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SELECTIVE FEEDING BY BLACK-TAILED DEER: FORAGE QUALITY OR ABUNDANCE?

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Selectivity of forages by ungulates may be in response to the abundance of forages (forage-abundance hypothesis) or the nutrient quality of palatable forages (selective-quality hypothesis). I examined predictions of both hypotheses by measuring feeding behaviors of free-ranging black-tailed deer (*Odocoileus hemionus columbianus*) at Hopland Field Station, Mendocino Co., California. I observed 98 foraging sessions (foraging bout of 7–10 min) of adult males and females in all seasons and measured the number of bites, time the head was in the feeding position, type of forage, and biomass of plants along foraging paths. Selection (seconds per bite) was strongly correlated with biomass of forages only when deer foraged on dried grass or forbs. Seconds per bite varied considerably among types of forages: green grass-forbs ($\bar{X} = 1.3$ s), leafy browse (3.8 s), dry grasses and forbs (6.1 s), acorns (19.6 s). The head was in the feeding position significantly less when foraging on dry grasses and forbs, and acorns than when deer foraged on green grass-forbs and leafy browse. Selectivity (seconds per bite) of leafy browse and acorns by deer was correlated with Julian date, an index to nutrient content. Number of bites was positively related to time the head was in the feeding position only when deer foraged on green grass-forbs. Selectivity of deer ostensibly varied in response to nutrient content, and searching was probably the dominant process influencing selectivity on most types of forages.

Key words: black-tailed deer, *Odocoileus hemionus columbianus*, forage selectivity, California

Deer (*Odocoileus*) are selective foragers (Hofmann, 1989; Robbins, 1983); yet, how selectivity changes with abundance and quality of resources is poorly understood (Weckerly and Kennedy, 1992). Animals with a large breadth of diet may become more selective with increases in forage biomass because of an increase in foraging efficiency, or they may become more selective with a decrease in quality of available forage because of a small breadth of diet imposed by constraints of digestive anatomy (Hofmann, 1989; Jarman and Sinclair, 1979; Robbins, 1983; Schoener, 1971; Weckerly and Kennedy, 1992).

Weckerly and Kennedy (1992) provided

indirect evidence from white-tailed deer (*Odocoileus virginianus*) that suggested selectivity was related more to forage quality than to abundance. They reported seasonal composition of diet varied with nutritional composition (selective-quality hypothesis) more than the abundance of forages (forage-abundance hypothesis). I determined if selectivity of free-ranging black-tailed deer (*Odocoileus hemionus columbianus*) was correlated with the biomass of forages along feeding paths, the direction of selection (i.e., positive or negative) in relation to forage quality, and relationships between number of bites taken and the time the head is in a position to take a bite. If the forage-

abundance hypothesis is correct, selectivity (seconds per bite) should be positively correlated with total biomass of forage along paths of foraging deer. The selective-quality hypothesis predicts that if selectivity is correlated with forage biomass, it is during periods when food resources of high quality are scant and the association is with specific, more palatable, types of forages. Also, selectivity should be less when high-quality resources are more abundant.

Determining relationships between bites taken and time the head is in the "feeding position" (a posture where it is possible for an animal to take a bite) is examined to understand how changes in forage quality affect search and handling time of large herbivores (*sensu* Spalinger et al., 1988). While foraging to maximize nutrient intake, animals that are not searching, and have constant handling or chewing time per bite, should exhibit a positive relationship between number of bites and time the animal's head is in the feeding position. The slope, furthermore, should be a function of handling time; longer handling times result in shallower slopes. If the amount of time spent searching and handling forage is dynamic within foraging bouts, even if searching overlaps handling (Hobbs and Spalinger, 1992), the relationship between number of bites taken and time the head is in the feeding position may be obscured.

Measuring these relationships for foraging deer across a spectrum of forage types that vary in quality helps decide which hypothesis is more appropriate. When forage quality is low, assuming forage quantity is not limiting, animals that have wide breadths of diet (*i.e.*, forage-abundance hypothesis) should be less selective because there is little search time and animals take bites as quickly as they can process or handle one to several bites. There is variable search and handling time between bites, according to the selective-quality hypothesis, when forage quality is low, because animals choose less-available items that are relatively high in nutrients or that reduce han-

dling time (Murden and Risenhoover, 1993; Spalinger et al., 1988).

When feeding on abundant forages of high quality, animals with a wide breadth of diet should become more selective. Hence, search time becomes variable and feeding time should not be coupled with number of bites. Animals with a narrow breadth of diet, however, should have little search time and more constant handling time because they are taking bites as quickly as they can process them. Hence, number of bites taken should be coupled with feeding time within foraging bouts.

MATERIALS AND METHODS

Black-tailed deer were observed on Hopland Field Station, Mendocino Co., northern California (39°N, 123°4'W). The field station was 2,149 ha and located on the east side of the Russian River Valley. Topography was rough with elevation ranging from 180 to 855 m. The climate was Mediterranean with hot, dry summers, and cool, moist winters. Average minimum and maximum temperatures at 245 m elevation were 1 and 12°C, respectively, for January and 11 and 33°C for July. Rainfall mostly occurred between October and May, averaging 91.7 cm annually, but varied widely from year to year.

A mosaic of oak (*Quercus*), annual grassland, and chamise (*Adenostoma fasciculatum*) chaparral occurred at the station. About 52% of the station was oak-type habitat, 32% was grassland, and 13% was chaparral. Ubiquitous trees of oak-woodland and oak-grassland habitats (Weckerly, 1993) were blue oak (*Quercus douglasii*), black oak (*Q. kelloggii*), interior live oak (*Q. wislizenii*), valley oak (*Q. lobata*), and madrone (*Arbutus menziesii*). Grasslands were composed of mostly introduced annual grasses (*Avena*, *Bromus*) and forbs (*Erodium*, *Medicago*), that grow during the rainy season. Chaparral habitats were mostly dense stands of chamise that contained scrub oak (*Q. durata*), ceanothus (*Ceanothus*), and manzanita (*Arctostaphylos*).

I observed free-ranging, foraging deer through a 45× monocular telescope at distances of 100–400 m during daylight hours. The first observable adult I detected was selected, and no more than four deer were measured at any site. I selected observation sites that had multiple types of forages for consumption. Foraging ob-

servations lasted 7–10 min. If an animal ceased foraging for >1 min or if it detected my presence, the trial was terminated. I recorded 98 foraging sessions (53 males, 45 females) from April 1990 to June 1991 (1 in spring 1990, 15 in autumn 1990, 45 in winter 1991, 29 in spring 1991, and 8 in summer 1991).

For each foraging session, I recorded the number of bites taken, type of forage, time the head was in the feeding position (seconds per minute), the biomass along the foraging path, and Julian date. Additional variables measured that did not have detectable influences on selectivity by deer included distance traveled while foraging and number of deer within 20 m of the focal animal (Weckerly, 1993).

Type of forage was categorized with respect to my capability of precisely and accurately measuring number of bites and time the head was in the feeding position. The types of forages, which included all kinds of foods deer consumed throughout the seasons (Longhurst et al., 1979; Weckerly, 1993), were green grass or forbs, leafy browse, dry forage, and acorns. Green grass or forbs were consumed from October to May. Commonly consumed species were *Erodium*, *Medicago*, and new growth of grasses (Longhurst et al., 1979). Green grass-forbs was high in crude protein and relatively low in fiber (Jones, 1967; Jones et al., 1990), and I considered this type of forage to be a high-quality food. Leafy browse was consumed mostly from February to May and included blue oak, black oak, live oak, valley oak, chamise, and scrub oak. I considered leafy browse a nutritious food (Longhurst et al., 1979). Deer grazing during the dry season, May to September, were classified as feeding on dry forage. This was a heterogeneous category because animals foraged on dried grasses and forbs and fallen leaves and lichens from trees and shrubs. Dry forages were considered a poor-quality diet because of low values of fecal nitrogen during months when these foods predominated (Massey et al., 1994) and the reported low nutrient and high-fiber content of dried grasses and forbs (Jones, 1963) and dried leaves (Weckerly, 1988). Acorns of blue oak, valley oak, and live oak were consumed from September to February. I considered acorns to be a high-quality source of food. Although acorns are high in fiber (Weckerly and Nelson, 1990) they contain high levels of digestible carbohydrates and lipids (McCullough,

1979; McCullough and Ullrey, 1985; Pekins and Mautz, 1988).

For a grazing deer, I defined the head to be in the feeding or searching position if the head was below the plane of its dorsum; when browsing; the feeding position was the head oriented toward the shrub or tree the animal was eating. I assumed that when the head was in the feeding position it was solely for purposes of foraging.

Biomass of plants along the path (1 m in width) traveled by foraging deer was estimated as reported in Weckerly (1993). Acorns collected from wire traps (60 cm in diameter) were shelled, oven-dried, and weighed to the nearest 0.01 g to determine their average mass. Available biomass of acorns was estimated as the product of the number of acorns along the foraging path of deer and average mass of an acorn. For the remaining plants, an index from percent cover and plant height was calibrated with mass of dry matter from plant parts clipped in 30.5-cm² plots. When deer foraged on grass-forbs, dry forage, and acorns, there were a number of food types along the foraging path. In statistical analyses, biomass was grouped into total biomass along foraging path and by forage type that the animal presumably was consuming. Lichens were pooled with fallen leaves because they were scant (1 g for all foraging paths combined) and always occurred under canopies of trees.

My measure of selectivity was time the head was in the feeding position per number of bites when the head was in the feeding position (reported as seconds per bite). I chose this variable over the more typical measure of selectivity (amount consumed versus amount available) because I wanted to examine behaviors that influence forage choice, not the outcome of that choice (Spalinger et al., 1988).

Correlation analyses (Zar, 1984) were used to examine relationships between biomass and selectivity and number of bites and time the head was in the feeding position. Because number of bites and time the head was in the feeding position was significantly different on the different types of forage (Weckerly, 1993), correlations between seconds per bite and biomass were examined for each type of forage. Relationships also were examined between selectivity and date when deer fed on acorns and leafy browse. Julian day, for leafy browse, and date since first-recorded foraging on acorns were used as indices of forage quality. The nutritional content of

TABLE 1.—*Descriptive statistics from foraging sessions of seconds per bite (also reported as bites per minute), time head in feeding position, and dry biomass of various types of plants along foraging path of black-tailed deer at Hopland Field Station, California, 1990–1991.*

Forage type	\bar{X}	SE	n
Seconds/bite (bites/min)			
Grass-forbs	1.3 (46.0)	0.05 (1.77)	42
Leafy browse	3.8 (15.8)	0.56 (2.32)	17
Dry forage	6.1 (9.8)	1.60 (2.57)	12
Acorns	19.6 (3.1)	3.01 (0.48)	27
Time head in feeding position (s/min)			
Grass-forbs	49.6	1.2	42
Leafy browse	49.6	1.4	17
Dry forage	40.9	2.4	12
Acorns	42.7	1.5	27
Dry biomass (g/m ²)			
Grass-forbs	24.1	0.81	42
Leafy browse	9.1	1.41	17
Dry forage			
Total ^a	28.6	4.2	12
Dried grass-forbs	23.6	5.11	12
Acorns			
Total ^b	37.7	3.28	27
Acorns	11.7	2.63	27

^a Fallen leaves, lichens, and grass-forbs.

^b Grass-forbs, fallen leaves, and acorns.

acorns was assumed to decline in late autumn and winter because the percentage of damaged and nonviable acorns on the ground is higher (McShea and Schwede, 1993; Sork and Boucher, 1977; Sork et al., 1983), and the nutrient content of leafy browse was assumed to increase in spring with the onset of rapid growth (Scrivner et al., 1988; Taber, 1956; Taber and Dasmann, 1958). For some correlations, the natural logarithm of seconds per bite was used to improve linearity. When using stepwise regression, criteria for variables to be entered, at each step, was $P < 0.015$, and no variable with $P > 0.05$ was allowed to remain in the equation. Because many of the correlation analyses were on the same family of data, probability values were adjusted with the sequential Bonferroni technique (Rice, 1989). Unadjusted probability values, however, are reported in tables. Differences among forage types in the natural logarithm of seconds per bite and time the head was in the

TABLE 2.—*Pearson's correlation coefficients between seconds per bite and various types of plant dry biomass along forage paths of black-tailed deer at Hopland Field Station, California, 1990–1991.*

Seconds/bite ^a versus	r	P ^b	n
Green grass-forbs			
Biomass	0.28	0.08	42
Percentage forbs along path	0.01	0.97	29
Leafy browse			
Biomass	0.31	0.23	17
Dry forage			
Total biomass ^c	-0.64	0.02	12
Biomass dried grass-forbs	-0.90	<0.01	11
Acorns			
Total biomass ^d	-0.13	0.51	27
Acorn biomass	-0.13	0.51	27

^a The natural logarithm of seconds per bite was used for correlations between dry forage and acorns.

^b $P < 0.05$ were significant after Bonferroni adjustment.

^c Fallen leaves, lichens, and dried grass-forbs.

^d Fallen leaves, grass-forbs, and acorns.

feeding position were examined with one-way analysis of variance (ANOVA—Sokal and Rohlf, 1981). Fisher's protected least significant difference (LSD) procedure for multiple comparisons was used to identify nonsignificant subsets if the ANOVA detected significant differences (Zar, 1984).

RESULTS

Feeding behavior exhibited by deer changed dramatically among forage types (Table 1). Averages for seconds per bite ranged from 1.3 on grass-forbs to 19.6 on acorns. Mean time the head was in the feeding position was greatest ($\bar{X} = 49.6$ s/min) when deer fed on grass-forbs and browse, and least ($\bar{X} = 40.9$) when they grazed on dry forage. Mean biomass (grams of dry matter per square meter) of plants along the feeding paths of deer ranged from 9.1 when deer ate leafy browse to 37.7 when animals foraged acorns.

Biomass of green grass-forbs and percentage of foraging path that was covered with forbs were not associated with selec-

tivity by deer (Table 2). Also, biomass of leafy browse, total plant biomass when foraging on acorns, and biomass of acorns were not associated with selectivity. Seconds per bite exhibited an inverse relationship with total biomass for dry forage. The inverse relationship was much stronger, however, when only considering biomass of dried grass-forbs.

Black-tailed deer showed considerable variation among forage types in selectivity (ANOVA, $F = 15.45$, $d.f. = 3$, 94 , $P = 0.0001$; Table 1). Using the Fisher's protected LSD for multiple comparisons, no differences were detected in seconds per bite on grass-forbs, browse or dry forage, although dry forage was marginally nonsignificant from grass-forbs ($P = 0.08$). Deer were much more selective when feeding on acorns ($P < 0.0001$).

Seconds per bite did not vary between the sexes among the four types of forages (Table 1; ANOVA, $F = 2.15$, $d.f. = 1$, 90 , $P = 0.15$), and the lack of an intersexual difference was consistent among types of forages (sex-by-forage interaction; $F = 0.94$, $d.f. = 3$, 90 , $P = 0.42$). Also, the risk of predation to foraging deer in more open habitats did not appear to influence selectivity or time the head was in the feeding position. When foraging on green grass-forbs, there was no significant difference between deer in forested (oak grassland, oak woodland, chaparral grassland) and those in open (grassland) habitats in seconds per bite (forest, $\bar{X} = 1.61$; grassland, $\bar{X} = 1.55$; $F = 0.87$, $d.f. = 1$, 40 , $P = 0.36$) and in the time the head was in the feeding position (forest, $\bar{X} = 50.6$ s/min; grassland, $\bar{X} = 48.6$ s/min; $F = 0.67$, $d.f. = 1$, 40 , $P = 0.42$). Deer were more selective when grazing on dry forage in forested than open habitats (forest, $\bar{X} = 8.72$ s/bite; grassland, $\bar{X} = 2.58$ s/bite; $F = 4.89$, $d.f. = 1$, 10 , $P = 0.05$). The difference in selectivity may have been influenced by differences in total biomass between habitat categories because there was significantly more total forage biomass in grassland than forested habitats

(forest, $\bar{X} = 21.8$ g/m²; grassland, $\bar{X} = 38.8$ g/m²; $F = 14.07$, $d.f. = 1$, 10 , $P = 0.004$). Furthermore, there was little difference in time the head was in the feeding position between animals in forested habitats and those in open habitats when grazing on dry forage (forest, $\bar{X} = 40.8$ s/min; grassland, $\bar{X} = 41.4$ s/min; $F = 0.02$, $d.f. = 1$, 10 , $P = 0.90$).

There was a significant positive relationship between number of bites and time the head was in the feeding position for deer foraging on grass-forbs (Fig. 1). A lack of association between these variables ($P \geq 0.38$) was apparent when deer fed on the remaining types of forages.

Deer foraging on acorns often lifted their heads after taking a bite, presumably to handle the bite because acorns are larger and often are shelled in their mouths (Weckerly, 1993). This behavior influenced the time that the animal's head was in the feeding position. Time the head was in the feeding position was significantly shorter when eating acorns and dry forage than when eating grass-forbs and leafy browse (Table 1; $F = 8.0$, $d.f. = 3$, 94 , $P = 0.0001$; Fisher's protected LSD).

There were significant relationships between my index of nutrient quality, Julian date, and selectivity when deer fed on acorns and leafy browse (Fig. 2). Deer spent more time searching for acorns in January and February. Conversely, selectivity was less in spring than winter when animals fed on leafy browse.

The relationships between date and seconds per bite was not confounded by forage biomass along the feeding path for acorns and leafy browse. There was no relationship between browse biomass and Julian day ($r^2 = 0.01$, $n = 17$, $P = 0.66$). The relationship between acorn biomass and date approached significance ($r^2 = 0.12$, $n = 27$, $P = 0.08$; $\hat{y} = 12.32 - 2.55x$). When an outlier was removed, however, the relationship between these two variables was significant ($r^2 = 0.28$, $n = 26$, $P = 0.006$; $\hat{y} = 10.07 - 2.17x$). Yet, a stepwise regres-

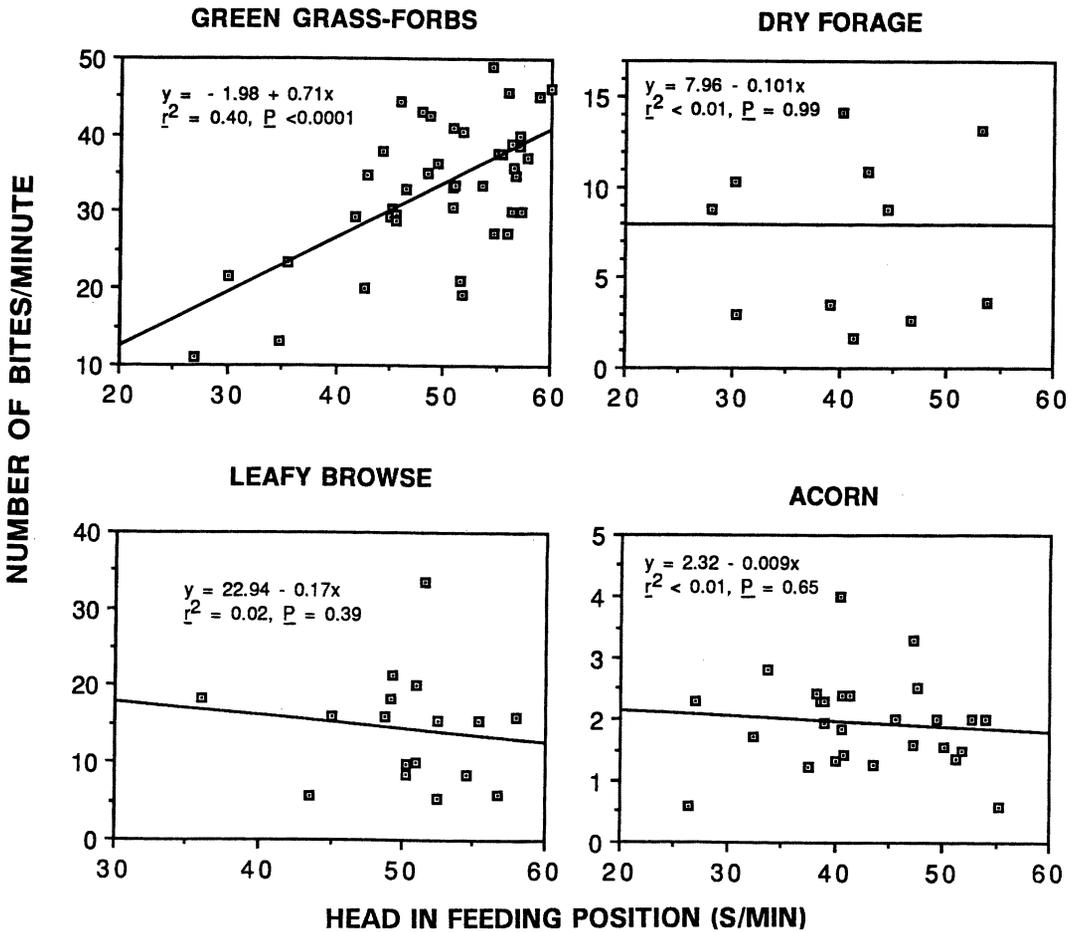


FIG. 1.—Relationships between number of bites and time the head is in the feeding position of foraging black-tailed deer on four types of forages at Hopland Field Station, California, 1990–1991.

sion (outlier removed), with seconds per bite as dependent variable and date and acorn biomass as possible predictor variables, only entered date ($r^2 = 0.194$, $n = 26$, $P = 0.024$; $\hat{y} = 7.66 + 0.138x$).

DISCUSSION

Black-tailed deer appear to alter their selective feeding behavior more in accord with the selective-quality hypothesis. Apparently, nutrient content was the predominant factor that influenced seconds per bite of deer foraging on browse, acorns, and dry forage. Selectivity was lowest on the easily processed and nutritious green grasses and forbs. Furthermore, deer were more selec-

tive of acorns and leafy browse when their nutritional content was probably lower. Only when deer fed on dry forage was selectivity associated with biomass. Nonetheless, the strongest correlation was with the herb component of total plant biomass along the foraging path, and the direction of the correlation (higher selectivity with lower biomass) was opposite to the predictions of the forage-abundance hypothesis (Schoener, 1971; Weckerly and Kennedy, 1992). The inverse correlation probably is a reflection of less searching because of a higher density of suitable bites at high biomass of dried grass-forbs (Hobbs and Spalinger, 1992; Spalinger et al., 1988). Fur-

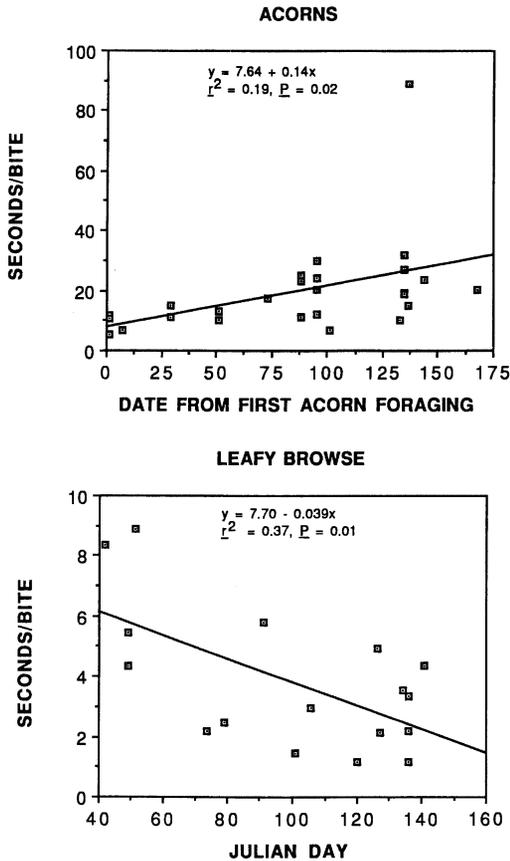


FIG. 2.—Regressions of selectivity (seconds per bite) with Julian day (leafy browse) and date (acorns). Date represents sequential days starting from the first recorded foraging session of black-tailed deer eating acorns (2 October 1990) on Hopland Field Station, California.

thermore, this outcome would be expected with animals possessing a smaller breadth of diet (Weckerly and Kennedy, 1992).

The selective-quality hypothesis cannot by itself, however, explain the change in selectivity among the different forage types. Acorns are a nutritious food source (McCullough and Ullrey, 1985; Pekins and Mautz, 1988) so, according to this hypothesis, selectivity should have been less because of a more constant handling and search time, when feeding under oak canopies, or number of bites should have been correlated with time the head is in the feed-

ing position. The likely reason for the high selectivity when deer are eating acorns is the constraint of high handling time (\bar{X} mass of acorn endosperm = 2.06 g; Weckerly, 1993) associated with a large bite (Spalinger et al., 1988) and shelling. Because of the long handling time, which can restrict food intake (Spalinger et al., 1988), it would be advantageous to select acorns that are whole and undamaged (Duvendek, 1962; Weckerly et al., 1989a, 1989b) and perhaps high in nutrient content.

Searching for whole and undamaged acorns probably requires a great effort by deer (Murden and Risenhoover, 1993) because animals rarely took bites of grass-forbs; whether the acorns were in dried vegetation or more nutritious green grass-forbs. Although acorns are concentrated under the canopies of oaks, the effort to select nutritious acorns probably is not less than the effort expended on many other forages (Pekins and Mautz, 1988).

As evident by the positive relationship between number of bites and time the head is in the feeding position, grazing on green grasses and forbs was the only type of forage in which handling may have directly dictated (i.e., little searching) selectivity. Searching appeared to be the process that influenced selectivity when feeding on leafy browse, acorns, and dry forage. The reason deer searched extensively is probably because of the high handling time. Deer should select bites that yield the greatest amount of nutrients in relation to their digestive constraints. Those constraints are probably a relatively short time of retention of digesta (Robbins, 1983) and restricted buccal processing capabilities of forages that vary in size and amount of fiber (Shipley and Spalinger, 1992). The importance of selecting a nutritious bite in relation to restricted digestive capabilities is illustrated when deer foraged on acorns. Feeding time within a foraging session was less than for other forages as was bite rate. Assuming deer were maximizing forage intake, they

had to select acorns that maximized nutrient assimilation.

Another reason why animals had a high searching time, excluding feeding on green grass-forbs, may be related to their physical condition. If animals are on a higher nutritional plane, such as eating acorns and leafy browse in winter when green grass-forbs may be abundant, they may be even more selective about bites they choose (Murden and Risenhoover, 1993).

An intriguing finding was that selectivity was not influenced by vigilance behavior as indexed by whether animals were grazing in grass-forbs in open or more closed types of habitats. The time an animal's head was in the feeding position has been shown to vary dramatically with distance to escape cover for bighorn sheep (*Ovis canadensis*), pronghorn (*Antilocapra americana*), moose (*Alces alces*), and mule deer (*O. hemionus*) in open habitats (Berger, 1991; Berger and Cunningham, 1988; Molvar and Bowyer, 1994). Possibly, animals on Hopland Field Station failed to alter selectivity in relation to presumed increases in risk of predation because of a localized absence of effective predators of adults. Mountain lions (*Felis concolor*) probably were rare and infrequent on Hopland Field Station (pers. obser.).

When examining vigilance of ungulates via the commonly used measure of time the head is in the feeding position (Berger and Cunningham, 1988) it may be necessary to consider types of forages as well. For example, when deer on Hopland Field Station foraged in green grass-forbs the time their heads were in the feeding position was ca. 9 s longer than when feeding in dried grass-forbs. Deer may have been motivated to forage more intensely on nutritious green grass-forbs and, when grazing in dried pastures, there may not have been sufficient reward to warrant intense searching (Robbins, 1983). I consider it unlikely that risk of predation was the only factor that could explain that difference in time the head was in the feeding position.

Black-tailed deer exhibited distinctive selective behavior on each type of forage at Hopland Field Station. Animals grazing in green pastures had a high bite rate and a relatively long feeding time. Browsing deer had a relatively lower bite rate. Individuals were selective when consuming acorns and grazing in dried pastures, and the feeding time within a foraging bout was relatively short. When initiating a foraging bout, animals may choose what kind of forage they will feed upon as opposed to evaluating all kinds of forages along their foraging path. How this choice affects the spatial patterns of black-tailed deer (habitat selection, home-range size and fidelity) remains poorly understood (Weckerly, 1993) and warrants further investigation.

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LITERATURE CITED

- BERGER, J. 1991. Pregnancy incentives, predation constraints and habitat shifts: experimental and field evidence for wild bighorn sheep. *Animal Behaviour*, 41:61-77.
- BERGER, J., AND C. CUNNINGHAM. 1988. Size-related effects on search time in North American grassland female ungulates. *Ecology*, 69:177-183.
- DUVENDECK, J. P. 1962. The value of acorns in the diet of Michigan deer. *The Journal of Wildlife Management*, 26:371-379.
- HOBBS, N. T., AND D. E. SPALINGER. 1992. Mechanisms of foraging in mammalian herbivores: new models of functional response. *The American Naturalist*, 140:325-348.
- HOFMANN, R. R. 1989. Evolutionary steps of eco-physiological adaptation and diversification of ruminants: a comparative view of their digestive system. *Oecologia* (Berlin), 78:443-457.

- JARMAN, P. J., AND A. R. E. SINCLAIR. 1979. Feeding strategy and the pattern of resource-partitioning in ungulates. Pp. 130–163, *in* Serengeti: dynamics of an ecosystem (A. R. E. Sinclair and M. Norton-Griffiths, eds.). University of Chicago Press, Chicago, 389 pp.
- JONES, M. B. 1963. Yield, percent nitrogen, and total nitrogen uptake of various California annual grassland species fertilized with increasing rates of nitrogen. *Agronomy Journal*, 55:254–257.
- . 1967. Forage and nitrogen production by subclover-grass and nitrogen-fertilized California grassland. *Agronomy Journal*, 59:209–214.
- JONES, M. B., M. W. DEMMENT, C. E. VAUGHN, G. P. DEO, M. R. DALLY, AND D. M. CENTER. 1990. Effects of phosphorus and sulfur fertilization on subclover-grass pasture production as measured by lamb gain. *Journal of Production Agriculture*, 3:534–539.
- LONGHURST, W. M., G. E. CONNOLLY, B. M. BROWNING, AND E. O. GARTON. 1979. Food interrelationships of deer and sheep in parts of Mendocino and Lake counties, California. *Hilgardia*, 47:191–247.
- MASSEY, B. N., F. W. WECKERLY, C. E. VAUGHN, AND D. R. MCCULLOUGH. 1994. Correlations between fecal nitrogen and diet composition in free-ranging black-tailed deer. *The Southwestern Naturalist*, 39:165–170.
- MCCULLOUGH, D. R., AND D. E. ULLREY. 1985. Chemical composition and gross energy of deer forage plants on the George Reserve, Michigan. Michigan State University Agriculture Experiment Station, Research Report, 465:1–19.
- MCCULLOUGH, Y. 1979. Carbohydrate and urea influences on *in vitro* deer forage digestibility. *The Journal of Wildlife Management*, 43:650–656.
- MCSHEA, W. J., AND G. SCHWEDE. 1993. Variable acorn crops: responses of white-tailed deer and other mast consumers. *Journal of Mammalogy*, 74:999–1006.
- MOLVAR, E. M., AND R. T. BOWYER. 1994. Costs and benefits of group living in a recently social ungulate: the Alaskan moose. *Journal of Mammalogy*, 75:621–630.
- MURDEN, S. B., AND K. L. RISENHOVER. 1993. Effects of habitat enrichment on patterns of diet selection. *Ecological Applications*, 3:497–505.
- PEKINS, P. J., AND W. M. MAUTZ. 1988. Digestibility and nutritional value of autumn diets of deer. *The Journal of Wildlife Management*, 52:328–332.
- RICE, W. R. 1989. Analyzing tables of statistical tests. *Evolution*, 43:223–225.
- ROBBINS, C. T. 1983. *Wildlife feeding and nutrition*. First ed. Academic Press, New York, 343 pp.
- SCHOENER, T. W. 1971. Theory of feeding strategies. *Annual Review of Ecology and Systematics*, 2:369–404.
- SCRIVNER, J. H., C. E. VAUGHN, AND M. B. JONES. 1988. Mineral concentrations of black-tailed deer diets in California chaparral. *The Journal of Wildlife Management*, 52:37–41.
- SHIPLEY, L. A., AND D. E. SPALINGER. 1992. Mechanics of browsing in dense food patches: effects of plant and animal morphology on intake rate. *Canadian Journal of Zoology*, 70:1743–1752.
- SOKAL, R. R., AND F. J. ROHLF. 1981. *Biometry: the principles and practice of statistics in biological research*. Second ed. W. H. Freeman and Company, San Francisco, 859 pp.
- SORK, V. L., AND D. H. BOUCHER. 1977. Dispersal of sweet pignut hickory in a year of low fruit production, and the influence of predation by a curculionid beetle. *Oecologia* (Berlin), 28:289–299.
- SORK, V. L., P. STACEY, AND J. E. AVERETT. 1983. Utilization of red oak acorns in a non-bumper crop year. *Oecologia* (Berlin), 59:49–53.
- SPALINGER, D. E., T. A. HANLEY, AND C. T. ROBBINS. 1988. Analysis of the functional response in foraging in the Sitka black-tailed deer. *Ecology*, 69:1166–1175.
- TABER, R. D. 1956. Deer nutrition and population dynamics in the north coast range of California. *Transactions of the North American Wildlife Conference*, 21:159–172.
- TABER, R. D., AND R. F. DASMANN. 1958. The black-tailed deer of the chaparral. *California Department of Fish and Game Bulletin*, 8:1–163.
- WECKERLY, F. W. 1988. Ecological studies relating to white-tailed deer in Tennessee. I. Evaluation of surveys for determining use of woody browse by white-tailed deer. II. Seasonal feeding strategies of white-tailed deer in Tennessee. Ph.D. dissert., Memphis State University, Memphis, Tennessee, 330 pp.
- . 1993. Intersexual resource partitioning of black-tailed deer: a test of the body size hypothesis. *The Journal of Wildlife Management*, 57:475–494.
- WECKERLY, F. W., AND M. L. KENNEDY. 1992. Examining hypotheses about feeding strategies of white-tailed deer. *Canadian Journal of Zoology*, 70:432–439.
- WECKERLY, F. W., AND J. P. NELSON, JR. 1990. Age and sex differences of white-tailed deer diet composition, quality, and calcium in Tennessee. *The Journal of Wildlife Management*, 54:532–538.
- WECKERLY, F. W., K. E. NICHOLSON, AND R. D. SEMLITSCH. 1989a. Experimental test of discrimination by squirrels for insect-infested and noninfested acorns. *The American Midland Naturalist*, 122:412–415.
- WECKERLY, F. W., D. W. SUGG, AND R. D. SEMLITSCH. 1989b. Germination success of acorns (*Quercus*): insect predation and tannins. *Canadian Journal of Forest Research*, 19:811–815.
- ZAR, J. H. 1984. *Biostatistical analysis*. Second ed. Prentice-Hall, Inc., Englewood Cliffs, New Jersey, 718 pp.

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