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USE OF QUAKING ASPEN FLOWER BUDS BY RUFFED GROUSE: ITS RELATIONSHIP TO GROUSE DENSITIES AND BUD CHEMICAL COMPOSITION[1]

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Abstract. Quaking aspen (*Populus tremuloides*) staminate flower buds are an important winter food for Ruffed Grouse (*Bonasa umbellus*); however, use of these buds can vary among years. One explanation for this differential use of aspen flower buds is that the buds' nutritional value or palatability changes. It has been proposed that fluctuations in the chemical content of aspen buds may affect their utilization by Ruffed Grouse, and that the utilization of aspen may be positively related to the population density these birds can maintain. This paper focuses on three key links of the above hypothesis: whether there are significant annual changes in the chemistry of aspen buds, whether aspen utilization by Ruffed Grouse is mediated by the chemistry of the buds, and whether there is a correlation between aspen use and changes in grouse densities. We monitored chemical changes in aspen flower buds periodically over 11 years and related chemical changes to aspen use and Ruffed Grouse densities. Additionally, previous studies were re-examined to determine the relationship between aspen consumption and changes in grouse densities. Significant differences were observed in coniferyl benzoate and protein levels among years. Data suggest that there may be inherent differences among aspen clones in their ability to chemically defend themselves. Use of aspen buds by grouse appears to be mediated by coniferyl benzoate and protein levels. Quaking aspen use was highly correlated to Ruffed Grouse densities. Lack of suitable or available aspen in the winter may increase predation risks and energetic costs for Ruffed Grouse.

Key words: Bonasa umbellus; Populus tremuloides; *coniferyl benzoate; secondary metabolite; population cycles; feeding behavior; phenylpropanoid;* Malacosoma disstria.

INTRODUCTION

Quaking aspen (*Populus tremuloides*) is widely recognized as an important food source for northern Ruffed Grouse (*Bonansa umbellus*) (Svoboda and Gullion 1972 and references therein). During many years, the winter diet of these birds consists primarily of quaking aspen staminate flower buds (Gullion 1966a, Vanderschaegen 1970, Svoboda and Gullion 1972, Doerr et al. 1974, Huempfner 1981). However, long term studies in Minnesota and Alberta indicate that winter use of quaking aspen may vary periodically and that low aspen use has coincided with declining or low grouse densities (Gullion 1970, 1984; Doerr et al. 1974; Huempfner 1981). Low use of quaking aspen can occasionally be attributed to a failure in the aspen bud crop (Gullion 1977); however, during many years of low use, the aspen bud crop has been ample (Doerr et al. 1974; Gullion 1977, 1984, and unpubl. data).

One explanation for this differential use of aspen flower buds (hereafter, bud will refer to staminate flower bud) is that the buds' nutritional value or palatability changes. Bud suitability is an important selection factor when Ruffed Grouse select an aspen in which to feed (Huff 1970, Jaku-

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bas et al. 1989, Jakubas 1989). Typically, winter use of aspen is restricted to certain trees or clones, with preference for specific trees changing over time (Gullion 1966a, Huff 1970, Schemnitz 1970, Huempfner 1981). Preference for certain trees is due, in part, to the concentration of coniferyl benzoate in the buds (Jakubas et al. 1989). Coniferyl benzoate (a phenylpropanoid ester) is a plant secondary metabolite which occurs only in the flower buds (Jakubas et al. 1989). Feeding trials indicate that coniferyl benzoate is aversive to Ruffed Grouse (Jakubas and Gullion 1990), European Starlings (*Sturnus vulgaris*) (Jakubas et al., in press), and insects (B. Jacobson, W.J.J., R. L. Lindroth, University of Wisconsin, unpub. data). Given the repellency of coniferyl benzoate, we postulate that annual fluctuations in coniferyl benzoate levels may affect aspen utilization by Ruffed Grouse. Furthermore, we propose that aspen utilization may be positively related to the population density these birds can maintain.

The inference that Ruffed Grouse densities may be partly determined by the availability of aspen buds is suggested by the association between Ruffed Grouse and the North American distribution of quaking aspen (Fig. 1), the high density these birds attain in areas where aspen is prominent (Svoboda and Gullion 1972), and the reported concurrent declines in Ruffed Grouse densities and quaking aspen use, as mentioned above. It is also in areas where aspen is prominent that the most pronounced 8–10 year cyclic fluctuations occur in Ruffed Grouse densities (Svoboda and Gullion 1972; Gullion 1977, 1984). Gullion (1984) speculated that fluctuations in the use of aspen buds by grouse may be due to changes in the buds' chemical composition, and that these chemical changes could actuate the Ruffed Grouse population cycle. Gullion's (1984) hypothesis is similar to those of Lauckhart (1957), Haukioja and Hakala (1975), and Bryant (1981), which offer explanations for other herbivore cycles. The underlying principle of these hypotheses is that changes in the overall nutritional value of plants, through changes in secondary metabolite or nutrient levels, can affect herbivore densities by altering the suitability of the animal's principle food.

This paper focuses on three key links of the proposed hypothesis that annual fluctuations in the chemistry of aspen buds are related to changes in Ruffed Grouse densities. The primary purpose of this study was to test for significant annual changes in the chemical composition of quaking aspen buds. Secondly, we investigated the relationship between changes in bud chemistry and annual use of aspen by Ruffed Grouse. Finally, we tested for a correlation between aspen use and Ruffed Grouse densities and reviewed the factors that might be responsible for such a correlation. All of the data necessary to accomplish these objectives were not available in any one study. Therefore, we investigated the relationship between quaking aspen use and grouse densities by reanalyzing previously published studies by Doerr et al. (1974) and Keith and Rusch (1989). Our investigation on the chemical changes in aspen buds focused on protein and coniferyl benzoate levels. Protein was the nutrient of choice for three reasons. First, Ruffed Grouse show a slight preference for buds with higher protein levels (Huff 1970, Doerr et al. 1974, Jakubas et al. 1989). Secondly, protein levels may influence the toxicity or repellency of certain plant secondary metabolites (Lindroth and Batzli 1984, Remington 1990). Finally, dietary protein levels can affect Ruffed Grouse reproductive success (Beckerton and Middleton 1982).

METHODS

POPULATION ESTIMATES

Minnesota Ruffed Grouse populations were monitored during the spring drumming season as part of on-going studies at the Cloquet Forestry Center and the Mille Lacs Wildlife Management Area using methods well described in earlier papers (Gullion 1965, 1966b; Gullion and Marshall 1968). The Mille Lacs and Cloquet study sites have been described, respectively, in Gullion (1981) and Gullion and Marshall (1968). Minnesota Department of Natural Resources (DNR) annual roadside drumming counts, for the north census zone, were used as regional estimates of grouse densities (Schultz 1985, Minnesota DNR, pers. comm.). The north census zone, which includes the Cloquet and Mille Lacs study sites, is a 10 county region near the middle of the state extending from the Canadian border to Sherburne county in the south (Schultz 1985).

Ruffed Grouse population estimates in Rochester, Alberta, were obtained from earlier studies (Keith and Rusch 1989, Rusch, pers. comm.). The Rochester study area has been described previously in Doerr et al. (1974) and Keith and Windberg (1978). Spring densities for drumming males were acquired using the methods in Gullion (1966b).

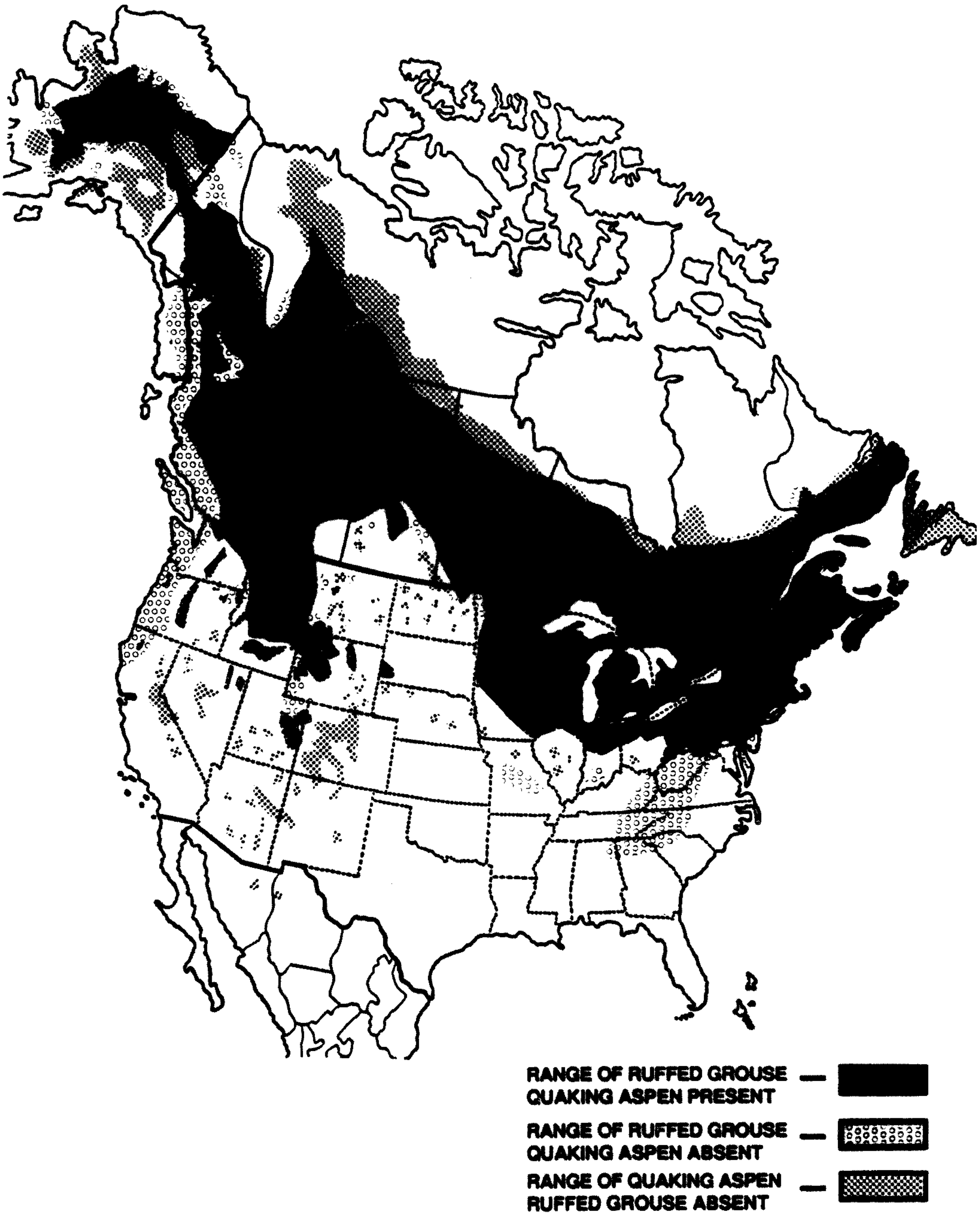

FIGURE 1. The distribution of Ruffed Grouse and quaking aspen in North America (data from Little 1971, Johnsgard 1973).

QUAKING ASPEN USE

Feeding observations were made approximately three times a week, from December to March, at Mille Lacs from 1985 to 1988 as described by Svoboda and Gullion (1972). In addition, records documenting Ruffed Grouse use of individual aspen since 1963 for Cloquet and since 1979 for Mille Lacs were available. Quaking aspen were classified as "used" trees if grouse were currently feeding on them. Quaking aspen classified as "unused" had no previous record of grouse use.

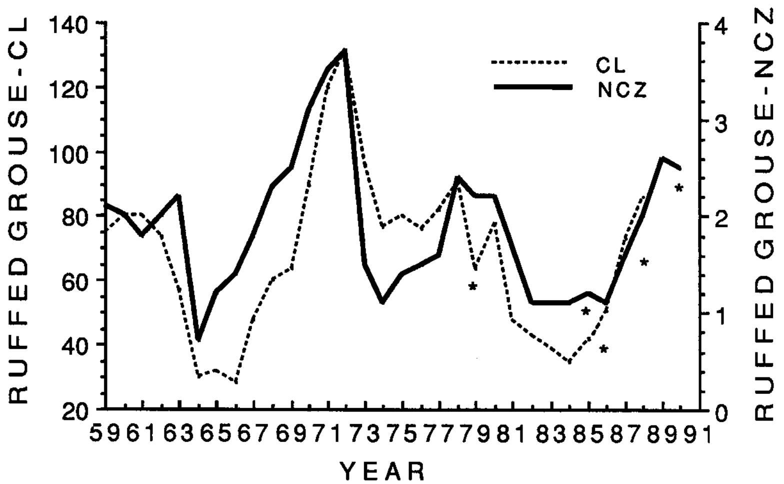

FIGURE 2. Spring Ruffed Grouse population at the Cloquet Forestry Center (CL), Minnesota (drumming male Ruffed Grouse) (data from Gullion [1985] and unpubl. data), and spring Ruffed Grouse population index of the north census zone of Minnesota (NCZ) (drumming males per stop) (data from Minnesota DNR). Asterisks indicate quaking aspen bud collection years.

The unused classification does not indicate that buds from these trees were unfit for use by grouse.

Annual use of quaking aspen by Ruffed Grouse was quantified from feeding observations in the Devil's Hole unit (409.9 ha; approximately 77 ha observable) of the Mille Lacs study site in 1985, 1986, and 1988. The number of observation days, and miles of observation routes driven were 25/52, 27/33, and 42/67 (days/miles); with eight, none, and six birds observed feeding in aspen, respectively, for each year. Using these data, an index of aspen use (AUI) was derived from the number of grouse seen feeding on aspen divided by the number of miles of observation routes driven. A correction factor for changes in Ruffed Grouse densities was not used in calculating the index. There was no correlation between the number of grouse seen feeding in quaking aspen and their densities, as indicated by feeding observations from 1982 to 1988 and corresponding grouse densities in the Devil's Hole unit. Admittedly, this observation technique is not intensive enough to provide precise information on the use of quaking aspen by Ruffed Grouse; however, it should be adequate as an annual index of quaking aspen use.

Data on the crop contents of Ruffed Grouse near Rochester, Alberta, were obtained from an earlier study by Doerr et al. (1974). Briefly, from 1966 to 1971 (December to April) feeding aggregations of grouse were located at dawn and dusk. Birds were shot while eating buds and their crop contents examined. Crop contents were reported as percent volume (dry displacement) and percent frequency of food items. Comparisons of annual dietary differences should be possible since sampling methods were consistent throughout the study (Doerr et al. 1974:609).

Annual changes in Ruffed Grouse densities and consumption of quaking aspen buds, willow (*Salix* sp.), beaked hazel (*Corylus cornuta*), rose (*Rosa acicularis*), and Juneberry (*Amelanchier vitisidaea*) were analyzed by linear correlation. The percent volume of the food item in the winter crop contents of Ruffed Grouse (Doerr et al. 1974), and the percent annual change in grouse densities (weighted mean of spring drumming males/40.5 ha) from the same study area (Keith and Rusch 1989, D. Rusch, pers. comm.) were used in all the above correlations.

BUD COLLECTION

Quaking aspen buds were collected at Cloquet and Mille Lacs from January through March. It is during these months that grouse consumption of aspen buds is heaviest and when physiological changes in aspen are relatively minor (Huff 1970, Huempfner 1981). Used and unused trees were sampled in 1979, 1985, 1986, and 1988; in 1990 only unused trees were sampled. This sampling scheme includes the initial decline during a Ruffed Grouse cycle, a period of low densities, a year in which the density was rapidly increasing, and a year that the population declined slightly (Fig. 2).

All used quaking aspen having an adequate number of buds were sampled in 1985, 1986, and 1988. When a used tree was sampled, the nearest unused tree that was > 61 m from the used tree (to avoid sampling in the used tree's clone) was sampled. Additionally, in years when few or no used trees were located (e.g., 1986, 1990), unused trees were randomly selected from throughout the study sites. Approximately 100 g of buds from the upper crown of each tree (where Ruffed Grouse preferentially feed [Huempfner and Tester 1988]) were sampled by shooting down branches with a small caliber rifle. Buds samples from 1979 were from an earlier study at Cloquet and had been stored at approximately −18°C in plastic bags since their original collection.

To investigate annual changes in bud chemistry of individual trees, nine quaking aspen from Cloquet and Mille Lacs were consecutively sampled in 1985, 1986, and 1988. These trees consisted of trees that Ruffed Grouse had fed on in 1985, trees which had been used by grouse in previous years (previously used trees), and unused trees ($n = 3$ for each tree group). The number of trees that could be sequentially sampled was lower than expected due to tree death and poor bud production during a given year. Since the sampling method involved shooting down branches in order to collect buds, it is possible that tree damage may have affected the chemistry of the flower buds in subsequent years (see Haukioja and Niemelä 1976, Baldwin and Schultz 1983).

CHEMICAL ANALYSES

Flower buds were analyzed for coniferyl benzoate and Kjeldahl nitrogen content following the procedures in Jakubas et al. (1989) and Jakubas and Gullion (1990). Nitrogen levels in the 1979 bud samples were determined by Corey Lerbs, Minnesota Department of Natural Resources, in 1979. Crude protein levels were calculated by multiplying the Kjeldahl nitrogen content by 6.25.

It is possible that the long storage (1979–1986) of the 1979 bud samples could have affected the level of coniferyl benzoate in the buds through oxidation or polymerization processes. Although it is the senior author's experience that coniferyl benzoate is fairly stable when stored in dark, cold conditions, the 1979 coniferyl benzoate levels should be regarded as minimum values.

SUITABILITY OF QUAKING ASPEN

Annual mean concentrations of protein or coniferyl benzoate may not accurately reflect the parameter most important to grouse, which is the number of quaking aspen on which they can feed. Therefore, an index was developed to ascertain the proportion of quaking aspen (out of the local population) that were suitable for Ruffed Grouse use. This index classified trees as being theoretically preferred trees (TPT) based on the level of coniferyl benzoate and protein in their flower buds. The protein level used in the TPT index was calculated from the weighted mean protein level of buds from used trees $\frac{\Sigma \mathrm{PiNi}}{\Sigma \mathrm{Ni}}$ from 1985, 1986, and 1988; where P is the mean protein level, N is the number of trees sampled, and i represents a given year. The coniferyl benzoate level used in the TPT index was determined from the highest level of coniferyl benzoate found in used trees during the same years. With these parameters in mind, a TPT value is equal to the percent of unused trees, in a given year, that have protein levels ≥ the index's protein level and have coniferyl benzoate levels ≤ the index's coniferyl benzoate level. Unused trees were used to calculate this index since their selection was basically random. The maximum level of coniferyl benzoate in used trees was chosen for the index because it is likely representative of the upper threshold of coniferyl benzoate that Ruffed Grouse can tolerate in aspen buds. The index was not calculated for 1979 since coniferyl benzoate and protein levels could only be measured on four unused tree samples. Protein samples from used trees in 1985 and 1986 were combined in calculating the TPT minimum protein level since only one used aspen with sufficient buds for sampling was found in 1986.

Use of this index is dependent on similar aspen bud crops between years. The relative production index (RPI) (Svoboda and Gullion 1972), which measures aspen flower bud production, was used to assess the aspen bud crops for 1985, 1986, and 1988 in random tree plots at Mille Lacs. The average RPI values for these years were 140, 159, and 225, respectively. At these relatively high RPI levels, bud availability likely was not a limiting factor in determining Ruffed

TABLE 1. Mean concentration (% dry wt.) and standard error for coniferyl benzoate and crude protein levels in quaking aspen flower buds[a] from used and unused trees from Cloquet and Mille Lacs, Minnesota. Within a column, mean values with a similar Greek subscript were not significantly different ($P > 0.05$) among years (Duncan's Multiple Range Test).

	Coniferyl benzoate				Protein			
Year	Unused	*n*	Used	*n*	Unused	*n*	Used	*n*
1979	$2.21 \pm 0.26_{\alpha}$	5	$1.24 \pm 0.20_{\alpha}$	7	$10.0 \pm 0.7_{\alpha\beta}$	8	$10.8 \pm 0.95_{\alpha}$	8
1985	$2.15 \pm 0.28_{\alpha}$	12	$1.04 \pm 0.13_{\alpha}$	10	$11.3 \pm 0.6_{\beta}$	11	13.9 ± 0.9	7
1986	$1.78 \pm 0.32_{\alpha\beta}$	9	—[b]		$9.3 \pm 0.4_{\alpha}$	10	—[b]	
1988	$1.07 \pm 0.23_{\beta}$	8	$1.13 \pm 0.23_{\alpha}$	9	$10.0 \pm 0.6_{\alpha\beta}$	8	$9.8 \pm 0.4_{\alpha}$	9
1990	$2.81 \pm 0.30_{\alpha}$	23	—[c]		$10.3 \pm 0.3_{\alpha\beta}$	23	—[c]	

[a] All flower bud samples from unused trees were staminate buds; bud samples from used trees include one sample from a female tree in 1985 and 1988.

[b] There were insufficient used samples in 1986 to give an accurate estimate.

[c] Ruffed Grouse feeding observations were not conducted in 1990, hence, no used trees were sampled.

Grouse use of aspen. However, in years when the RPI value is considerably lower (i.e., in 1972 the RPI value was 53 [Gullion, unpub. data]), some type of correction factor should be added to the TPT index.

STATISTICAL ANALYSES

Mean coniferyl benzoate and protein levels were compared among years using one-way analysis of variance (ANOVA). A check of the data, in relation to ANOVA model assumptions, indicated that the coniferyl benzoate concentrations in unused trees did not have a constant variance. A Box-Cox analysis indicated that a square root transformation was the best transformation for these data (Montgomery 1984). Other data appeared to fit the ANOVA model assumptions.

Mean coniferyl benzoate levels of trees that were consecutively sampled for three years were compared using two-factor ANOVA with repeated measures. The independent factors were tree classification and year. Trees that Ruffed Grouse used before or during 1985 and unused trees were the two tree classifications. A one-factor ANOVA, with repeated measures, was used to analyze yearly changes in coniferyl benzoate levels among unused trees.

In all cases, a Duncan's Multiple Range Test was used to isolate significant differences among means (Montgomery 1984). Simple linear regressions were used for all correlations. Results for all analyses were considered significant if $P < 0.05$.

RESULTS

CHANGES IN BUD CHEMISTRY

Coniferyl benzoate levels in unused trees varied significantly among years ($F = 4.84$; df = 4, 51; $P = 0.002$). Post-hoc tests revealed that mean coniferyl benzoate levels in 1988 were lower than in 1979, 1985, and 1990. However, mean coniferyl benzoate levels were not significantly different in 1979, 1985, 1986, and 1990 (Table 1). In addition, mean coniferyl benzoate levels were not significantly correlated ($r^2 = 0.46$, $P > 0.1$) to annual changes in Ruffed Grouse densities (Minnesota, north census zone). Used trees did not vary significantly in coniferyl benzoate levels in 1979, 1985, and 1988 ($F = 0.25$; df = 2, 23; $P = 0.93$) (Table 1).

Bud protein levels in unused aspen varied significantly among years ($F = 2.03$; df = 4, 55; $P = 0.036$). Post-hoc tests indicated that mean protein levels in 1985 were significantly higher than in 1986; however, levels were similar in 1979, 1986, 1988, and 1990 (Table 1). Similarly, there were significant differences ($F = 8.71$; df = 2, 21; $P = 0.002$) among years for bud protein levels in used quaking aspen. Again, post-hoc tests indicated mean protein levels in 1985 were higher than in 1979 or 1988 (Table 1).

The TPT index indicated that the percentage of trees available for use by Ruffed Grouse in 1985, 1986, 1988, and 1990 was 27%, 0%, 25%, and 8.7%, respectively. The protein level used for calculating the index was 11% (dry wt.) and the coniferyl benzoate level used was 1.8% (dry wt.). The TPT index appears to be highly associated with Ruffed Grouse use of aspen, with the highest level of aspen use occurring in 1985 (AUI = 0.15), no use in 1986 (AUI = 0.0), and moderate use in 1988 (AUI = 0.09). When presented graphically, TPT and AUI values are linearly related. Similarly, when TPT values are compared to annual changes (9.1%, −8.3%, 25%, −3.8%, respectively) in the regional Ruffed Grouse population (Minnesota, north census

TABLE 2. Mean concentration and standard error (SE) of coniferyl benzoate in trees that were sampled sequentially for three years.

Tree classification	Mean concentration of coniferyl benzoate (% dry wt.) ± SE		
	1985	1986	1988
Previously used	0.99 ± 0.12	0.83 ± 0.10	0.92 ± 0.02
Used	0.61 ± 0.10	0.85 ± 0.15	0.60 ± 0.06
Unused	1.25 ± 0.31	1.16 ± 0.23	0.95 ± 0.25
All groups	0.90 ± 0.13	0.92 ± 0.09	0.77 ± 0.09

zone) a positive correlation is apparent. More rigorous statistical tests of these associations cannot be made until additional data are collected.

Coniferyl benzoate levels in quaking aspen, sequentially sampled for three years, varied significantly among years depending on the classification of the tree. No significant differences in coniferyl benzoate levels occurred among years when used and unused trees were treated as one group ($F = 0.96$; df $= 1, 7$; $P = 0.36$). However, there was a significant interaction among year and tree classification ($F = 6.85$; df $= 1, 7$; $P = 0.04$). A comparison of mean coniferyl benzoate levels indicated that unused trees had decreased in coniferyl benzoate since 1985, while used and previously used trees had not changed (Table 2). Further analyses indicated that a significant ($F = 20.06$; df $= 1, 2$; $P < 0.05$) decrease in coniferyl benzoate concentrations among unused trees had occurred from 1985 to 1988.

IMPORTANCE OF QUAKING ASPEN

Data from the Alberta studies indicate that the percent of quaking aspen in the diet of Ruffed Grouse was highly correlated with changes in grouse densities ($r^2 = 0.87$, $P = 0.02$) (Fig. 3). A comparison of winter quaking aspen use and the proportion of juveniles in the fall population indicated that these factors were weakly correlated ($r^2 = 0.66$, $P = 0.09$). The volume of quaking aspen in the crop contents (used in these correlations) might be under represented since many of the birds were collected while still feeding in aspen. Conversely, the quantity of alternative foods should not be under-represented since Ruffed Grouse reportedly feed on lower vegetation first before moving up the tree canopy to feed on aspen (Huempfner 1981, Huempfner and Tester 1988).

Consumption of other dietary items was not correlated to Ruffed Grouse densities (Fig. 3). Willow bud consumption was negatively related to grouse densities; however, the slope of the regression was not significantly greater than zero ($r^2 = 0.547$, $P = 0.15$).

DISCUSSION

Coniferyl benzoate levels in quaking aspen changed significantly over an 11 year period. The lowest levels of this compound occurred in 1986 and 1988. This was just prior to, or during, an increase in grouse densities, whereas high coniferyl benzoate levels were observed during declining (1979, 1990) or low grouse densities (1985). However, there was no significant correlation between annual changes in grouse densities and coniferyl benzoate levels. Despite fluctuations in coniferyl benzoate levels, Ruffed Grouse consistently chose aspen with low levels of this compound, as indicated by samples from 1979, 1985, and 1988 (also see Jakubas et al. 1989).

Overall, crude protein levels were similar among years, with the exception of 1985. Mean protein levels in unused quaking aspen went from their highest level (1985) to their lowest level the following year. There does not appear to be any correlation between bud nitrogen and coniferyl benzoate levels in individual trees (Jakubas 1989, and unpub. data) or among years. This was unexpected, since nitrogen levels in aspen foliage were found to be inversely related to phenolic production (Bryant et al. 1987).

Coniferyl benzoate levels appear to fluctuate differently among used and unused trees. In trees that were consecutively sampled for three years, unused trees decreased in coniferyl benzoate levels from 1985 to 1988, while trees that grouse previously fed on showed no general trend. We propose that aspen clones have inherent differences in their capacity to chemically defend themselves or in their ability to respond to extrinsic factors (e.g., weather conditions). Clonal differences in chemical defense were evident at the Cloquet study site, where a clone with a long history of use by Ruffed Grouse did not produce

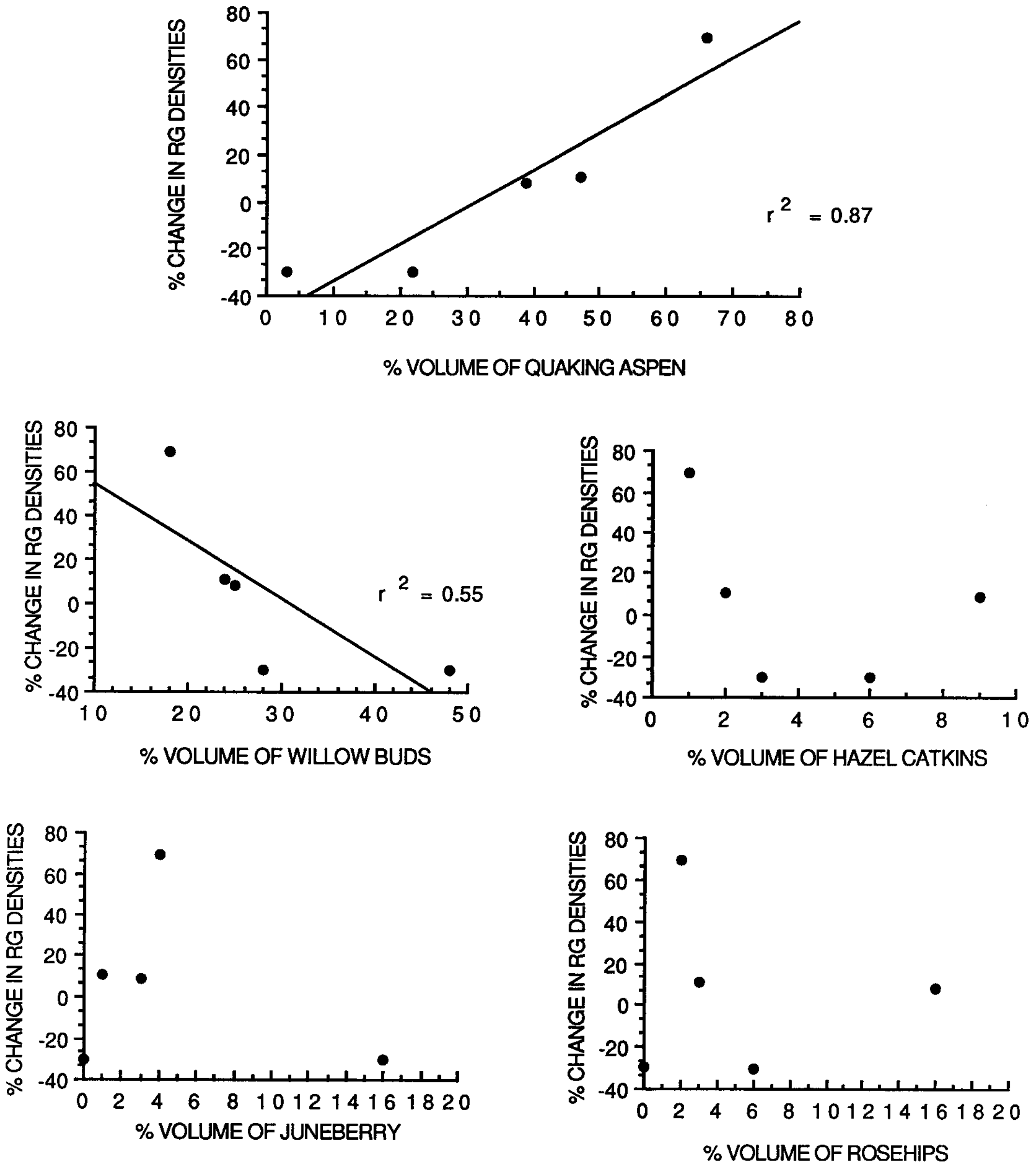

FIGURE 3. The annual change in grouse densities (weighted mean density of drumming male Ruffed Grouse per 40.5 ha) (Keith and Rusch [1989] and Rusch, pers. comm.) plotted against Ruffed Grouse crop contents of various food items from the preceding winter (percent crop volume) (Doerr et al. 1974). All data were collected near Rochester, Alberta.

any coniferyl benzoate, and a clone that had no record of grouse feeding activity for approximately 20 years had the highest level of coniferyl benzoate found at the Cloquet study site (Gullion and Jakubas, unpub. data).

Further evidence for variations in clonal chemical defense is suggested by studies of the occurrence of Hypoxylon canker (*Hypoxylon* sp.). The incidence of Hypoxylon canker among clones of aspen can vary markedly (Copony and Barnes 1974) and phenolic compounds in aspen bark inhibit growth of this canker (Takai and Hubbes

1973). Assuming a correlation exists between a clone's ability to produce phytoalexins and inhibition of canker growth, the differential incidence of Hypoxylon canker among clones may reflect differences in chemical defense capacities. If clones of quaking aspen vary in their ability to produce defensive compounds, as suggested by the above data, clones which are unable to produce high levels of coniferyl benzoate may be important food reservoirs for grouse during times when the general population of aspen is producing high levels of this compound.

We do not know why coniferyl benzoate levels changed significantly among years. Other phenylpropanoids closely related to coniferyl benzoate are proposed to have diverse physiological functions including flower induction, sex regulation (Lapa and Udre 1987, 1989), phytoalexin functions (Keen and Littlefield 1979, Kuc 1983, Lamb et al. 1989), and growth regulation (Lynn and Chang 1990). Consequently, the mechanisms regulating coniferyl benzoate levels may be related to physiological requirements other than herbivore defense.

It is possible that changes in coniferyl benzoate levels occur with an overall change in the secondary chemistry of quaking aspen. One mechanism that may induce such a chemical change is heavy defoliation of aspen by forest tent caterpillars (*Malacosoma disstria*). Forest tent caterpillars (FTC) prefer quaking aspen foliage, although at high densities they affect many of the woody species in northern forests (Duncan and Hodson 1958). During FTC outbreaks, such as those that occurred in Minnesota from 1951 to 1953, moderate to heavy defoliation occurred throughout aspen forests in northern Minnesota (2,428,123 ha) (Duncan and Hodson 1958, Hodson 1977). Defoliation of quaking aspen may significantly change foliar nutrients and phenolic compounds (Mattson and Palmer 1988). Additionally, severe defoliation by FTC may directly affect foliage and flower bud production (Duncan and Hodson 1958, Hodson, pers. comm.). This was evident at the Cloquet study site in the winter of 1989–1990 when only one aspen in 10 randomly chosen plots had noticeable flower buds. In the spring of 1989, the Cloquet site and surrounding area suffered moderate defoliation by FTC.

Conversely, changes in quaking aspen chemistry may be associated with environmental conditions that accompany FTC outbreaks. FTC outbreaks are usually preceded by relatively cold winters and warm springs, with this pattern continuing during FTC population increases (Witter et al. 1975, Hodson 1977). Weather patterns can affect nutrient and secondary metabolite levels in plants (Jonasson et al. 1986), but it is unknown what effect weather has on coniferyl benzoate levels. Forest tent caterpillar eggs were first noticed at the Cloquet study site in the winter of 1987–1988, the same year the level of coniferyl benzoate was significantly lower. It is interesting, that FTC outbreaks occurred near the peak of the Ruffed Grouse cycle in Minnesota, during the 1930s, 1950s, late 1970s and late 1980s (Duncan and Hodson 1958; Anonymous 1970, 1971, 1972, 1978, 1979; Cambell 1988). An exception was the outbreak of 1963–1967 in the northernmost part of the state. Grouse densities peaked in 1972 when there was little FTC activity (Witter et al. 1975). However, another important aspen defoliator, large aspen tortrix (*Choristoneura conflictana*) did peak that year in the St. Louis County/Cloquet area (Anonymous 1972). Although FTC outbreaks may co-occur with peak grouse populations, high FTC populations usually continue after the grouse population has declined.

Although Ruffed Grouse consistently prefer quaking aspen with low levels of coniferyl benzoate, a larger question to be answered is whether chemical changes in quaking aspen buds affect the extent to which they are utilized by Ruffed Grouse. To answer this question, we estimated the proportion of quaking aspen that should be suitable to Ruffed Grouse based on bud coniferyl benzoate and protein levels and compared this suitability index to the number of grouse observed feeding in aspen. Ruffed Grouse use of aspen closely matched the TPT index, indicating that the suitability of aspen buds may be related to both coniferyl benzoate and protein levels. The influence of low protein levels on quaking aspen use was evident in 1986 when none of the trees having low coniferyl benzoate levels had protein levels above 11%. During that winter, no grouse were observed feeding in aspen at the study site. Conversely, moderate use of quaking aspen in 1985 was correlated to a higher percentage of aspen having both high protein and low coniferyl benzoate levels (Fig. 4).

The TPT index is only an index and is not intended to indicate absolute values of coniferyl benzoate and protein aspen buds must have for

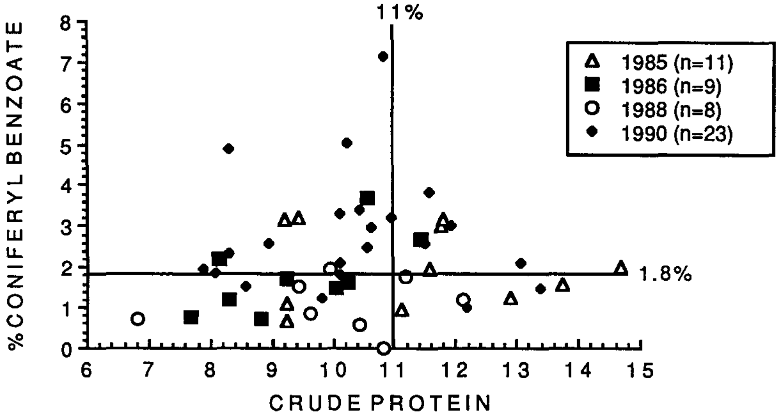

FIGURE 4. Ranking of male unused trees in 1985, 1986, 1988, and 1990 according to their coniferyl benzoate and crude protein levels in relationship to the parameters of the TPT index. Trees that have protein levels ≥ 11% (dry wt.) and coniferyl benzoate levels ≤1.8% (dry wt.) were considered theoretically preferred feeding trees.

grouse to feed on them. The 11% protein level used in the index is the average protein level for used trees, consequently many trees that grouse feed on are below this value. The 1.8% coniferyl benzoate limit used in the index may be close to the threshold amount of coniferyl benzoate that Ruffed Grouse will tolerate; however, this limit should be confirmed by laboratory feeding trials.

Annual changes in aspen chemistry may make factors that are normally associated with Ruffed Grouse selection of feeding trees, such as tree age and health, less important in some years. Overall, Ruffed Grouse tend to feed in older trees or trees that are poor in health (Svoboda and Gullion 1972, Doerr et al. 1974). Similarly, the majority of 23 feeding trees in our study were either older trees or in poor condition (52% old and in good health, 34% in obvious poor health, and 13% young trees). Low annual levels of coniferyl benzoate may allow grouse to feed on a greater number of young healthy trees. This was evident in 1988 when only 11% of the feeding trees that year were in poor condition, as compared to 54% that were in poor health in 1985. Changes in aspen bud chemistry may partially explain why other researchers (i.e., Schemnitz 1970) reported that Ruffed Grouse winter feeding mainly occurs in healthy young aspen.

Data from the Alberta studies indicate that the amount of quaking aspen flower buds in the diet of Ruffed Grouse is highly correlated with changes in the bird's population density. It is unlikely that the proportion of aspen in their diet was a consequence of the bird's population density. Heavy consumption of quaking aspen as a consequence of high grouse densities would infer that the birds were being "forced" onto an unfavorable species or that other food sources were lacking. It is well documented that quaking aspen use by grouse, relative to its abundance, is high compared to other tree species (Svoboda and Gullion 1972, Huempfner and Tester 1988). Although data on the availability of alternative food sources do not exist for the Alberta study, we can infer from grouse crop contents that other food sources were available and consumption of these foods was not density dependent (Fig. 3). Similarly, it is unlikely that the negative correlation between willow bud consumption and grouse densities indicates that demand for willow buds exceeded supply during high grouse densities. First, the percentage of birds having willow buds in their crops was highest when grouse densities were highest, indicating birds had no trouble finding willow. Although the number of grouse that had consumed willow was high at peak densities, the amount of willow eaten was at its lowest level. This contrasts to the high amount of aspen eaten during that period. Secondly, laboratory feeding trials confirm that Ruffed Grouse preferentially consume aspen flower buds but not willow buds (C. Guglielmo, University of Wisconsin, unpub. data).

An alternative explanation for the correlation between Ruffed Grouse densities and consumption of aspen flower buds is that grouse densities may be partially dependent on the amount of aspen on which they can feed. A significant decrease in the suitability or availability of quaking aspen could potentially affect the bird's breeding condition, susceptibility to predation, or energetics. It does not appear that changes in Ruffed Grouse densities in Alberta were due to decreased fecundity or hatching success. Keith and Rusch (1989) indicated that average clutch size, hatching success, and initial brood size did not differ among years. However, the proportion of juveniles in the fall population was positively correlated to annual changes in grouse densities (Keith and Rusch 1989). One explanation for a low ratio of adult to juvenile birds during declining densities is that poor winter food conditions may lead to a high proportion of unsuccessful breeding birds in the population (see Andreev 1988). Although the Alberta data indicate that winter aspen use and the proportion of juveniles in the fall population may be correlated, the correlation was not highly significant ($0.1 > P > 0.05$). Alternatively, Keith and Rusch (1989) attributed the low proportion of juveniles during declining densities to higher summer predation rates on juveniles as compared to adults. However, their data on summer survival rates are limited since marked birds were not used (Keith, pers. comm.). Overall, there is very little evidence that a decline in the use of aspen flower buds affected the breeding success of grouse in Alberta.

Ruffed Grouse likely expend a greater amount of energy and are more susceptible to predation when feeding on trees other than aspen. A grouse can typically fill its crop with aspen flower buds in 15 min, after which it is free to seek cover from predation or harsh weather conditions (Svoboda and Gullion 1972). When feeding on alternative foods such as paper birch (*Betula papyrifera*) buds and catkins, it would likely take them much longer to fill their crops, due to the small size and inaccessibility of these items. Additionally, birch branches are thinner and more flexible than those of quaking aspen, making it necessary for Ruffed Grouse to frequently use their wings to maintain their balance while feeding. Increased feeding time and the higher visibility of the bird, due to its movements, could make the bird more susceptible to avian predation. Similarly, in regions where aspen is not prevalent, the increased effort grouse expend in finding adequate food resources is associated with more frequent movements, increased predation risks, and lower survival (Thompson and Fritzell 1989). This may ultimately account for low grouse densities in these areas (F. Thompson, 1990 Biennial Grouse Group Meeting).

Given the increased energetic costs and predation risks that may be associated with loss of the winter aspen food resource, one would predict that annual changes in grouse densities would correlate with winter survival in the Alberta study. Overall, the Alberta data on winter survival rates are not strong enough to draw any firm conclusions. The accuracy of the survival data of Keith and Rusch (1989) may not be high given that winter survival was estimated without using marked birds. Rather, winter survival was estimated by dividing the previous fall's population estimate (line transects) by the April population estimate (based on drumming males) (Rusch, pers. comm.). Keith and Rusch (1989) report that survival from September–April was not related to the annual rate of increase. Rather, it was summer survival that was positively correlated with changes in grouse densities. However, it is difficult to explain ecologically why summer survival was inversely correlated to winter predation rates, whereas winter survival was positively related. Notably, other studies indicate an important inverse relationship between winter predation rates and survival (Gullion and Marshall 1968, Keith and Rusch 1989).

Given these data on winter survival, apparent predation rates, and lack of information on dispersal, it is impossible to tell if differential survival rates would explain the correlation between aspen use and changes in grouse densities. However, recognition that aspen suitability changes and that use of aspen may influence grouse survival may help explain why grouse densities decline or stay at low levels during years when predation rates are relatively low.

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