mean age at capture was 2.07 days (SE = 0.33). Survival between male and female collared fawns did not differ (Z = -0.32, P = 0.75). The remaining 25 uncollared fawns were monitored through systematic field observation (see description in Methods). Survivorship of collared fawns (20.0%) and uncollared fawns (32%) did not differ (Z = -0.25, P = 0.81). Survivorship of all fawns (both collared and uncollared; 26.7%) did not differ from that found for other populations (29.4%, N = 995) as reported by O’Gara and Shaw (2004) (Z = 0.22, P = 0.82). Annual fawn productivity and survival were variable across years (mean productivity = 15.0 fawns, SE = 3.5 and mean survival = 30.7%, SE = 8.5). Of 13 recovered collars, 10 functioned properly while deployed (i.e., they consistently recorded locations); of these 10 functioning collars, 9 were from deceased fawns. The mean number of days lived for the 9 collared fawns that died was 14.4 days (SE = 2.9) and all but one of these fawns died at ≤18 days of age.

Causes of mortality for the 20 collared fawns and 1 uncollared fawn included predation (28.6%; n = 6), health-related issues (9.5%; n = 2) and undetermined causes (61.9%; n = 13). For the 6 predator-related mortalities, evidence of coyote (n = 6) or golden eagle (n = 1) was detected. Results from laboratory necropsies performed for the two health-related mortalities indicated that death was caused by an infected umbilical cord for one individual, and a lacerated liver (possibly from being stepped on by its mother) for the other.

*Fawn habitat selection model.*—To model fawn habitat selection, eight candidate models were developed using 70 locations from collared individuals and 61 random locations (Table 1). The habitat parameters used in the global model are indicated at the bottom of Table 1. Two candidate models, Model 1 (w_i = 0.56) and Model 2 (w_i = 0.36), showed substantial support as the best approximating models (ΔAIC_c <2). Parameter estimates (β), standard errors (SE) of the estimates, odds ratios, and 95% confidence intervals (CI) for the odds ratios of the variables in the two models are shown in Table 2. Model 1 showed that fawn locations were negatively associated with increased vegetation height at 5 m, fawn visibility at 50 m, slope of terrain, and distance to saltbush and water, yet positively associated with increased forb composition and fawn visibility at 100 m. Model 2 consisted of the same parameters and respective negative and positive associations as Model 1 for all variables excluding forb composition and fawn visibility at 50 m. A generalized map of fawn habitat selection within the CPNM (Figure 1) was created using Model 1 and Model 2 variables that could be measured with standard GIS layers (i.e., slope of terrain and distance to water and saltbush).
Fawn survival model.—To model fawn survival, six candidate models were developed (Table 3) using 1,417 locations from 10 GPS-collared individuals. Two candidate models, Model 1 (\(w_i = 0.55\)) and Model 2 (global model; \(w_i = 0.32\)), showed support as the best approximating models (\(\Delta AIC < 2\)). Parameter estimates (\(\beta\)), standard errors (SE) of the estimates, odds ratios, and 95% confidence intervals (CI) for the odds ratios of the variables in the two models are shown in Table 4. Model 1 showed that locations of individuals that lived >17 days were positively associated with increased slope and distance to main roads, but were negatively associated with increased distance to water, fences, and all roads. Model 2, in addition to the same parameters and respective positive or negative associations as
Model 1, showed a negative association with distance to saltbush. A generalized map of fawn survival within the CPNM (Figure 2) was created using Model 1 and Model 2 (the global model) variables that could be measured with standard GIS layers (e.g., slope of terrain and distance to water, saltbush, and all roads).

**Discussion**

**Fawn productivity and survival.**—Pronghorn fawn survivorship on the CPNM, overall, did not differ from that reported for other populations across the geographic distribution of pronghorn based on the results of O’Gara and Shaw (2004). However, variability in offspring productivity and survivorship was observed during 2009–2011 and only three to five fawns survived during any one season. Pronghorn commonly exhibit high variability in annual recruitment (Vriend and Barrett 1978, Kohlmann 2004), and years of low offspring survival generally do not impact long-term demographics of large populations. For small or sparse populations, however, low annual recruitment, particularly during consecutive years, increases extinction risk (Courchamp et al. 2008). Increased rates of fawn survival are likely required to sustain a viable population of pronghorn at this site and management actions that increase recruitment could reduce the risk of localized extinction.

Of the four primary mortality factors (predation, starvation, exposure, disease) described by O’Gara and Shaw (2004), we detected evidence only of predation. Although predation is not generally considered to drive pronghorn population dynamics, the importance
of predation increases for static or declining populations, as well as for populations occupying marginal habitats or areas where the number of predators is high in relation to the number of pronghorn (Lee et al. 1998, O’Gara and Shaw 2004). In addition, the abundance of alternative prey (e.g., lagomorphs, rodents) can alleviate predation on pronghorn fawns (Beale 1986). Mortalities related to health (infected umbilical cord and lacerated liver) appeared to be separate and unrelated events. Due to the high percentage of unknown mortality (65%), meaningful comparisons between predation on the CPNM (29%) and predation on other populations (53%; O’Gara and Shaw 2004) were not possible. The high number of undetermined causes of death was due primarily to technical malfunctions of VHF telemetry signals, which were often weak or non-existent. Poor signal quality delayed the time in which deceased fawns could be located. Often fawns were consumed entirely before being found, or only small tooth and bone fragments remained. Scavengers (e.g., vultures, corvids, coyotes) are abundant on the CPNM, and differentiating between scavenging and predation events becomes increasingly difficult with delayed recovery times (e.g., >24 hours).

**Fawn habitat selection model.**—Results from the fawn habitat selection model

| Table 3. | Comparison and relative ranking of candidate models for pronghorn fawn survival, on the Carrizo Plain National Monument, California from 2009 to 2011. Akaike’s Information Criterion corrected for small sample sizes (AICc) was used for model selection. Included for each candidate model are values for log-likelihood, number of parameters (k), AICc values, ΔAICc values, and Akaike weights (wi). Relative ranking of models was determined using ΔAICc. |
|-------------------------------------------------------------|
| **Model**       | -2LogL | k | AICc | ΔAICc | wi    |
| 1. dmr+dar+df+dw+ps | 478.20 | 5 | 488.25 | 0 | 0.5540 |
| 2. Global modela | 477.30 | 6 | 489.36 | 1.12 | 0.3172 |
| 3. dmr+dar+df+dw | 483.16 | 4 | 491.19 | 2.94 | 0.1275 |
| 4. dmr+dar+df   | 494.34 | 3 | 500.35 | 12.11 | 0.0013 |
| 5. dmr+dar     | 508.19 | 2 | 512.19 | 23.95 | <0.0001 |
| 6. dmr+dw+ps   | 527.97 | 3 | 533.98 | 45.74 | <0.0001 |

aGlobal model included percent slope of terrain (ps) and distances to saltbush (dsb), water (dw), main roads (dmr), all roads (dar) and fences (df).

| Table 4. | Parameter estimates, standard errors of the estimates, odds ratios, and 95% confidence intervals for the odds ratios of the variables in the two best approximating models of pronghorn fawn survival, (β, SE, Odds ratio, 95% CI, respectively) on the Carrizo Plain National Monument, California, 2009–2011. |
|-------------------------------------------------------------|
| **Effect**       | β    | SE  | Odds ratio | 95% CI       |
| Model 1:         |      |     |            |              |
| dmr              | 0.001 | <0.001 | 1.001 | 1.000-1.001 |
| dar              | -0.003 | 0.001 | 0.997 | 0.996-0.998 |
| df               | -0.002 | <0.001 | 0.998 | 0.997-0.999 |
| dw               | -0.0004 | <0.001 | 1.000 | 0.999-1.000 |
| ps               | 0.0403 | 0.019 | 1.041 | 1.004-1.080 |
| Model 2:         |      |     |            |              |
| dmr              | 0.001 | <0.001 | 1.001 | 1.000-1.001 |
| dar              | -0.003 | 0.001 | 0.997 | 0.996-0.998 |
| df               | -0.002 | 0.001 | 0.998 | 0.997-0.999 |
| dw               | -0.0004 | <0.001 | 1.000 | 0.999-1.000 |
| ps               | 0.051 | 0.022 | 1.052 | 1.009-1.097 |
| dsb              | -0.002 | <0.001 | 1.000 | 0.999-1.000 |

Variables include percent slope of terrain (ps) and distances to water (dw), main roads (dmr), all roads (dar), fences (df), and saltbush (dsb).
indicate that females and their fawns both selected for a combination of environmental parameters at both macro- and microhabitat scales. At the microhabitat scale, the negative associations for variables measured close to fawn locations and the positive associations for similar variables measured 100 m from fawns reveal that the relationship between these variables and choice of bed-sites is scale-dependent. Fawn locations had lower visibility at close distances compared to random locations. However, fawn locations within low visibility vegetation patches were, on average, located on a larger scale in open areas with greater visibility compared to surrounding habitat. Fawns appeared to choose sites in isolated patches of cover within larger areas containing less concealment from predators, rather than in continuous habitat with dense cover. Movement between those isolated patches is likely to increase the risk of detection by predators. However, pronghorn females may choose areas with higher visibility surrounding hidden fawns as a means of enhancing their own ability to detect predators.

Females with fawns exhibit increased vigilance and aggressive behavior toward predators (Byers 1997b), and fawn survival can be higher in habitat containing open areas with shorter vegetation height than in other areas (Bodie 1978, Autenrieth 1992). Additionally, our results show that fawn locations had higher forb cover than random locations. Forbs are a critically important source of nutrients for lactating females (Yoakum 2004c) and our results indicate that fawns are selecting bed-sites within areas pre-selected by females for forage quality.

At the macrohabitat scale, fawn locations, in comparison to random locations, were in areas with lower slope and closer to water sources and large saltbush shrub communities.
Flat terrain increases the ability of adult pronghorn to detect and avoid predators (Yoakum 2004a). The availability of surface drinking water for adult pronghorn can be important in arid environments such as the CPNM, particularly for lactating females (Yoakum 2004a). Ockenfels et al. (1992) suggested that water on arid grasslands is an important, if not critical, factor in determining the location of fawn bed-sites (Yoakum 2004a). We did not anticipate that proximity to saltbush would be an important habitat variable for fawns because saltbush communities on the CPNM tend to be clustered in dense stands along the valley floor with heights that are indicative of low quality habitat (>50 cm; Longshore and Lowrey 2008). Although moderate dispersion of shrubs in grassland habitats can increase fawn survival (Autenrieth 1982), sites with shrubs >75 cm in height can have higher predator-related mortality of fawns (Bodie 1978).

Fawn survival model.—Results from the fawn survival model indicate that locations of individuals who lived beyond 17 days, in comparison to those who lived ≤17 days, were closer to water sources, farther from high-use main roads, and on steeper terrain. Postnatal fawns acquire water strictly from nursing, and females inhabiting more mesic areas than the CPNM typically meet most of their water requirements through the consumption of succulent forage items (Yoakum 2004b). For pronghorn occupying arid ranges, however, availability and dispersion of open water sources can directly affect adult health and reproduction, as well as fawn productivity and survival (McKee and Wolf 1963, Beale and Smith 1970, Ockenfels et al. 1992).

The positive association between survival and distance from high-use main roads suggests that anthropogenic disturbance during the fawning season influences survival. Model results also indicated that these survivors were located closer to fences and all roads (small dirt roads as well as main roads). This result is most likely due to the fact that fences and dirt roads are abundant and well dispersed throughout the monument, and not because proximity to either resulted in increased survival times. It was unexpected that survival would be positively influenced by steeper terrain because pronghorn typically select habitat with the lowest slope (Ockenfels et al. 1994). Einarsen (1948) reported, however, that the best physiography for fawning sites was among basins surrounded by low ridges or hills. On the CPNM, areas with high percent slope may offer environmental conditions such as improved forage quality, increased vegetative and topographic concealment, or even the absence of human disturbance, that increase fawn survival and outweigh the risks associated with steep terrain (e.g., decreased range of predator detection).

Collectively, these findings highlight the importance of both micro- and macrohabitat-scale environmental attributes for recruitment in pronghorn. Ecological studies on recruitment, as well as conservation strategies aimed at increasing rates of recruitment, should consider the habitat requirements of females and fawns simultaneously. Methods and results reported herein, when combined with results reported by others, can be used as guidelines for conservation and management of pronghorn within the CPNM.

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