Do browsing ungulates diminish avian foraging?

Autor(en): **Scher, Stanley**

Objekttyp: **Article**

Zeitschrift: **Schweizerische Zeitschrift für Forstwesen = Swiss foresty journal = Journal forestier suisse**

Band (Jahr): **149 (1998)**

Heft 5

PDF erstellt am: **13.09.2024**

Persistenter Link: https://doi.org/10.5169/seals-766109

Do Browsing Ungulates Diminish Avian Foraging?
Studies of Woodpeckers in Forest Understory Communities of Central Europe and Western North America Show Cause for Concern

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Keywords: Browsing; ungulates; *Capreolus; Odocoileus;* songbirds; *Passeriformes;* woodpeckers; *Picidae; Colaptes; Dendrocopos; Hypopicus; Picoides; Picus;* sapsuckers; *Sphyrapicus;* foraging substrates; forest understory; vegetation structure; Common yew; *Taxus baccata;* Pacific yew; *Taxus brevifolia.* FDK 174.7 Taxus: 148.2: 149: 181.42: (73): (494.34)

1. Introduction

In forest communities, vegetation structure is a key determinant of avian abundance and diversity *(MacArthur* and *MacArthur,* 1961; *Moss,* 1978). Forest understory structure can be modified by browsing pressure from herbivores, subcanopy fires, silvicultural practices, application of herbicides, and other anthropogenic i.e. human-caused disturbances *(McShea* and *Rappole,* 1997). In a previous report, we called attention to interactions between browsing damage from ungulates such as deer, elk, and moose, to Pacific yew *(Taxus brevifolia),* an understory tree or shrub, and avian foraging in the Siskiyou Mountains and Cascade Range of southern Oregon *(Scher,* 1997). This paper addresses the following questions: How does ungulate herbivory change the structure and accessibility of foraging substrates? How do such changes influence avian abundance and local diversity? Do ungulate-induced structural changes in forest vegetation and their impact on bird populations represent cause for concern? To set this work in context, we provide background information on herbivore damage to understory trees and shrubs, briefly review the foraging ecology of woodpeckers, cite case studies to document ungulate damage to *Taxus* species in Central Europe and western North America, and explore impacts on woodpeckers with similar foraging strategies that occur on both continents.

2. Background

Many songbirds *(Passeriformes)* depend upon forest understory vegetation for food resources. Where densities of ungulate populations exceed the carrying capacity, heavy browsing alters the understory vegetation structure used by songbirds as foraging substrates *(deCalesta,* 1994, 1997; *McShae* and *Rappole,* 1997; *Scher,* 1997).

Gill (1992) defines browsing damage as removal of buds, foliage, shoots, and uprooting of seedlings. Browsing of terminal buds results in loss of apical dominance, replacement of leaders by laterals, development of multiple stems, and reduction of height growth *(Eiberle,* 1987; *Welch et al.,* 1991; *Putman,* 1996). Some ungulates also strip and consume the bark from stems *(Parks* and *Tiedemann,* 1993; *Putman,* 1996).

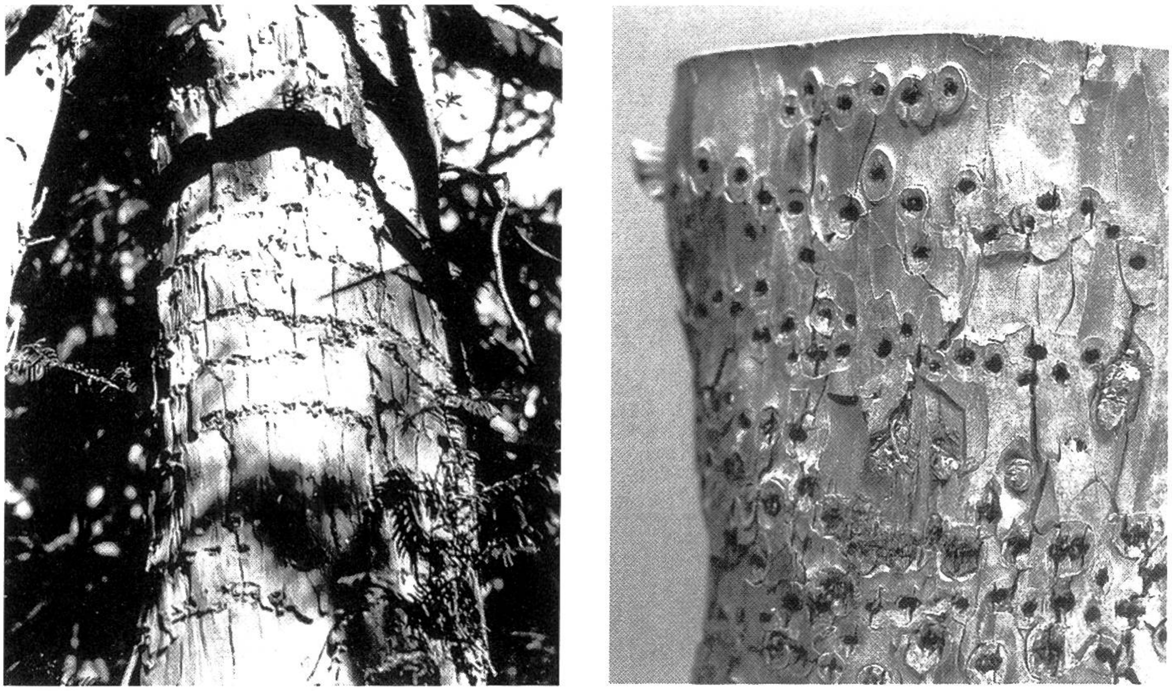
In Central Europe, the influence of deer browsing on understory forest vegetation has been documented for centuries *(Bechstein,* 1821; *Burckhardt,* 1865; *Brueckner,* 1993; *Roth,* 1996). In Switzerland, *Leuthold* (1980) noted decline of the common yew *(Taxus baccata)* as a consequence of damage from excessive roe deer *(Capreolus capreolus)* populations.

In North America, browsing damage by white-tailed deer *(Odocoileus virginianus)* influences reproductive biology of Canada yew *(Taxus canadensis)* *(Allison,* 1990a, 1990b). Deer and other ungulates – elk and moose – retard vertical growth, reduce abundance, and supress natural regeneration of Canada yew *(Snyder* and *Janke,* 1976; *Reisenhoover* and *Maass,* 1987; *Balgooyan* and *Waller,* 1995) and Pacific yew *(Taxus brevifolia)* *(Nelson* and *Leege,* 1974; *Pierce,* 1984; *Parks* and *Tiedmann,* 1993; *Scher,* 1997).

Woodpecker Foraging Ecology

Members of the *Picidae* family display a wide range of foraging strategies. Flickers *(Colaptes)* obtain their food primarily by foraging on the ground. Sapsuckers *(Sphyrapicus)* capture insects from the air like flycatchers *(Muscicapidae)* *(Bent,* 1939; *Howell,* 1952; *Kilham,* 1977; *Raphael* and *White,* 1984; *Shuford,* 1993); but most woodpeckers drill holes in the bark of trees to collect insects.

The North American Acorn Woodpecker *(Melanerpes formicivorus)* *(MacRoberts,* 1970; *Winkler et al.,* 1995) and four species of sapsuckers *(Sphyrapicus)* *(Tate,* 1969, 1973; *Scher,* 1997) drill small (approximately 3 – 8 mm diameter), evenly-spaced holes in horizontal rows or rings, often arranged in vertical columns or in spiral patterns to produce characteristic arrays in the bark of trees or other woody plants *(McAtee,* 1911; *Rushmore,* 1969) *(Figure 1).* Sapsuckers revisit and maintain thousands of drill holes as a food resource. Other birds, mammals, and insects visit woodpecker holes to



a b

Figure 1. Woodpecker drill-hole patterns on the bark of: a. Common yew *(Taxus baccata), (Kučera,* 1972) and b. Pacific yew *(Taxus brevifolia), (Scher,* 1997).

consume sap, inner bark, and glean associated insects *(Bolles,* 1891; *Kilham,* 1953, 1958; *Nickell,* 1956; *Foster* and *Tate,* 1966; *Miller* and *Nero,* 1983; *Ehrlich* and *Daily,* 1988; *Williams,* 1990; *Daily et al.,* 1994).

Several genera of European and Middle-Eastern woodpeckers – *Dendrocopus, Picoides, Picus* – *(Turcek,* 1954; *Klima,* 1959; *Ruge,* 1970; *Kučera,* 1972; *Miech,* 1986; *Mossadegh,* 1997; see reviews by *Cramp et al.,* 1985, and *Winkler et al.,* 1995) and at least one Asian sapsucker *(Dendrocopus, Picoides* or *Hypopicus) (Osmaston,* 1916; *Abdulali,* 1968; *Zusi* and *Marshall,* 1970) also create sapsucker-like drill-hole patterns in the bark of selected trees where they function as community feeding stations.

3. Study sites and Methods

In western North America, we investigated ungulate damage to Pacific yew in a mixed conifer forest on the Dead Indian Plateau in the Cascade Range, approximately 32 km (20 miles) east of Ashland in Jackson County, southwestern Oregon. Slopes on the plateau are gentle to flat, and elevations range from 1340 to 1830 m (4500 to 6000 ft.) *(Minore,* 1978).

In Central Europe, we observed evidence of ungulate damage to the common yew *(Taxus baccata)* in the beech- *(Fagus sylvatica)* dominated forests of Üetliberg in the lower Alps, just southwest of Zurich where slopes are steep and elevations range from 480–870 m (1575–2854 ft.) *(Koch,* 1975).

We used hedging of yew as a measure of ungulate browsing. In southwestern Oregon, we estimated the number and distribution of drill holes as evidence of woodpecker activity on understory and overstory conifers, and compared cumulative counts to integrate foraging activity over multiple years *(Scher,* 1997).

4. Results

We found evidence of ungulate damage to unprotected yew trees and shrubs in the forest understory on both continents. Terminal bud browsing by ungulates resulted in formation of multiple leaders, reduced rate of height growth, and increased production of lateral branches compared with unbrowsed controls.

In western North America, the number of sapsucker drill holes per tree ranged over several orders of magnitude, approaching several thousand on Pacific yew stems greater than 10 cm (4 inches) diameter at breast height (DBH) *(Scher,* 1997). At two sites in Central Europe – one near St. Gallen in the Canton of Appenzell, Switzerland *(Kučera,* 1972), and another at Guggenberg bei Adnet, about 10 km (6 miles) southeast of Salzburg, Austria *(Eichberger* and *Heiselmayer,* 1995) – attempts to quantify the number of woodpecker drill holes on common yew were impeded by attenuated horizontal spacing resulting in an overlapping pattern *(Figure 1).*

Yew trees heavily browsed by ungulates lacked evidence of woodpecker foraging. Absence of woodpecker drill holes on yew modified by growth responses to ungulate damage suggests that the altered branching structure of heavily browsed plants may limit access to woodpeckers and other bark-foraging birds in North America and Eurasia.

5. Discussion

Using hedging as a measure of ungulate damage and drill-hole patterns as evidence of woodpecker foraging activity, we explored the relationship between ungulate browsing and bark-foraging on Pacific yew in southwestern Oregon and the common yew in Central Europe. Our early observations lead us to the hypothesis that ungulate damage induces growth responses in yew species resulting in modified branching patterns which serve as a barrier to restrict or exclude access of woodpeckers and other bark-foraging bird species to foraging substrates and food resources. By modifying the forest understory structure, large populations of ungulates can strongly influence resource availability to other organisms *(Jones et al.,* 1997).

As noted above, drill holes created and maintained by sapsuckers and other woodpeckers with similar foraging strategies serve as feeding stations for other birds, mammals, and insects (*Bolles,* 1891; *Batts,* 1953; *Kilham,* 1953, 1958; *Nickell,* 1956: *Foster* and *Tate,* 1966; *Miller* and *Nero,* 1983; *Ehrlich* and *Daily,* 1988; *Williams,* 1990). Avian visitors to such feeding stations include other woodpeckers, other bark-foraging bird species such as creepers *(Certhidae)* and nuthatches *(Sittidae),* as well as wrens *(Troglodytidae),* warblers *(Parulidae),* chickadees *(Paridae),* hummingbirds *(Trochilidae),* kinglets *(Sylviidae),* siskins and goldfinches *(Fringillidae)* (*Ehrlich* and *Daily,* 1988). Accordingly, by restricting access to woodpecker foraging substrates, ungulate browsing may indirectly impact bird abundance and local diversity. These observations are consistent with previous work demonstrating declines in forest understory bird populations (*Boone* and *Dowell,* 1986; *Baird,* 1990) and diversity (*Casey* and *Hein,* 1983; *Dessecker* and *Yahner,* 1987) attributed to high deer densities.

This work, taken together with other relevant studies (*deCalesta,* 1994, 1997; *McShea* and *Rappole,* 1997; *Scher,* 1997) raises the question: At what point should action be taken to prevent further ungulate-induced damage to forest understory communites? In response to this question, *Noy-Meier* (1981) and *McShea* and *Rappole* (1997) agree on one criterion: when damage by ungulate populations interferes with conservation efforts to protect other species.

Summary

This paper explores impacts of ungulate browsing on avian access to bark-foraging substrates in the forest understory of Central Europe and southwestern Oregon. We used hedging as a measure of growth responses to ungulate damage to the common yew *(Taxus baccata)* and Pacific yew *(Taxus brevifolia).* To study woodpecker foraging behavior, we estimated the number and distribution of woodpecker drill holes on the bark of yew stems. The absence of drill holes on hedged plants provides evidence of an indirect effect of browsing on woodpecker foraging activity. The widespread use of woodpecker drill holes as a food resource by other woodpeckers, other bark-foraging bird species, other songbirds, as well as mammals and insects suggests that structural changes in forest understory vegetation resulting from ungulate browsing may influence abundance and local diversity of songbirds and other woodpecker-dependent members of the understory community.

Résumé

L'abroutissement de l'If par les ongulés diminue-t-il les perforations corticales par les oiseaux? Des études de Pics dans des communautés du sous-étage forestier d'Europe Centrale et de l'Ouest de l'Amérique du Nord révèlent des relations de cause à effet

Ce travail explore les impacts de l'abroutissement par des ongulés sur l'accès à des substances nutritives corticales pour des oiseaux, dans les sous-bois d'Europe Centrale et de l'Oregon du sud-ouest. La réaction à des dommages causés par des ongulés à l'If commun *(Taxus baccata)* et à l'If du Pacifique *(Taxus brevifolia)* fut établie par l'intermédiaire de tailles expérimentales. Pour l'étude du comportement nutritif du Pic, il fut procédé à l'estimation du nombre et de la distribution des points de perforation dans l'écorce de fûts d'ifs. L'absence de perforations sur les plantes soumises à une taille met en évidence un effet indirect de l'abroutissement sur l'activité du Pic. L'utilisation générale de ces points de perforation par d'autres pics, d'autres espèces d'oiseaux à comportement nutritif analogue, de même que par des mammifères et des insectes suggère que des changements de structure du sous-étage forestier suite à l'abroutissement par des ongulés pourraient influencer l'abondance et la diversité locale des oiseaux chanteurs et des autres membres de cette communauté liée au Pic.

Traduction: *Ernst Zürcher*

Zusammenfassung

Wirkt sich Wildverbiss nachteilig auf die Nahrungssuche von Vögeln aus? Untersuchungen über Spechte in der Unterschicht von Wäldern in Mitteleuropa und im Nordwesten von Amerika geben Anlass zur Besorgnis

Diese Arbeit handelt von den Auswirkungen des Schalenwildverbisses in der Unterschicht von Wäldern in Mitteleuropa und im südwestlichen Oregon auf die Zugänglichkeit der Gehölze für Vögel, die ihre Nahrung von der Rinde ablesen. Um die Wuchsreaktion der Gemeinen Eibe *(Taxus baccata)* und der Pazifischen Eibe *(Taxus brevifolia)* auf Wildverbiss bemessen zu können, wurden diese Gehölze wie Hecken geschert. Um das Verhalten von nahrungssuchenden Spechten zu untersuchen, wurde die Anzahl und die Verteilung von Spechtlöchern in der Rinde von Eibenstämmen ermittelt. Das Fehlen von Spechtlöchern an zurückgeschnittenen Gehölzen legt eine indirekte Wirkung des Verbisses auf die Nahrungssuche der Spechte nahe. Es ist üblich, dass vorhandene Spechtlöcher von weiteren Spechten, anderen rindenabsuchenden Vogelarten, anderen Singvögeln sowie auch von Säugetieren und Insekten als Nahrungsquelle benutzt werden. Strukturelle Veränderungen der Vegetation der Unterschicht aufgrund von Wildverbiss können deshalb Einfluss haben auf die Abundanz und die lokale Diversität von Singvögeln und anderen Bewohnern der Unterschicht, die von der Aktivität der Spechte abhängig sind.

Übersetzung: *Erica Zimmermann*

Abdulali, H., (1967): Sap sucking by Indian woodpeckers. J. Bombay Historical Society *65:* 219–221.
Allison, T.D., (1990a): The influence of deer browsing on the reproductive biology of Canada yew *(Taxus canadensis* marsh.) I. Direct effects on pollen, ovule, and seed production. Oecologia *83:* 523–529.
Allison, T.D., (1990b): The influence of deer browsing on the reproductive biology of Canada yew *(Taxus canadensis* marsh.) II. Pollen limitation: an indirect effect. Oecologia *83:* 530–534.
Baird, T.H., (1990): Breeding Bird Populations. New York State Museum Bull. 477, State of New York, Albany.
Balgooyen, C.P., Waller, D.M., (1995): Use of *Clintonia borealis* and other indicators to gauge impacts of white-tailed deer on plant communities in northern Wisconsin. Natural Areas Journal *15:* 305–318.
Batts, H.L., (1953): Siskin and goldfinch feeding at sapsucker tree. Wilson Bull. *65:* 198.
Bechstein, J.M., (1821): Forstbotanik, In: Zeitlinger, H. J., (1990): Die Eibe. Österr. Forstzeitung *9:* 43–46.
Bent, A.C., (1939): Life Histories of North American Woodpeckers. United States National Museum Bulletin *174.*
Bolles, F., (1891): Yellow-bellied sapsucker and their uninvited guests. Auk *8:* 256–270.
Boone, D.D., Dowell, B.A., (1986): Catoctin Mountain Park bird study. National Park Service CX-3000-4-0152.
Brueckner, E., (1993): Development of the red deer population and the forest biotope in the west Ertz Mountains, Vogtland from 1591 to 1990. Z. für Jagdwiss. *39:* 46–59.
Burckhardt, A., (1865): Der Eibenbaum im Plesswalde bei Göttingen. Aus dem Walde *1:* 88–92.
Casey, D., Hein, D., (1983): Effects of heavy browsing on a bird community in a deciduous forest. J. Wildl. Manage. *47:* 829–836.
Cramp, S. et al., (eds) (1985): Handbook of the Birds of Europe, the Middle East, and North Africa. The Birds of the Western Palearctic.Vol *IV:* Terns to Woodpeckers. Oxford Univ. Press. Oxford, New York.
Daily, G.C. et al., (1994): Double keystone bird in a keystone species complex. Proc. Natl. Acad. Sci, USA *90:* 592–594.
deCalesta, D.S., (1994): Impact of white-tailed deer on songbirds within managed forests in Pennsylvania. J. Wildlife Manage. *58:* 711–718.
deCalesta, D.S., (1997): Deer and ecosystem management. In: The Science of Overabundance. Smithsonian Institution Press, Washington, London, 267–279.
Desseker, D.R., Yahner, R. H. (1987): Breeding bird communities associated with Pennsylvania northern hardwood clearcut stands. Proc. Pennsylvania Acad. Sci *61:* 170–173.
Ehrlich, P.R., Daily, G.C., (1988): Red-naped sapsuckers feeding at willows: possible keystone herbivores. American Birds *42:* 357–365.
Eiberle, K., Nigg, H., (1987): Grundlagen zur Beurteilung des Wildverbisses im Gebirgswald. Schweiz. Z. Forstwes. *138:* 747–785.
Eichberger, C., Heiselmayer, P., (1995): Die Eibe *(Taxus baccata* L.) in Salzburg: Versuch einer Monographie. Schriftenreihe für systematische Botanik, Floristik und Geobotanik, Band *7.* Universitätsverlag. Wien, Salzburg.
Foster, W.L., Tate, J. Jr., (1966). Activities and co-actions of animals at sapsucker trees. Living Birds *5:* 87–113.
Gill, R.M.A., (1992): A review of damage by mammals in north temperate forests: 3. Impact on trees and forests. Forestry *65:* 363–388.
Howell, T.R., (1952): Natural history and differentiation in the yellow-bellied sapsucker. Condor *54:* 237–282.
Jones, C.G. et al., (1997): Positive and negative effects of organisms as physical ecosystem engineers. Ecology *78:* 1946–1957.
Kilham, L., (1953): Warblers, hummingbirds, and sapsuckers feed on sap of yellow birch. Wilson Bull. *65:* 198.
Kilham, L., (1958): Red squirrels feeding at sapsucker holes. J. Mammal. *39:* 4–5.
Kilham, L., (1977): Nesting behavior of yellow-bellied sapsuckers. Wilson Bull. *89:* 310–324.

Klima, M., (1959): Einige Beobachtungen über das Spechtringeln an Bäumen. Zool. Listy *8:* 33–36.
Koch, N., (1975): Oekologische Beziehungen zwischen den Vögeln und den Biotopen des Üetliberges und des Reppischtales bei Zürich. Sonderabdruck aus Vierteljahrsschrift der Naturforschenden Gesellschaft in Zürich. Buchdruckerei und Verlag Leemann AG, Zürich. S. 299–428.
Kučera, L., (1972): Durch Spechte *(Picidae)* verursachte Baumschäden mit besonderer Berücksichtigung des Ringelns. Schweiz. Z. Forstwes. *123:* 107–116.
Leuthold, C., (1980): Die ökologische und pflanzensoziologische Stellung der Eibe *(Taxus baccata)* in der Schweiz. Veröff. Geobot. Inst. Rübel *67:* 1–217.
MacArthur, R.H.; MacArthur, J.W. (1961): On bird species diversity. Ecology *42:* 594–598.
MacRoberts, M.H., (1970): Notes on the food habits and food defense of the Acorn Woodpecker. Condor *72:* 196–204.
McAtee, W.L., (1911): Woodpeckers in relation to trees and wood products. United States Department of Agriculture, Biological Survey Bull. *39.* Washington.
McShea, W.J., Rappole, J.H., (1997): Herbivores and the ecology of understory birds. In: The Science of Overabundance. Smithsonian Institution Press. Washington, London. 298–309.
Miech, P., (1986): Zum Ringeln einiger Spechtarten *(Picinae)* im Flachland. Orn. Ber. Berlin (West) *11:* 39–76.
Miller, R.S., Nero, R.W. (1983): Hummingbird-sapsucker associations in northern climates. Can. J. Zool. *61:* 1540–1546.
Minore, D., (1978): The Dead Indian Plateau. General Technical Report PNW-72 Pacific Northwest Forest and Range Experiment Station, U.S. Department of Agriculture, Forest Service. Portland, OR. 23pp.
Moss, D. (1978): Diversity of woodland song-bird populations. J. Animal Ecology *47:* 521–527.
Mossadegh, A. (1997): Woodpecker drill-hole patterns in the bark of *Taxus baccata* in the Elburz Mountains, on the Caspian coast of Northern Iran. (personal communication).
Nelson, R.J., Leege, T.A., (1974): Nutritional requirements and food habits. In: Elk of North America: Ecology and Management. Stackpole Books, Harrisburg, PA. 323–368.
Nickell, W.P., (1956): Birds and insect guests at a sapsucker tree. Jack-Pine Warbler *34:* 117.
Noy-Meir, I., (1981): Responses of vegetation to the abundance of mammalian herbivores. In: Problems in the Management of Locally Abundant Wild Mammals. Academic Press, New York. 233–246.
Osmaston, A. E., (1916): Curius habits of woodpeckers in the Kumaon Hills. J. Bombay Natural History Society *24:* 363–366.
Parks, C.A., Tiedemann, A.R., (1993): Browsing ungulates cause decline of a Pacific yew *(Taxus brevifolia)* stand in northeastern Oregon. In: International Yew Resources Conference: Yew *(Taxus)* Conservation Biology and Interactions. Berkeley, CA.
Pierce, J. D., (1984): Shiras moose forage selection in relation to browse availability in north-central Idaho. Can. J. Zool. *62:* 2404–2409.
Putman, R. J., (1996): Ungulates in temperate forest ecosystems: perspectives for future research. In: A.J. Kuiters *et al.*, eds.: Ungulates in Temperate Forest Ecosystems. Elsevier. Amsterdam. 205–214.
Raphael, M. G., White, M., (1984): Use of snags by cavity-nesting birds in the Sierra Nevada. Wildl. Monogr. *86.*
Reisenhoover, K.I., Maass, S.A., (1987): The influence of moose on the composition and structure of Isle Royal forests. Can. J. For. Res. *17:* 357–364.
Roth, R., (1996): The effect of deer on the natural regeneration of mixed forests. Z. für Jagdwiss. *42:* 143–156.
Ruge, K., (1970): Zum Ringeln der Spechte. J. Ornithol. *111:* 496.
Rushmore, F. M., (1969): Sapsucker damage varies with tree species and seasons. General Technical Report NE-136. Northeastern Forest Experiment Station, U.S. Department of Agriculture, Forest Service, Radnor, PA. 19pp.
Scher, S., (1997): Sapsucker *(Sphyrapicus)* foraging ecology in Pacific yew stands, southwestern Oregon. In: J.K. Beigel *et al.*, eds.: First Conference on Siskiyou Ecology. Siskiyou Regional Education Project. Cave Junction, OR. 132–136.
Shuford, W. D., (1993): Marin County Breeding Bird Atlas. Bushtit Books. Bolinas, CA.
Snyder, J. D., Janke, R. A., (1976): Impact of moose browsing on boreal type forests of Isle Royal National Park. American Midland Naturalist *95:* 79–92.

Tate, J. Jr., (1969): Foraging behavior of the eastern yellow-bellied sapsucker *(Sphyrapicus varius varius).* Ph.D. dissertation. University of Nebraska, Lincoln.
Tate, J. Jr., (1973): Methods and annual sequence of foraging by the sapsucker. Auk *90:* 840–856.
Turcek, F., (1954): The ringing of trees by some European woodpeckers. Ornis Fennica *31:* 33–41.
Welch, D. et al., (1991): Leader browsing by red and roe deer on young Sitka spruce trees in western Scotland. II. Effects on growth and tree form. Forestry *65:* 309–330.
Williams, C.E., (1990): Late winter foraging by honeybees *(Hymenoptera: Apidae)* at sapsucker holes. Great Lakes Entomol. *23:* 29–32.
Winkler, H. et al., (1995): Woodpeckers: A Guide to the Woodpeckers of the World. Houghton Mifflin. Boston, New York.
Zusi, R.I., Marshall, J.T., (1970): A comparison of Asiatic and North American sapsuckers. Natural History Bull. Siam Society. *23:* 395–407.

Acknowledgements

I thank Johann Visser and Gerald Mandell for guidance in identifying study areas on the Dead Indian Plateau, John Obst and Jerald Morse for assistance with photography, B. Shimon Schwarzschild for reviewing the manuscript and offering constructive comments and suggestions, George Chang and Joe McBride for providing research and computer facilities on the University of California, Berkeley Campus, Rosmarie Louis for calling my attention to relevant library resources at the Swiss Federal Institute of Technology, and Ladislav Kučera for sharing insights on woodpecker damage to yew.

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