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FORAGING BEHAVIOR BY MULE DEER: THE INFLUENCE OF CATTLE GRAZING

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Abstract: We studied the effects of different cattle stocking rates on activity patterns of female mule deer (*Odocoileus hemionus*) on a summer range in the Sierra Nevada of California. Using an automated telemetry system, we determined that deer averaged 32 ± 2.2 (SE)% of the time feeding, 8 ± 1.1% traveling, and 60 ± 2.4% resting per 24-hour period. Deer spent more time feeding and less time resting with increased cattle stocking rates. During 1984, a year of average precipitation, deer spent more time feeding per day in late summer than in early summer in range units grazed by cattle but did not do so in ungrazed range units. In 1985, a drier year, deer spent less time feeding per day in late summer in grazed range units. Time spent feeding by deer was negatively correlated with standing crop of herbaceous forage in meadow-riparian habitats. Deer increased their time spent feeding by shortening the length of resting bouts and including more feeding bouts each day, not by increasing the length of each foraging bout. Companion studies indicated that with cattle grazing, deer home-range sizes were larger (Loft 1988), and hiding cover for fawns was reduced (Loft et al. 1987). The results are consistent with the hypothesis that cattle competed with deer, particularly at high stocking rates and during a year of below-average precipitation. We suggest that female mule deer were acting as time-minimizers to meet the high energetic demands of lactation while minimizing their exposure to predators. Management options to reduce adverse effects include reducing or eliminating cattle grazing during early summer on all or part of the grazing allotment.

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The debate over competition between livestock and native ungulates is centuries old (Stover 1985). Competition between 2 species occurs in the broad sense if an increase in either one harms the other (MacArthur 1972). Specifically, 2 species compete when they both use a resource in short supply, or if the resource is not in short supply, when 1 species seeking the resource harms the other in the process (Birch 1957). Competition between large herbivores is difficult to measure at the population level because of logistics associated with manipulating numbers of 1 species and measuring changes in another. However, studies of foraging behavior in a multi-species system can be used as a first step in examining interspecific competition, particularly where numbers of one or both species can be manipulated.

Traditional optimal foraging theory predicts that animals either maximize the amount of energy gained over time or minimize the amount of time needed to obtain some fixed level of energy (Schoener 1971, Belovsky 1984, Pyke 1984, Stephens and Krebs 1986). However, some of the underlying simplifications of optimal foraging theory have been criticized (Stephens and Krebs 1986, Pierce and Ollason 1987). Mangel and Clark (1986), McNamara and Houston (1987), and Lima and Dill (1990) argued that an animal must not only maximize its rate of energy intake, but also must avoid predators and reproduce. When those factors are considered, optimal foraging theory can provide a framework for understanding the foraging behavior of mule deer.

We examined activity patterns of free-ranging female mule deer on a summer range stocked with varying numbers of cattle. Unlike studies using tame deer, deer in our study were free-ranging, and as such, subject to constraints on foraging behavior imposed by predator-avoidance strategies and by the need to bear and raise fawns. We attempt to show how mule deer must balance those sometimes conflicting needs and how potential competition with cattle affects that balance. Specifically, we discuss changes in the amount of time spent feeding by deer, number and duration of feeding bouts, and changes in the times of the day that foraging occurs, and use optimal foraging theory to suggest reasons behind those changes.

This 2-year study was part of a series of investigations conducted during 1983–85 on the

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effects of cattle stocking rate on deer hiding cover (Loft et al. 1987), habitat selection (Loft et al. 1991), home-range sizes and spatial patterns (Loft 1988), migration routes (Loft et al. 1989), and tame deer foraging behavior in montane meadows (Winckel 1989).

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STUDY AREA

Our study was conducted during June–September 1984–85 in McCormick Creek Basin (38°24′N, 119°54′W). The 490-ha basin lies between 2,230 and 2,750 m elevation in the Sierra Nevada of California. It is important summer range for migratory mule deer. Deer usually arrive in early June and remain through October. Fawns are born from about 15 June to 15 August with a peak in mid-July (Leopold et al. 1951). McCormick Creek Basin was grazed by cattle from 6 July to 16 September 1984 and from 6 July to 17 September 1985.

Average daily minimum and maximum temperatures were about 6 and 23 C, respectively. Most annual precipitation falls as snow during winter, but the area receives an average of 7.5 cm of summer rainfall (Loft et al. 1987). In 1984, patches of snow remained in the basin through late May. In 1985, most snow had melted by early May, soil moisture was depleted more rapidly during the summer, and the effects were that of a mild drought.

There are 5 major habitats in McCormick Creek Basin (in general decreasing importance to deer): meadow-riparian (12% of the total area), aspen (5%), conifer (29%), montane shrub (34%), and timberline sagebrush (20%) (Loft et al. 1991).

METHODS

Grazing Treatments

The study area was fenced into 3 range units of 140, 155, and 185 ha. Three cattle stocking rates (no grazing, moderate grazing, heavy grazing) were rotated among range units during 1983–85 to avoid confounding grazing treatment and range unit effects. Because our study was not replicated outside McCormick Creek Basin, we caution against applying these results elsewhere. Additional research is needed on other sites in the Sierra Nevada.

During the 2 years of this study, the moderate stocking rate equaled 0.65 animal unit months per ha (AUM/ha) in 1984 and 0.76 AUM/ha in 1985. These rates were based on the area of primary range (meadow-riparian plus aspen habitats) in each unit, included cows and calves, and matched U.S. Forest Service recommendations (T. W. Beck, pers. commun.). Heavy stocking rates were 1.31 AUM/ha (1984) and 1.70 AUM/ha (1985). Additional details are given by Loft et al. (1987).

Carryover effects of the previous year's grazing were assumed negligible (Loft et al. 1991). McCormick Creek Basin had a long history of cattle grazing during summer, and studies there and elsewhere in the Sierra Nevada indicate little effect of a single previous year's grazing on plant species composition, standing crop, or cover (Kie and Myler 1987, Loft et al. 1987).

Monitoring Deer Activity

Adult female deer were captured throughout the basin with modified corral traps (Rempel and Bertram 1975) and fitted with radio-telemetry collars. Deer were assigned to range units according to location of the 30% isopleths of their home range distributions (Loft 1988). Between 4 and 6 deer were collared in each of the 3 range units. In addition, 3–7 adult cows in each range unit also were fitted with radio-telemetry collars.

Radio-telemetry collars were constructed with mercury-based tip-switches that varied signal pulse rate as a function of head position. Tip-switches are more accurate in predicting animal activity patterns than reset-motion or variable-pulse collars (Garshelis et al. 1982, Gillingham and Bunnell 1985). Radio signals were received by omnidirectional antennas placed on 4-m-tall masts at locations that gave line-of-sight reception to most of the basin.

Radio signals were received and processed with a receiver-scanner and digital data processor (Telonics, Mesa, Ariz.). Two channels of output from the data processor (signal strength and pulse period) were then routed in millivolt form to an automatic datalogger (Polycorder, Omnidata International, Inc., Logan, Ut.). The datalogger was programmed to store 6 readings of signal strength and pulse period at 5-second intervals, repeated every 10 minutes. To allow recording of information for multiple animals, we modified the scanner to accept a 5-volt excitation signal from the datalogger instructing it to change to the next programmed frequency. Using a datalogger with 16K of storage, we accumulated information on 4 animals for a 12-hour period. Changing dataloggers after 12 hours enabled us to gather data over a 24-hour period.

We used criteria of signal strength and pulse period (head position) to distinguish 3 activity classes: feeding, traveling, and resting (Green and Bear 1990). Head-down signals or head-up and head-down combinations within any single block of readings, coupled with moderate to high signal variability, were classified as feeding behavior. Head-up signals of high variability were classified as traveling, and head-up signals of low variability were classified as resting behavior. We classified the rare cases of head-down signals of very low or no variability as resting also.

We conducted 5 validation tests each from 2 to 4 hours duration in which we observed actual behaviors while collecting telemetry data. In 3 tests, we used cows (1 test in McCormick Creek Basin with 9 observation sessions, and 2 tests at the San Joaquin Experimental Range in central California with 14 and 9 sessions). By comparing observed with estimated times spent feeding, traveling, and resting during each observation session (with resulting total sample sizes of 3 times the number of sessions), we obtained r^2 values of 0.91, 0.91, and 0.97 for each of the 3 tests, respectively. In 2 tests, we used tame mule deer (1 test at nearby Bell Meadow with 6 sessions and 1 test at the University of California, Davis with 7 sessions). The resulting r^2 values were 0.97 in both cases.

Feeding behavior included both sustained feeding activity as well as walking-feeding. Feeding behavior also encompassed other activities such as grooming, nursing, and drinking. Similar activities in elk (*Cervus elaphus*) in Alberta never exceeded 6% during any season (Gates and Hudson 1983). Although our validation tests did not perfectly duplicate the potential range of activities by animals in the field (for example, a relative lack of sustained head-up browsing among tame deer), we believe resulting biases, if any, to be small and of little consequence to our results (Green and Bear 1990).

Table 1. Number of 24-hour monitoring periods (deer-days, cow-days) used as independent subsamples in McCormick Creek Basin, California.

	Deer		Cattle	
	Early summer	Late summer	Early summer	Late summer
1984				
No grazing	5	4		
Moderate grazing	6	4	6	4
Heavy grazing	4	5	6	6
1985				
No grazing	6	5		
Moderate grazing	5	5	5	4
Heavy grazing	4	4	4	4

Traveling behavior included only those bouts of sustained head-up, cross-country travel. Because relatively little time was spent traveling by either deer or cattle, our estimates of traveling were less accurate than those for feeding and resting behaviors. Finally, resting behavior also included rumination.

Data Analysis

We attempted to monitor each radio-collared deer and cow for at least 1 24-hour period during each half of the summer. We treated each deer-day or cow-day as an independent subsample within McCormick Creek Basin. We analyzed dependent variables such as percent time in activity class, length of activity bouts, number of activity bouts per 24-hour day, and number of activity bouts during each quarter of the day with a general linear model ANOVA (Freund and Littell 1981). Main factors examined were grazing level (none, moderate, and heavy cattle stocking rates), year (1984, 1985), and season (early summer was 6 Jul–10 Aug and late summer was 11 Aug–17 Sep). Separate ANOVA's were performed for deer and cattle. We used Duncan's multiple range test to determine differences between mean values of variables (Steel and Torrie 1980). Sample sizes varied from 4 to 6 deer-days or cow-days in each cell of the experimental design (Table 1).

We used linear regression to examine percent time spent feeding and average duration of resting bouts as functions of year and standing crop of herbaceous forage in meadow-riparian habitats (kg/ha dry matter measured at 3-week intervals throughout the summer [Loft et al. 1987]).

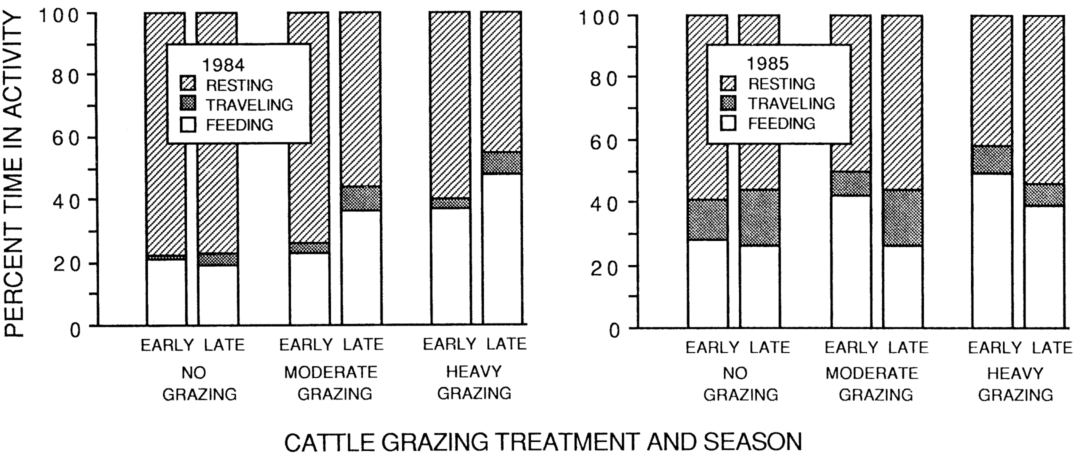

Fig. 1. Percent time spent feeding, traveling, and resting by mule deer in McCormick Creek Basin as a function of year (1984, 1985), season (early summer was 6 Jul to 10 Aug and late summer was 11 Aug to 17 Sep), and cattle stocking rate (none, moderate, heavy).

We used the number of days away from the nearest full moon in linear regressions to explore deer foraging behavior under differing amounts of moonlight.

RESULTS

Percent Time in Activity

Overall, deer spent 32 ± 2.2 (SE)% of the time feeding ($n = 57$ deer-days total), 8 ± 1.1% of the time traveling, and 60 ± 2.4% of the time resting. They spent more time feeding with increasing cattle stocking rates, averaging 24, 31, and 44% of the time feeding with no, moderate, and heavy cattle stocking rates, respectively ($P < 0.01$) (Fig. 1). In contrast, time spent resting declined from 67% in the absence of cattle to 60% with moderate stocking and 50% with heavy stocking ($P < 0.01$) (Fig. 1).

Time spent traveling by deer did not differ between stocking rates ($P > 0.10$) but increased from 6% in early summer to 11% in late summer when averaged for both years ($P = 0.03$) (Fig. 1). Time spent traveling increased from a summer-long average of 4% during 1984 to 12% in 1985, the drier year ($P < 0.01$). Time spent resting decreased from 66% in 1984 to 54% in 1985 ($P < 0.01$) (Fig. 1).

In the 2 range units grazed by cattle in 1984, deer spent more time feeding during late summer than during early summer (43 vs. 29%) ($P = 0.04$) (Fig. 1). Conversely, in 1985 deer in the 2 range units grazed by cattle spent less time feeding in late summer (32 vs. 45%) ($P = 0.04$). The differences in time spent feeding by deer between early and late summer were accompanied by inverse changes in time spent resting ($P = 0.05$) (Fig. 1).

Cattle exhibited few differences in behavior with respect to stocking rate (2 levels, moderate and heavy), year, and season. Overall, cattle spent an average of 45 ± 1.3% of their time feeding ($n = 39$ cow-days total), 6 ± 0.9% traveling, and 50 ± 1.4% resting. During both 1984 and 1985, they spent more time feeding in late summer (49%) than they did in early summer (41%) ($P < 0.01$). Cattle spent more time traveling in 1985 (9%) than they did in 1984 (3%) ($P < 0.01$).

Duration of Activity Bouts

Average duration of a deer feeding bout did not differ among cattle stocking rates ($P > 0.10$) (Table 2). In 1984, deer spent less time per feeding bout in early summer than in late summer ($P = 0.02$). In 1985, they spent more time per feeding bout in early summer ($P = 0.02$) (Table 2). These changes paralleled those in percent time spent feeding by deer (Fig. 1). The average duration of a traveling bout was less in 1984 than in 1985 ($P < 0.01$) (Table 2).

Average duration of deer traveling bouts was greater in 1985 than in 1984 ($P < 0.01$) (Table 2). Deer resting bouts were longest with no grazing, shorter with moderate cattle stocking rates, and shortest with heavy stocking rates ($P = 0.04$) (Table 2).

Mean length of cattle activity bouts was 35.3

Table 2. Mean number of minutes per deer activity bout in McCormick Creek Basin, California. Values are means of individual deer-day means, sample sizes are given in Table 1. See text for significant differences.

	Early summer						Late summer					
	Feeding		Traveling		Resting		Feeding		Traveling		Resting	
Yr and treatment	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
1984												
No grazing	16.5	2.85	9.0	2.45	111.9	47.18	21.1	6.83	8.3	2.85	73.8	19.65
Moderate grazing	19.7	3.64	7.1	2.25	56.3	7.57	27.0	6.07	15.0	2.49	65.0	34.35
Heavy grazing	19.9	1.60	7.8	2.62	31.8	4.92	25.4	2.23	11.7	1.07	27.9	7.02
1985												
No grazing	19.5	3.15	13.9	1.49	35.7	2.29	20.2	1.66	16.7	2.36	27.5	1.37
Moderate grazing	27.9	5.49	15.0	2.27	33.4	6.43	20.0	1.01	12.9	1.44	32.1	4.23
Heavy grazing	30.8	6.15	13.9	2.05	24.9	2.68	21.4	2.24	12.2	0.92	31.3	4.29
All years and treatments	22.0	1.75	12.8	0.71	50.2	9.19	22.4	1.43	13.4	0.75	41.4	6.48

± 1.44 minutes feeding, 11.8 ± 0.40 minutes traveling, and 39.2 ± 1.64 minutes resting. Average traveling bouts by cattle were longer in 1985 (12.5 min) than in 1984 (11.1 min) (P = 0.02). No significant differences were detected between stocking rates, years, or early versus late summer in the duration of cattle feeding or resting bouts ($P > 0.10$).

Activity Bouts Per Day

Increase in percent time spent feeding by deer with heavy cattle grazing (Fig. 1) was a result of more feeding bouts per day rather than an increase in the duration of each bout (Table 3). On average, deer fed fewest times per day in ungrazed range units, more in moderately grazed units, and most in heavily grazed units ($P < 0.01$).

Number of deer traveling bouts per day did not differ among stocking rates ($P > 0.10$) (Table 3). However, deer traveled more often in late summer than in early summer ($P = 0.03$) and more often in 1985 than in 1984 ($P < 0.01$) (Table 3).

The number of deer resting bouts varied as a function of cattle stocking rate ($P = 0.03$), year ($P < 0.01$), and the interaction between these 2 factors ($P = 0.03$) (Table 3). In 1984, deer rested fewest times per day in the ungrazed range unit, more in the moderately grazed unit, and most in the heavily grazed unit. During the drier year in 1985, differences in number of resting bouts per day were less pronounced (Table 3). These changes in the number of resting bouts per day were related to changes in the length of each resting bout (Table 2).

Cattle averaged 18.1 ± 0.60 feeding bouts per day, regardless of stocking rate, year, or

Table 3. Mean number of deer activity bouts per day in McCormick Creek Basin, California. Values are means of individual deer-day means, sample sizes are given in Table 1. See text for significant differences.

	Early summer						Late summer					
	Feeding		Traveling		Resting		Feeding		Traveling		Resting	
Yr and treatment	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
1984												
No grazing	14.8	4.49	1.6	0.68	17.0	4.60	10.5	3.40	4.3	2.98	15.8	1.93
Moderate grazing	15.2	2.12	3.7	1.89	19.5	1.67	17.0	3.54	7.3	3.61	17.0	3.49
Heavy grazing	25.5	2.72	4.0	2.04	27.5	2.36	25.4	2.11	7.4	2.36	22.8	1.39
1985												
No grazing	20.3	1.98	12.7	1.98	22.8	0.98	15.6	2.73	14.2	3.88	27.0	0.78
Moderate grazing	21.6	2.34	8.0	2.05	22.0	1.64	18.4	2.11	17.8	3.32	25.6	1.75
Heavy grazing	23.3	1.44	9.3	1.25	24.3	1.93	25.0	2.74	7.3	1.44	25.0	3.49
All years and treatments	19.7	1.23	7.7	1.00	21.9	1.08	18.8	1.42	10.5	1.49	22.5	1.15

Table 4. Number of feeding bouts initiated by deer as a function of time of the day and cattle grazing treatment, McCormick Creek Basin, California, 1984–85.

Treatment	Dawn (0300–0900 hr)	Day (0900–1500 hr)	Dusk (1500–2100 hr)	Night (2100–0300 hr)
No grazing	4.5A[a]	3.0A	4.5A	3.9A
Moderate grazing	3.6A	5.4B	5.4AB	3.7A
Heavy grazing	6.2A	6.8B	6.2B	5.6B

[a] Means within a column followed by the same letter are not significantly different ($P > 0.10$).

early versus late summer periods. They traveled on average 3.8 ± 0.66 times per day in 1984 but 9.9 ± 1.51 times per day in 1985 ($P < 0.01$). Cattle averaged 20.2 ± 1.07 resting bouts per day with moderate stocking rates and only 16.7 ± 0.67 bouts per day with heavy stocking rates.

Feeding Bout Start Times

Number of feeding bouts initiated by deer during each quarter of the day (times defined as dawn: 0300–0900; day: 0900–1500; dusk: 1500–2100; and night: 2100–0300 hr) varied as a function of cattle stocking rate (Table 4). In the absence of cattle, most feeding bouts were initiated during dawn and dusk. More feeding bouts were added during the day under moderate grazing and during both day and night under heavy grazing (Table 4).

A significant effect of year on feeding bout starts occurred during day and dusk only. Deer initiated feeding bouts an average of 4.3 times during the day in 1984 but 5.7 times in 1985 ($P = 0.01$). They initiated feeding bouts an average of 4.5 times during dusk in 1984, but 6.0 times during 1985 ($P = 0.01$).

Number of feeding bout starts by cattle within quarters of the day did not differ with respect to any main factor ($P > 0.10$), averaging 4.2, 5.3, 4.8, and 3.8 starts during dawn, day, dusk, and night, respectively.

Effects of Forage Availability on Foraging Behavior

Percent time spent feeding by deer increased ($P < 0.10$) with declining standing crop of herbaceous forage in meadow-riparian habitats. However, the relationship was very weak ($r^2 = 0.06$) and of no value in predicting the amount of time an individual deer would spend feeding.

Average duration of deer resting bouts increased with forage standing crop and was greater in 1984 than in 1985. But again, although the relationship was significant ($P < 0.01$), it was of no predictive value ($r^2 = 0.18$).

Percent time spent feeding by cattle also increased with declining forage standing crop ($P < 0.05$, $r^2 = 0.10$). Average duration of cattle resting bouts did not differ with year or forage standing crop.

Effects of Moon Phase on Foraging Behavior

Deer initiated more feeding bouts during the night (2100–0300 hr) with increasing number of days to the nearest full moon ($r^2 = 0.07$, $P < 0.05$). However, total percent time feeding by deer was not affected by the number of days to the nearest full moon ($P > 0.10$). Deer decreased the proportion of, but not the total, time spent feeding each 24-hour period during nights with bright moonlight.

Cattle initiated fewer feeding bouts during the night with increasing number of days to the nearest full moon ($r^2 = 0.14$, $P < 0.05$). Also, total percent time feeding by cattle declined as a function of the number of days away from a full moon ($r^2 = 0.10$, $P < 0.05$). Cattle increased the number of nighttime feeding bouts during nights with bright moonlight, and these extra feeding bouts were additive to the total time spent feeding.

DISCUSSION

The Influence of Cattle Grazing

The mean percent time spent feeding by mule deer in our study (32%) was less than that reported for mule deer in Utah (40–46%) (Collins and Urness 1983) and black-tailed deer (*Odocoileus hemionus columbianus*) in Washington (54%) (Hanley 1982). The mean percent time spent feeding by cattle (45%) was similar to that previously reported on foothill rangelands in California (41–45%) (Wagnon 1963), in Montana (47–50%) (Peterson and Woolfolk 1955), and in Colorado (48%) (Ellis and Travis 1975).

In McCormick Creek Basin, deer and cattle spent more time feeding with declining quantity of available herbaceous forage in meadow-riparian habitats. These relationships, although significant, were characterized by low r^2 and high standard errors of the estimates. However, deer fed on woody species as well as herbaceous plants, both in meadow-riparian (Loft et al. 1987) and other habitats (Loft et al. 1991). In contrast, cattle spent proportionally more time in meadow-riparian habitats and likely fed less on woody plants. As a result, the relationship between percent time feeding by cattle and standing crop of herbaceous forage was less variable than that for deer.

Companion studies at nearby Bell Meadow indicated that cattle grazing reduced the availability of forbs preferred by tame mule deer, especially in late summer. Deer responded by increasing the proportion of sedges in their diet and decreasing overall diet diversity (Winckel 1989). Cattle grazing had relatively few effects on the quality of herbaceous forage available to deer (e.g., a reduction in in vitro digestible dry matter with grazing in 1985 but not in 1984 [Winckel 1989]). Deer were forced to decrease bite size and increase biting rate with decreased forage availability. Unlike the free-ranging deer in McCormick Creek Basin, the tame deer in Bell Meadow did not have access to browse or to other habitats (Winckel 1989).

In McCormick Creek Basin, cattle grazing reduced availability of herbaceous forage for deer (Loft et al. 1987). Deer responded by decreasing the length of their resting bouts and increasing the number of feeding bouts each day and the total time spent feeding. This strategy was partially successful; however, during late summer 1985 (a dry yr) deer in range units grazed by cattle decreased the time they spent feeding. The declines under those conditions may have resulted from the inability of deer to further adjust their feeding patterns (Green and Bear 1990), from reductions in water availability caused by the drier year and resulting in reduced intake (Lautier et al. 1988), or from some combination of these factors (Bowyer 1984). These results suggest that competition between mule deer and cattle on summer range occurred, particularly at higher cattle stocking rates and during the year of below-average precipitation.

Optimal Foraging and the Potential Role of Predation

Current advances in optimal foraging theory suggest that animals must not only gain energy by feeding, but they must also avoid predators and reproduce (Mangel and Clark 1986, McNamara and Houston 1987, Lima and Dill 1990). Although some large ungulates such as moose (*Alces alces*) are believed to maximize the rate of energy gain (Belovsky 1978), others may be time-minimizers during some seasons of the year (Belovsky 1984:109).

We believe that female mule deer in McCormick Creek Basin acted as time-minimizers, and they attempted to meet the high energetic demands of lactation (Hanley 1984, Carl and Robbins 1987) while minimizing their exposure to predators and ensuring the survival of their offspring (Lima and Dill 1990). In the absence of cattle, deer spent less time feeding than has been reported elsewhere. We believe competition with cattle adversely affected deer, resulting in increased time spent feeding.

Home-range size in deer increased with increasing cattle stocking (Loft 1988). A reanalysis of home-range sizes using the adaptive kernel method (Worton 1989) indicated averages of 88 ha with no grazing, 103 ha with moderate grazing, and 124 ha with heavy grazing (Loomis et al. 1991). In addition, as home-range size increased with increased cattle stocking rate, a greater proportion of those home ranges included the steeper slopes surrounding McCormick Creek Basin (Loft 1988). The energetic costs to deer of both upslope and downslope locomotion are greater than for horizontal movements (Parker et al. 1984). Assuming females are central-place foragers during summer because of the need to find and nurse fawns, and must traverse their home ranges frequently (Swihart et al. 1988), home ranges that are larger and include more steep terrain increase energetic costs.

Successful reproduction in mule deer involves not only conception and the birth of fawns, but also the survival of those fawns to reproductive age. Fawns are hider-type neonates and rely on hiding cover to escape predation early in life (Geist 1981). Cattle grazing may limit deer numbers by reducing hiding cover for fawns (Bowyer and Bleich 1984, Bowyer 1986). Cattle grazing in McCormick Creek Basin resulted in reduced hiding cover for fawns in both aspen and meadow-riparian habitats (Loft et al. 1987). Increased loss of hiding cover may have resulted in increased predation on young fawns.

Heavy cattle grazing also may influence rates of predation on adult female deer. There is a trade-off between obtaining energy and reducing the risk of predation (Mangel and Clark 1986, McNamara and Houston 1987, Berger and Cunningham 1988) and that trade-off is particularly acute during the reproductive season (Lima and Dill 1990). Other ungulates are known to change foraging behavior to minimize predation. In Michigan, female moose with calves sacrifice high-quality diets in choosing home ranges on small islands free from wolves (*Canis lupus*) (Edwards 1983). Populations of caribou (*Rangifer tarandus*) persist on islands in Lake Superior with lower predation pressure despite reduced quantity and variety of forage (Ferguson et al. 1988). When pronghorns (*Antilocapra americana*) are faced with increased probabilities of predation, they spend less time feeding and more time searching for predators (Berger et al. 1983). We believe that the need by deer in our study to spend more time feeding under heavy cattle stocking rates reduced the time available to rest and search for predators.

In addition, changes in the timing of feeding bouts by deer also may have affected their susceptibility to predation. In the absence of cattle grazing, most feeding bouts were initiated by deer during the dawn and dusk periods. Fewer bouts were begun during the middle of the day because of the potential added energetic costs of thermoregulation (Parker and Robbins 1984, Beier and McCullough 1990, Schmitz 1991), and at night, possibly because of increased chances of predation. Mountain lions (*Felis concolor*) are efficient predators of adult mule deer, are abundant in the Sierra Nevada (Neal et al. 1987), and may be more active at night (Seidensticker et al. 1973). With moderate cattle stocking rates, deer in our study added feeding bouts during the day but not at night. Only with heavy cattle stocking did deer initiate more feeding bouts at night (Table 4). During nights with bright moonlight, deer fed less and shifted feeding activities to other times of the day.

Conversely, stocking rates did not affect the time cattle spent feeding. Cattle also increased, not decreased, the number of feeding bouts initiated during nights with bright moonlight. There were no efficient predators on adult cows in McCormick Creek Basin.

We again caution that this study was not replicated outside McCormick Creek Basin, and that these results and our interpretation of them are specific to that site. We hypothesize that similar results would be obtained in other similar areas of the Sierra Nevada, but testing of such hypotheses remains to be done. Management as scientific experimentation can provide some of those opportunities (Macnab 1983).

MANAGEMENT IMPLICATIONS

Results of our study suggest that competition occurs between cattle and female mule deer in McCormick Creek Basin, and that such competition likely has adverse population consequences for deer. Several cattle management strategies could reduce these adverse effects:

1. Hold cattle stocking rates at moderate levels, particularly through the end of the first week of August. The goals would be to minimize the loss of hiding cover for fawns until they are at least a month old, to ensure maximum levels of forage for adult females to allow them to meet the energetic demands of lactation while minimizing their exposure to predators, and to ensure good carryover of forage until the time the fawns are weaned.
2. Delay grazing entirely until early August, and then graze at moderate levels for the remainder of the summer, with the same goals as above.
3. Institute a deferred-rotation grazing system. One half of each allotment would be grazed in early summer and ½ in late summer, both at moderate levels. Rotate the order of grazing each year.
4. Institute a multi-allotment, rest-rotation grazing system. Only graze each allotment 1 or 2 years out of every 3. This alternative represents the greatest change from the current situation, but the economic benefits would be great as well (Loomis et al. 1991).

LITERATURE CITED

BELOVSKY, G. E. 1978. Diet optimization in a generalist herbivore: the moose. Theoretical Population Biol. 14:105–134.

———. 1984. Herbivore optimal foraging: a comparative test of three models. Am. Nat. 124:97–115.

BEIER, P., AND D. R. MCCULLOUGH. 1990. Factors influencing white-tailed deer activity patterns and habitat use. Wildl. Monogr. 109:1–51.

BERGER, J., AND C. CUNNINGHAM. 1988. Size-related effects on search times in North American grassland female ungulates. Ecology 69:177–183.

———, D. DANEKE, J. JOHNSON, AND S. BERWICK. 1983. Pronghorn foraging economy and predator avoidance in a desert ecosystem: implications for the conservation of large mammalian herbivores. Biol. Conserv. 25:193–208.

BIRCH, L. C. 1957. The meanings of competition. Am. Nat. 91:5–18.

BOWYER, R. T. 1984. Sexual segregation in southern mule deer. J. Mammal. 65:410–417.

———. 1986. Habitat selection by southern mule deer. Calif. Fish and Game 72:153–169.

———, AND V. C. BLEICH. 1984. Effects of cattle grazing on selected habitats of southern mule deer. Calif. Fish and Game 70:240–247.

CARL, G. R., AND C. T. ROBBINS. 1988. The energetic cost of predator avoidance in neonatal ungulates: hiding versus following. Can. J. Zool. 66: 239–246.

COLLINS, W. B., AND P. J. URNESS. 1983. Feeding behavior and habitat selection of mule deer and elk on northern Utah summer range. J. Wildl. Manage. 47:646–663.

EDWARDS, J. 1983. Diet shifts in moose due to predator avoidance. Oecologia (Berlin) 60:185–189.

ELLIS, J. E., AND M. TRAVIS. 1975. Comparative aspects of foraging behavior of pronghorn antelope and cattle. J. Appl. Ecol. 12:411–420.

FERGUSON, S. H., A. T. BERGERUD, AND R. FERGUSON. 1988. Predation risk and habitat selection in the persistence of a remnant caribou population. Oecologia 76:236–245.

FREUND, R. J., AND R. C. LITTELL. 1981. SAS for linear models: a guide to the ANOVA and GLM procedures. SAS Inst., Inc., Cary, N.C. 231pp.

GARSHELIS, D. L., H. B. QUIGLEY, C. R. VILLARRUBIA, AND M. R. PELTON. 1982. Assessment of telemetric motion sensors for studies of activity. Can. J. Zool. 60:1800–1805.

GATES, C. C., AND R. J. HUDSON. 1983. Foraging behavior of wapiti in a boreal forest enclosure. Nat. Can. (Que.) 110:197–206.

GEIST, V. 1981. Behavior: adaptive strategies in mule deer. Pages 157–223 *in* O. C. Wallmo, ed. Mule and black-tailed deer of North America. Univ. Nebraska Press, Lincoln.

GILLINGHAM, M. P., AND F. L. BUNNELL. 1985. Reliability of motion-sensitive radio collars for estimating activity of black-tailed deer. J. Wildl. Manage. 49:951–958.

GREEN, R. A., AND G. D. BEAR. 1990. Seasonal cycles and daily activity patterns of Rocky Mountain elk. J. Wildl. Manage. 54:272–279.

HANLEY, T. A. 1982. Cervid activity patterns in relation to foraging constraints: western Washington. Northwest Sci. 56:208–217.

———. 1984. Relationships between Sitka black-tailed deer and their habitat. U.S. For. Serv., Pac. Northwest For. and Range Exp. Stn. Gen. Tech. Rep. PNW-168. 21pp.

KIE, J. G., AND S. A. MYLER. 1987. Use of fertilization and grazing exclusion in mitigating lost meadow production in the Sierra Nevada, California, USA. Environ. Manage. 11:641–648.

LAUTIER, J. K., T. V. DAILEY, AND R. D. BROWN. 1988. Effect of water restriction on feed intake of white-tailed deer. J. Wildl. Manage. 52:602–606.

LEOPOLD, A. S., T. RINEY, R. MCCAIN, AND L. TEVIS, JR. 1951. The Jawbone deer herd. Game Bull. 4, Calif. Dep. Nat. Resour., Div. Fish and Game, Sacramento. 139pp.

LIMA, S. L., AND L. M. DILL. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Can. J. Zool. 68:619–640.

LOFT, E. R. 1988. Habitat and spatial relationships between mule deer and cattle in a Sierra Nevada forest zone. Ph.D. Thesis, Univ. California, Davis. 144pp.

———, R. C. BERTRAM, AND D. H. BOWMAN. 1989. Migration patterns of mule deer in the central Sierra Nevada. Calif. Fish and Game 75:11–19.

———, J. W. MENKE, AND J. G. KIE. 1991. Habitat shifts by mule deer: the influence of cattle grazing. J. Wildl. Manage. 55:16–26.

———, ———, ———, AND R. C. BERTRAM. 1987. Influence of cattle stocking rate on the structural profile of deer hiding cover. J. Wildl. Manage. 51:655–664.

LOOMIS, J. B., E. R. LOFT, D. R. UPDIKE, AND J. G. KIE. 1991. Cattle-deer interactions in the Sierra Nevada: a bioeconomic approach. J. Range Manage. 44:395–399.

MACARTHUR, R. H. 1972. Geographical ecology—patterns in the distribution of species. Harper and Row, New York, N.Y. 269pp.

MACNAB, J. 1983. Wildlife management as scientific experimentation. Wildl. Soc. Bull. 11:397–401.

MANGEL, M., AND C. W. CLARK. 1986. Towards a unified foraging theory. Ecology 67:1127–1138.

MCNAMARA, J. M., AND A. I. HOUSTON. 1987. Starvation and predation as factors limiting population size. Ecology 68:1515–1519.

NEAL, D. L., G. N. STEGER, AND R. C. BERTRAM. 1987. Mountain lions: preliminary findings on home-range use and density in the central Sierra Nevada. U.S. For. Serv., Pac. Southwest For. and Range Exp. Stn., Res. Note PSW-392. 6pp.

PARKER, K. L., AND C. T. ROBBINS. 1984. Thermoregulation in mule deer and elk. Can. J. Zool. 62:1409–1422.

———, ———, AND T. A. HANLEY. 1984. Energy expenditures for locomotion by mule deer and elk. J. Wildl. Manage. 48:474–488.

PETERSON, R. A., AND E. J. WOOLFOLK. 1955. Behavior of Hereford cows and calves on short grass range. J. Range Manage. 8:51–57.

PIERCE, G. J., AND J. G. OLLASON. 1987. Eight reasons why optimal foraging theory is a complete waste of time. Oikos 49:111–117.

PYKE, G. 1984. Optimal foraging theory: a critical review. Annu. Rev. Ecol. Syst. 15:523–575.

REMPEL, R. D., AND R. C. BERTRAM. 1975. The Stewart modified corral trap. Calif. Fish and Game 61:237–239.

SCHOENER, T. W. 1971. Theory of feeding strategies. Annu. Rev. Ecol. Syst. 2:369–404.

SCHMITZ, O. J. 1991. Thermal constraints and optimization of winter feeding and habitat choice in white-tailed deer. Holarctic Ecol. 14:104–111.

SEIDENSTICKER, J. C., IV, M. G. HORNOCKER, W. V. WILES, AND J. P. MESSICK. 1973. Mountain lion social organization in the Idaho Primitive Area. Wildl. Monogr. 35:1–60.

STEEL, R. G. D., AND J. H. TORRIE. 1980. Principles and procedures of statistics: a biometrical approach. Second ed. McGraw-Hill, New York, N.Y. 633pp.

STEPHENS, D. W., AND J. R. KREBS. 1986. Foraging theory. Princeton Univ. Press, Princeton, N.J. 247pp.

STOVER, S. L. 1985. Silviculture and grazing in the New Forest: rival land uses over nine centuries. J. Forest Hist. 29:32–42.

SWIHART, R. K., N. A. SLADE, AND B. J. BERGSTROM. 1988. Relating body size to the rate of home range use in mammals. Ecology 69:393–399.

WAGNON, K. A. 1963. Behavior of beef cows on a California range. Univ. Calif. Agric. Exp. Stn. Bull. 799. 58pp.

WINCKEL, J. 1989. Effects of cattle grazing in a mountain meadow on the feeding behavior and nutrition of mule deer. M.S. Thesis, Univ. California, Davis. 99pp.

WORTON, B. J. 1989. Kernel methods for estimating the utilization distribution in home-range studies. Ecology 70:164–168.

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