

Differential investment in twin offspring by female pronghorns (*Antilocapra americana*)

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Differential investment in offspring has been reported for many mammals, often in the context of the Trivers–Willard model of male-biased investment, but evidence of differential investment in pronghorns (*Antilocapra americana*) is largely lacking. We assessed the causes and consequences of different birth masses of littermate fawns in a pronghorn population in Oregon. The mass differential for co-twins ranged from 0% to 89% (median = 8.35%). Male-biased investment explained the mass differential in opposite-sex litters but not same-sex litters. The mass differential did not result from mothers producing 1 normal-size fawn and 1 runt fawn, and the smaller fawn was not deficient in physiological condition. Only 29% of fawns survived to 8 weeks and both fawns died in 56% of litters, but co-twin mortalities were largely separate events. Mass did not confer a survival advantage when considering all fawns through age 8 weeks, but there was evidence of such an advantage when comparing fawns within litters before age 18 days. Differential investment in fawns might be a bet-hedging strategy in which the mother accepts a lower expected reproductive success in exchange for a lower variance, but neither the mean nor the variance differed between mothers of different-size (>8.35% mass differential) and similar-size (<8.35%) litters. In fact, there was evidence of increased reproductive success for mothers of different-size litters, much of which stemmed from higher survival 4–6 days after birth. Having different-size fawns reduced the chances of sequential mortality, in which a predator killed one fawn then returned to kill the other.

Key words: *Antilocapra americana*, bet hedging, body mass, fawn survival, maternal investment, pronghorn, sex-biased investment, win–stay strategy

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Differential investment in offspring by female mammals has been reported for many species, often in the context of the Trivers–Willard model of sex-biased investment based on maternal condition (Trivers and Willard 1973). Females in good condition are expected to invest more in sons because of size-related advantages for males in adulthood, especially in polygynous mating systems (Hewison and Gaillard 1999; Maynard Smith 1980; Sikes 2007; Trivers and Willard 1973). Accordingly, males may be larger at birth than females, reflecting differential investment during gestation, or suckle more than females during lactation. However, the evidence is equivocal; for many species data on sex differences in birth mass or postparturition maternal care conform to expectations, but for some species the data do not conform (Byers and Moodie 1990; Hewison and Gaillard 1999; Sikes 2007).

Female pronghorns (*Antilocapra americana*) typically produce litters of 2 fawns of about 4 kg each, an exceptional maternal investment that results in a litter mass nearly 18% of maternal mass (Byers 1997). Twinning and large birth mass are traits thought to result from a long history of intense predation pressure on fawns (Byers 1997). Fawns grow rapidly, presumably because increased size and running speed enhance the ability to escape predators, especially coyotes (*Canis latrans*—Byers 1997; O’Gara and Yoakum 2004). Unlike some other species of polygynous ungulates (Hewison and Gaillard 1999), there is no evidence of male-biased maternal investment in pronghorns; birth masses, suckling rates, and



growth rates of male fawns are not greater than those of female fawns (Byers and Moodie 1990). Byers and Moodie (1990) proposed that given the resource demands of producing 2 fawns of exceptionally large size, pronghorn females are at the limit of their capacity for maternal investment and hence lack the additional resources to invest in sons.

In a study of pronghorn fawn mortality, we observed a striking disparity between the masses of twin littermate fawns in some litters. Our objective was to characterize this mass differential, assess its causes, and evaluate the fitness consequences for the fawns and their mother. The mass differential we observed might be the result of sex-biased maternal investment (Maynard Smith 1980; Trivers and Willard 1973). Although a male-biased difference in fawn mass is absent in some pronghorn populations (Byers and Moodie 1990), the trait apparently has not been studied in many populations, including the one we studied. The maximal maternal investment of female pronghorns suggests a 2nd explanation for a mass differential between co-twins; perhaps females in poor condition lack the resources to produce 2 normal-size fawns, and instead they produce 1 normal-size fawn and 1 runt fawn. If so, we hypothesized that the runt fawn might be deficient in physiological condition in addition to mass. Because of the importance of size and speed in escaping predators, we expected that survival of the lighter fawn in litters of different-size fawns would be reduced. However, the mother's fitness might not be reduced accordingly. A differential investment in fawns might be a type of bet-hedging strategy, in which the mother accepts a lower expected reproductive success in exchange for a lower variance (Seeger and Brockmann 1987). Pronghorn fawns frequently suffer high rates of predation (Byers 1997), and having only 1 fawn survive may be better than to risk losing both.

MATERIALS AND METHODS

Our study was conducted at Hart Mountain National Antelope Refuge, southeastern Oregon (42°30'N, 119°40'W). Elevation ranged from 1,500 to 2,450 m, and climate was characterized by hot, dry summers and cold winters, with annual precipitation ranging from 15 to 30 cm. Vegetation was mostly shrub-steppe dominated by low sagebrush (*Artemisia arbuscula*) and occasionally big sagebrush (*A. tridentata*), interspersed with a variety of forbs and grasses (Gregg et al. 2001). The refuge supported a population of about 1,400–2,000 pronghorns at the time of our study (Dunbar et al. 1999). Fawn mortality was high (84%), largely due to predation by coyotes (Gregg et al. 2001).

Female pronghorns employ a "hiding" strategy to deter predators (Byers 1997). Beginning shortly after birth, co-twin fawns bed separately and remain recumbent for long periods of time between brief visits by the mother for suckling (Autenrieth and Fichter 1975; Barrett 1984; Byers 1997; Kitchen 1974). Bedded fawns remain immobile when approached until about 3–5 days old, after which they become increasingly likely to jump up and run when threatened

(Autenrieth and Fichter 1975; Byers 1997). Mothers actively defend their fawns when threatened by predators (Autenrieth and Fichter 1975; Byers and Byers 1983; Kitchen 1974). At about 10 days of age fawns begin the transition out of the pure hiding strategy, and by about 20 days fawns join social groups of other fawns and their mothers (Byers 1997).

We captured neonatal pronghorn fawns from 13 to 25 May each year from 1998 through 2002. Capture teams of 2 or 3 people used vantage points to locate adult females just before parturition or newborn fawns after parturition. When parturition was observed, we waited 3–4 h before attempting capture, to facilitate mother–fawn imprinting (O'Gara and Yoakum 2004). We used long-handled nets to capture fawns, which were then blindfolded and handled using sterile gloves to minimize the transfer of human scent. Co-twin fawns typically were bedded within 5–10 m of each other, which facilitated capture of both littermates. We recorded sex and mass to the nearest 0.1 kg, and in all years except 2002 we drew 4–6 ml of blood from the jugular vein in ethylenediaminetetraacetic acid-treated tubes. Blood samples were chilled and transported to the Lake District Hospital, Lakeview, Oregon, for analysis of serum chemistry and complete blood cell counts. Age was known in the case of observed parturitions, or was estimated using a combination of status of the umbilicus, hoof wear, and behavior, based on established criteria (Byers and Moodie 1990; Trainer et al. 1983; Von Gunten 1978) and by comparison with known-age fawns. We instrumented both fawns in 46 litters during 1998–2001 with an ear-tag-mounted radiotransmitter (14 g; Advanced Telemetry Systems, Isanti, Minnesota) equipped with a mortality sensor that activated after the fawn had been stationary for 1–2 h. We monitored radiotagged fawns twice a day through mid-June and then daily until fieldwork was terminated mid-July. Upon receipt of a mortality signal, we used radiotelemetry homing to locate the fawn to confirm mortality. Capture and handling of fawns conformed to guidelines of the American Society of Mammalogists (Sikes et al. 2011).

We expressed the mass differential between co-twins as a percentage, by dividing the difference in mass between co-twins by the mass of the lighter co-twin and multiplying by 100. We calculated the median mass differential among litters, and we considered those litters greater than the median to be "different-size" and those less than the median to be "similar-size." If different-size litters result primarily from preferential investment in male fawns, then males should be larger at birth than females, which we analyzed with a *t*-test. However, because pronghorn mothers are at their maximal level of maternal investment, this male–female difference might be expressed primarily in opposite-sex litters. If so, males of opposite-sex litters should be larger at birth than females of those litters, and the mass differential between co-twins should be reduced in same-sex litters compared with opposite-sex litters. We evaluated the 1st expectation with a *t*-test, and the 2nd with a Mann–Whitney test.

If different-size litters result from mothers producing 1 normal-size fawn and 1 runt fawn, then total litter mass at birth

for different-size litters should be less than that for similar-size litters, and the mean birth mass of the heavier co-twin in each litter should not differ between the 2 types of litters. We evaluated both expectations using *t*-tests.

To determine if a mass difference between co-twins is associated with a difference in physiological condition at birth, we used paired-comparison *t*-tests to determine if serum chemistry and complete blood cell count parameters differed between the heavy and light co-twins of different-size litters. We compared those parameters considered potential indicators of nutritional status for pronghorns and other ungulates (Franzmann 1985; Kunkel and Mech 1994; Seal and Hoskinson 1978; Seal et al. 1978), and we restricted our analysis to fawns 3–4 h old to approximate birth conditions as closely as possible.

We determined survival of radiotagged fawns to 8 weeks of age, which was the age of the youngest fawn in our study when monitoring ended mid-July. We assessed the influence of mass on survival for all fawns by using a *t*-test to compare the masses of fawns that survived to 8 weeks versus those that died. However, fawn survival might be influenced by maternal effects such as the choice of parturition site (Wiseman et al. 2006) or the effectiveness of maternal defense, so we also used a paired-comparison approach within litters. We calculated the survival of heavy versus light co-twins in both different-size and similar-size litters using the Kaplan–Meier method modified for a staggered-entry design, and we compared the survival of heavy and light co-twins using a modified log-rank test (Pollock et al. 1989; White and Garrott 1990). For this analysis we compared survival to age 18 days because most predation mortality occurs before that age (Gregg et al. 2001). If mass affects survival, the heavy co-twin in different-size litters should have higher survival than the light co-twin, but survival of both heavy and light co-twins in similar-size litters should be similar. For those similar-size litters in which both co-twins had the same mass ($n = 4$), we assigned heavy and light status based on the flip of a coin. Bet-hedging involves a trade-off between the mean and variance in reproductive success, so we compared mean fawn survival to 8 weeks between similar-size and different-size litters using a Mann–Whitney test, and we compared variances using a variance-ratio test. To elucidate factors contributing to any differences found, we used the Kaplan–Meier method to compare fawn survival between similar-size and different-size litters to age 18 days.

For comparisons of means we used *t*-tests if the data met the assumption of normality; if not, we compared medians using a Mann–Whitney test. We used SAS version 9.2 (SAS Institute Inc. 2002) for the modified log-rank test, and Minitab version 15 (Minitab Inc. 2006) for all other tests. We used $P = 0.05$ for determining statistical significance in all tests.

RESULTS

We captured 84 pairs of co-twin fawns; 68 were 3–12 h old, 8 were 24 h old, and 8 were 36–72 h old. All fawns appeared healthy at the time of capture. Regression analysis revealed that

fawns did not exhibit significant growth from 3 to 12 h of age (mass in kg = $3.98 - 0.005 \times \text{age in hours}$, $r^2 = 0.001$, $P = 0.702$, $n = 136$ fawns). However, a comparison of mean mass between age classes indicated that growth was significant ($t_{150} = 7.46$, $P < 0.001$) between age 3–12 h ($\bar{X} = 3.96$ kg, $SD = 0.484$ kg, $n = 136$ fawns) and age 24 h ($\bar{X} = 4.63$ kg, $SD = 0.324$ kg, $n = 16$ fawns). Hence, we considered mass at ≤ 12 h of age to be birth mass.

The mass differential for co-twins ranged from 0% to 89% among 84 litters, with a median of 8.35% (Fig. 1). Birth mass of male fawns ($\bar{X} = 4.02$ kg, $SD = 0.500$ kg, $n = 71$) did not differ ($t_{134} = 1.64$, $P = 0.103$) from that of female fawns ($\bar{X} = 3.89$ kg, $SD = 0.458$ kg, $n = 65$) when considering all litters. However, when considering only opposite-sex litters, a paired-comparison *t*-test revealed that birth mass of male fawns was greater than that of females ($D = 0.31$ kg, $SD = 0.568$ kg, $n = 35$ litters, $t_{34} = 3.20$, $P = 0.003$). Despite this male–female difference, the median mass differential for same-sex litters (median = 8.35, $n = 40$) did not differ ($W = 1,732$, $P = 0.780$) from that for opposite-sex litters (median = 8.40, $n = 44$). The total mass at birth of different-size litters ($\bar{X} = 7.87$ kg, $SD = 0.706$ kg, $n = 35$) was not different ($t_{66} = 0.38$, $P = 0.708$) from that of similar-size litters ($\bar{X} = 7.94$ kg, $SD = 0.893$ kg, $n = 33$). The birth mass of the heavier of the 2 co-twins in different-size litters was greater ($t_{66} = 2.23$, $P = 0.029$) than that of the heavier co-twin of similar-size litters (Fig. 2). In comparisons of serum chemistry and complete blood cell count values for fawns of 16 different-size litters at 3–4 h of age, we found no differences between heavy and light co-twins for any blood parameter (Table 1).

We determined survival to 8 weeks for 46 litters of twin fawns, and the overall survival rate for the 92 fawns was 29%. Although we typically found co-twin fawns bedded close together at capture, mortalities of co-twins were largely separate events. In 13 litters 1 fawn survived to 8 weeks. In 26 litters both fawns died, but in 20 of those litters the fawns died on different days. In the 6 litters in which fawns died on the same day, fawns were very young; age was ≤ 2 days in 4

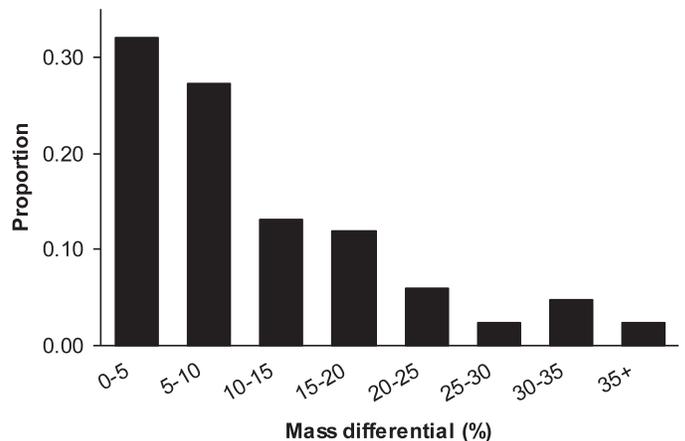


FIG. 1.—Frequency distribution of the mass differential between co-twins of 84 litters of pronghorn fawns at Hart Mountain National Antelope Refuge, Oregon, 1998–2002.

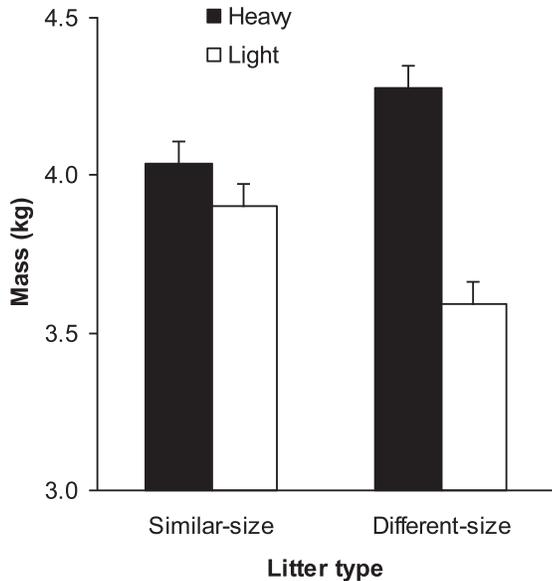


FIG. 2.—Mean (\pm SE) birth mass of heavy and light pronghorn fawns of similar-size ($n = 33$) and different-size ($n = 35$) litters at Hart Mountain National Antelope Refuge, Oregon, 1998–2002.

litters and 5 and 7 days in the other 2 litters. Hence, for litters in which 1 or both fawns died, in 33 (85%) of 39 cases only 1 fawn died at the 1st mortality event.

Mass at birth was not related to survival to 8 weeks; the mean birth mass of fawns that lived to 8 weeks ($\bar{X} = 3.78$ kg, $SD = 0.384$ kg, $n = 21$) was not different ($t_{70} = 1.53$, $P = 0.133$) from the mean birth mass of fawns that died ($\bar{X} = 3.96$ kg, $SD = 0.490$ kg, $n = 51$). However, comparisons within litters revealed evidence of a mass-based differential in survival (Fig. 3). The survival curve of the heavy co-twin of different-size litters was higher than that of the light co-twin, although the difference in survival was not statistically significant ($\chi^2_1 = 0.24$, $P = 0.623$). As expected, survival was indistinguishable between co-twins of similar-size litters ($\chi^2_1 = 0.02$, $P = 0.899$).

Contrary to the expectations of a bet-hedging strategy, the mean reproductive success for mothers of different-size litters (0.79 fawns living to 8 weeks) was greater than that of mothers of similar-size litters (0.44 fawns), a difference that fell short of statistical significance ($W = 570$, $P = 0.109$ adjusted for ties). Further, the variance in reproductive success did not differ ($F_{26,18} = 1.27$, $P > 0.50$) between mothers of similar-size litters ($s^2 = 0.487$) and different-size litters ($s^2 = 0.619$). Comparison of survival between litter types, in 3-day intervals from birth to age 18 days, revealed that much of the survival advantage of different-size litters over similar-size litters occurred shortly after birth (Fig. 4). Both litter types showed a rapid increase in survival with age, but survival of fawns in different-size litters was much higher at 4–6 days of age. Two of 24 fawns of different-size litters died during this period, compared with 12 of 38 fawns of similar-size litters ($\chi^2_1 = 5.15$, $P = 0.023$). The 2 mortalities from different-size litters were littermate fawns that died 1 day apart. The 12 mortalities from similar-size litters represented 10 different litters. In 8 of these 10 litters both co-twins died before 18 days, and they usually died in rapid sequence. In 1 of 8 litters both co-twins died on the same day, and in the other 7 litters the co-twins died 1–3 days apart.

DISCUSSION

The median mass differential between co-twins (8.35%) corresponds to a difference in birth mass of 0.33 kg for 4-kg fawns, which is equivalent to 1.3 days of growth at the mean daily rate of 0.25 kg (Byers 1997). Such a mass differential might have fitness consequences, considering the importance of rapid growth for eluding predators (Byers 1997; O’Gara and Yoakum 2004). The differential was much greater for some litters; 15% of litters showed a mass differential of $\geq 20\%$, corresponding to more than 3 days of growth.

When considering all fawns, birth mass of males was not greater than that of females, hence the mass differential in our study was not largely a result of a male-biased investment.

TABLE 1.—Comparison of mean values of selected blood parameters of heavy and light co-twin fawns of different-size pronghorn litters at Hart Mountain National Antelope Refuge, Oregon, 1998–2001.

Parameter	<i>n</i>	Heavy		Light		<i>t</i>	<i>P</i>
		\bar{X}	<i>SD</i>	\bar{X}	<i>SD</i>		
Sodium (meq/liter)	16	149.6	3.7	149.9	1.8	0.59	0.562
Chloride (meq/liter)	16	110.1	3.9	109.6	3.6	1.14	0.271
Calcium (mg/dl)	16	10.03	1.57	10.49	0.98	1.95	0.070
Phosphorus (mg/dl)	16	9.73	1.32	9.33	1.18	1.56	0.139
Alkaline phosphatase (U/liter)	16	1,008	499	888	406	1.12	0.278
Lactate dehydrogenase (U/liter)	16	920.2	268.3	926.7	317.8	0.16	0.876
Glucose (mg/dl)	16	154	52	134	52	1.45	0.168
Blood urea nitrogen (mg/dl)	16	20.8	4.1	20.1	4.0	1.07	0.300
Total protein (g/dl)	16	3.60	0.29	3.46	0.32	1.55	0.143
Cholesterol (mg/dl)	16	25.1	4.2	26.3	5.3	0.87	0.397
Red blood cells ($\times 10^6/\mu\text{l}$)	16	10.21	1.01	10.35	0.66	0.60	0.558
Hematocrit (%)	10	43.8	4.8	44.0	3.6	0.37	0.716
Hemoglobin (g/dl)	16	15.5	1.7	15.7	1.2	0.51	0.621
Mean corpuscular volume (fl)	16	42.9	2.5	43.1	2.8	0.72	0.480

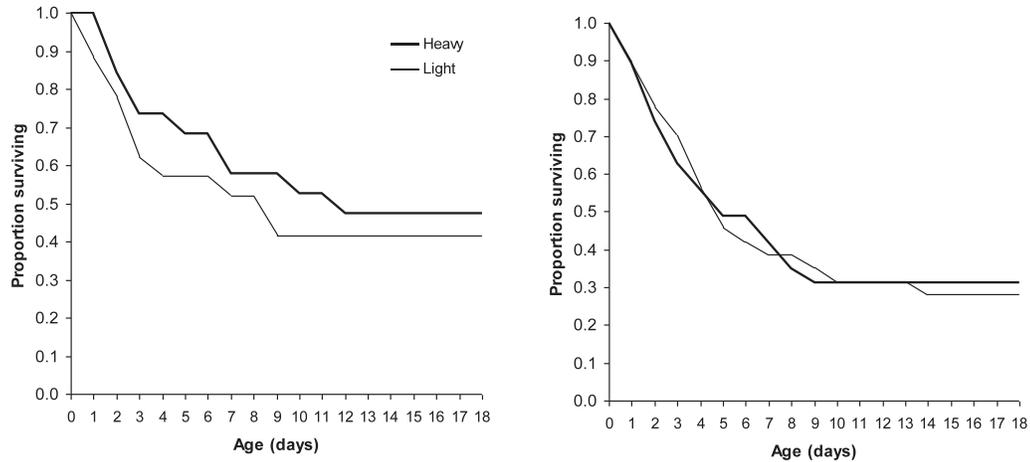


FIG. 3.—Survival of heavy and light co-twins of (left) different-size and (right) similar-size litters of pronghorn fawns at Hart Mountain National Antelope Refuge, Oregon, 1998–2001.

These results are consistent with those of other studies (Barrett 1981; Byers and Moodie 1990; Mitchell 1980; Wild et al. 1994), although Fairbanks (1993) found a female bias in mass of pronghorn fawns in Colorado. However, when considering only opposite-sex litters, we found that male mass was greater than that of female co-twins. Three factors may explain the difference between our findings of a male-biased birth mass and those of other studies. First, we restricted our analysis to birth mass, before postnatal growth began, whereas some studies used fawns older than 12 h, potentially increasing the unexplained variation. Second, we used a paired-comparison test that removed potential variation among mothers in their ability to generate litter mass, another possible source of unexplained variation. Third, we compared only opposite-sex co-twins, which is the litter type in which a male-based birth mass should be expressed if female pronghorns are at the limit of their capacity for maternal investment. Hence, our results support the Trivers–Willard hypothesis of male-biased maternal investment (Maynard Smith 1980; Trivers and Willard

1973), and male-biased investment explains some of the mass differential we found between co-twins, but only for opposite-sex litters. The mass differential between co-twins in same-sex litters was just as prevalent as in opposite-sex litters, as indicated by similar median values. Hence, a differential investment occurs in both same-sex and opposite-sex litters, but in opposite-sex litters the favored fawn is the male.

The total mass of different-size litters was similar to that of similar-size litters, indicating that mothers were not producing a runt fawn due to a lack of resources. Indeed, the heavier fawn of different-size litters was a “super-fawn” that exceeded the mass of both fawns of similar-size litters. Gestation of different-size fawns represents a difference in tissue quantity, but it does not also represent a difference in quality; we detected no difference in blood values that might suggest reduced physiological condition in the lighter fawn.

We did not find an association between birth mass and survival to 8 weeks, which agrees with results of previous studies that found no association or an inconsistent association between fawn mass and survival to ≥ 2 months old (Dunbar et al. 1999; Fairbanks 1993). However, we did find evidence, although not statistically significant, of a survival advantage for heavy fawns in different-size litters within 18 days of birth. Perhaps body mass does confer a survival advantage for pronghorn fawns, but it is only expressed early in life, and its detection might be obscured by variation in maternal effects such as degree of maternal defense and safety of bed locations chosen by the mother.

Pronghorn fawns typically suffer high rates of predation (Byers 1997), a generalization supported by our results; 71% of fawns died before 8 weeks of age, both fawns died in more than half of all litters (56%), and both fawns survived in only 15% of litters. Consequently, if size confers a survival advantage, preferential investment in one co-twin at the expense of the other might improve chances of the heavier fawn surviving, in the face of the likely outcome of both fawns dying. Some of our results are consistent with this possibility; the heavy fawn in different-size litters was a “super-fawn” that exceeded other fawns in

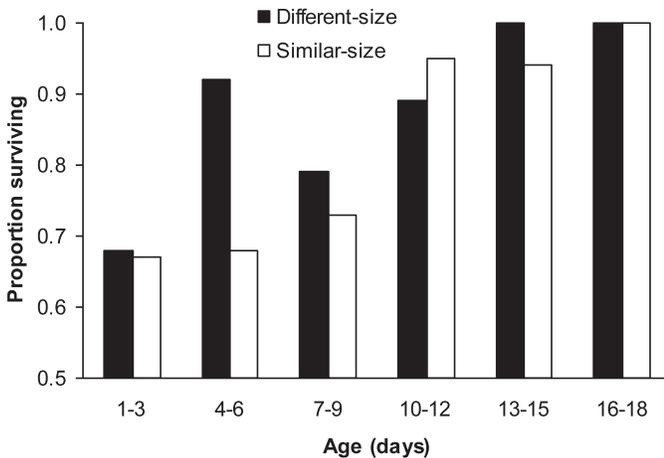


FIG. 4.—Survival of pronghorn fawns in different-size and similar-size litters during 3-day intervals from birth to age 18 days at Hart Mountain National Antelope Refuge, Oregon, 1998–2001.

mass, and we found evidence of a mass-based survival advantage for these fawns. However, neither the mean nor the variance in reproductive success for mothers of different-size litters was less than that for mothers of similar-size litters; in fact, there was evidence of increased reproductive success for mothers of different-size litters, much of which stemmed from higher fawn survival a few days after birth.

Analysis of survival to 18 days in 3-day intervals revealed the overall pattern that fawn survival increases rapidly from about 65–70% at age 1–3 days to $\geq 90\%$ by age 10–12 days, a pattern that supports the notion that rapid growth enhances the ability to escape predators. However, the exception to this pattern is that fawn survival in different-size litters during 4–6 days of age is strikingly higher than that for similar-size litters. The explanation for this difference is obscure, but it may be related to the temporal pattern of mortality in twin littermates. In ungulates, neonatal co-twins often are both killed at the same predation event, but sometimes survival of co-twins is substantially independent (Bishop et al. 2008; Panzacchi et al. 2009; Testa et al. 2000). Our results indicate that most mortality events involved only 1 co-twin, and the few same-day events were concentrated in the 1st few days after birth. This pattern probably results from the fact that mothers bed co-twin fawns apart from each other beginning shortly after birth (Barrett 1984). Hence, mortalities of co-twin fawns are mostly separate events, differing in time and presumably space as well, but our results suggest they might not be independent events. Panzacchi et al. (2009) reported a “win–stay” strategy for red foxes (*Vulpes vulpes*) when hunting littermate roe deer (*Capreolus capreolus*) fawns; foxes remembered a successful attack and returned within a few days to search for and kill the surviving littermate. The win–stay strategy might explain why most pronghorn fawn mortalities during age 4–6 days involved co-twins that died on different days, but ≤ 3 days apart. But the question remains, why did different-size litters suffer fewer of these apparently “win–stay” mortalities? In some fashion, the size differential appears to have reduced the likelihood of the 1st mortality. Age 3–5 days is the age at which some fawns flush when threatened (Autenrieth and Fichter 1975; Byers 1997); perhaps in different-size litters, the heavy fawn is large enough to flush—and also to escape, possibly aided by maternal defense—thereby luring the predator away from the still-hidden light fawn and generating a “lose–leave” response.

In conclusion, some female pronghorns produced twin fawns with substantially different body masses, a difference that is only partly explained by sex-biased investment. This mass differential could be a physiological side effect with no adaptive value (Marshall and Uller 2007). It also could result from interactions between fetuses in utero (Korsten et al. 2009; Kühn et al. 2007); such an explanation seems plausible for pronghorns, which are unusual in producing multiple embryos that are reduced to 2 before birth via sibling competition (O’Gara and Yoakum 2004). However, the mass differential was associated with higher survival for both co-twins and consequently a higher fitness for the mother, so perhaps it has an evolutionary basis. Predation on pronghorn fawns can vary

in magnitude considerably among years (e.g., 56–99%—Byers 1997), and mothers might produce different-size fawns in response to this uncertainty.

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