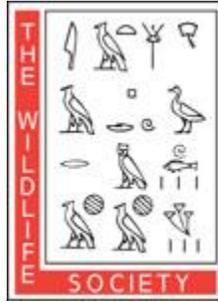


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Importance of early successional habitats to mammals in eastern forests

by John A. Litvaitis



Abstract

Populations of mammals that depend on early successional forests or shrub-dominated habitats are declining in portions of the eastern United States. Although much of this decline can be attributed to maturation of young forests that once dominated the East, fragmentation and suppression of natural disturbances also have been implicated. Responses by habitat specialists (e.g., New England cottontails [*Sylvilagus transitionalis*]) and carnivores with large area requirements that rely on prey associated with early successional habitats (e.g., bobcats [*Lynx rufus*]) have been most extreme. Populations of facultative or opportunistic users of early successional habitats (e.g., black bears [*Ursus americanus*] and little brown bats [*Myotis lucifugus*]) apparently have not been affected by fewer young stands. As eastern forests mature, biotic and abiotic forces will increase abundance of early successional habitats. However, maturation of these forests will take a century or more. In the meantime, using even-aged silviculture and applying controlled burns to native shrublands may be useful to alleviate current shortages. In landscapes modified substantially by suburban-urban developments and dense networks of roads, conventional management efforts likely will be insufficient. In these regions, increased populations of generalist predators are capable of exerting intense predation on mammalian herbivores that are restricted to small patches, and movement between patches by small mammals is limited. Mammals with large area requirements also are hampered in these landscapes by frequent road crossings. These limitations may require implementing habitat management programs for mammals that differ from those developed for other disturbance-dependent taxa. Large (>10-ha), clustered patches of early successional habitat may be necessary to maintain viable populations. The effectiveness of these managed habitats will be further enhanced by positioning them close to existing land uses that are characterized by early successional habitats (e.g., powerline corridors). In agricultural landscapes, the representation of old-field habitats could be increased in set-aside programs.

Key Words bats, black bears, bobcats, cottontails, disturbance, early successional habitat, mammals, snowshoe hares

Mammals are often overlooked as indicators of habitat change because many species are secretive, occur at low densities, or have generalized lifestyles that are satisfied by numerous habitats. These characteristics may limit

ability of natural resource managers to track any relationship between mammal abundance and habitat change. Despite these limitations, mammals respond to natural disturbances (e.g., MacMahon et al. 1989) and human

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land uses (e.g., Kirkland 1977) that alter habitat structure and ecological succession. In eastern forests, this response includes a fairly predictable succession of species that colonize a site as it progresses from grassy clearing to closed-canopy forest (Beckwith 1954, Golley et al. 1965). Depending on the region, meadow voles (*Microtus pennsylvanicus*) or oldfield mice (*Peromyscus polionotus*) are among the first to colonize abandoned fields (Beckwith 1954, Golley et al. 1965). As a woody understory develops, cottontails (*Sylvilagus*) or snowshoe hares (*Lepus americanus*) begin to occupy the site (Beckwith 1954, Burgason 1977). Eventually squirrels (*Glaucomys*, *Sciurus*, and *Tamiasciurus*) become residents as trees dominate the area (Wilson and Ruff 1999). Clearly, this sequence is a simplification of the habitat associations of mammals, but it does indicate that forests with a variety of seral stages will support a diverse mammal community (Hunter 1990).

Land-use patterns have had an obvious influence in shaping the age structure of eastern forests for centuries (Williams 1989, Lorimer 2001) and thus have affected the historic and current composition of forest wildlife communities (Litvaitis 1993, McWilliams et al. 1997). In portions of this region, early successional forests and shrub-dominated habitats are becoming increasingly scarce (Litvaitis et al. 1999, Trani et al. 2001). Seedling–sapling stands currently represent the smallest portion of forestlands in northeastern (e.g., Massachusetts: 4%) and north-central (e.g., Illinois: 3%) states (Trani et al. 2001). This compares to substantially larger amounts of young forests in other areas, especially the Coastal Southeast (e.g., seedling–sapling forests represent 35% of timberlands in Alabama and Mississippi, Trani et al. 2001). Populations of mammals associated with young forests also are declining in northeastern (Litvaitis 1993) and north-central states (Mankin and Warner 1999a). Although the ramifications of these declines on regional biological diversity are not understood completely, long-term viability of some species may be in jeopardy (Litvaitis and Villafuerte 1996). This situation warrants conservation attention now.

Approximately 140 species of mammals are native to the eastern United States, and about 90 of these are associated with forested habitats (estimated from Wilson and Ruff 1999). In this paper, I examine the relationships of forest mammals to shrub-dominated and disturbance-generated habitats in the eastern United States. First, I differentiate between species that are responsive to

changes in the abundance of these habitats and those that simply utilize them opportunistically. Next, I consider other factors that limit the suitability of early successional habitats to mammals in many contemporary landscapes. Finally, I describe approaches to manage disturbance-generated habitats in regions where these communities are in short supply and how management efforts can be placed in a landscape context to maximize their suitability to mammals.

Perhaps a logical first step in considering how to respond to reductions in early successional habitats would be to define an appropriate benchmark or baseline for comparison. If we could decide on the "normal" abundance of these habitats, then we should be able to respond to a shortfall or overabundance rather than simply react to changes.

Responses by mammals to forest disturbances

Early successional obligates

Among the mammals that depend on young forests or shrub-dominated communities in the eastern United States, lagomorphs may be the most widespread group. Cottontails and snowshoe hares occupy a variety of habitats in this region (Wilson and Ruff 1999), but local abundance depends on availability of dense understory vegetation (e.g., Litvaitis et al. 1985, Barbour and Litvaitis 1993).

In the Northeast, New England cottontails (*Sylvilagus transitionalis*) occupy wetlands, idle agricultural lands, powerline corridors, and patches of regenerating forest (Litvaitis 1993). In these habitats, secondary succession has progressed approximately 10–25 years and understory vegetation provides food and cover (Barbour and Litvaitis 1993). As trees on these sites mature and understories thin, local cottontail populations decline rapidly (Figure 1a). Historically, New England cottontails likely occupied native shrublands associated with rocky outcrops or wetlands and forests regenerating after a small-scale (e.g., inundation by beavers [*Castor canadensis*], lightning strike, or windthrow) or large-scale (e.g., hurricanes, wildfires, or fires intentionally set by native peoples) disturbance. Clearing of forests for agriculture by European settlers and subsequent abandonment of these lands was an extreme disturbance event that profoundly affected the abundance of early successional habitats (Litvaitis 1993). New England cottontails and other early

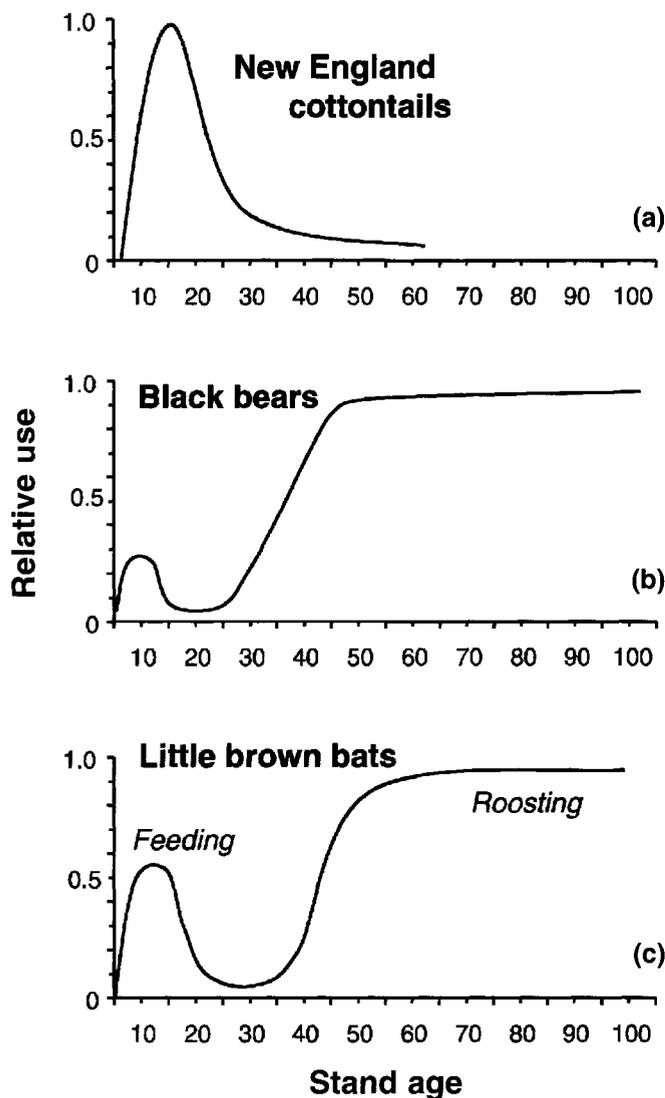


Figure 1. Conceptual representation of seral-stage associations of several mammals in eastern forests. New England cottontails (a) are considered obligate users of young stands because these habitats provide all food and cover needs. Black bears (b) are considered opportunistic users of young stands, and mature stands are used in all seasons. Little brown bats (c) also can be considered opportunistic users of young stands. Bats may congregate in these stands, but the stands do not contain a greater concentration of insects, and bats also forage in other habitats. Mature stands are used as diurnal roosts, and abundance of roosts may limit suitability of a forest to bats. Response curves were adapted from Giles (1978).

successional vertebrates reached unprecedented levels of abundance in the Northeast during the late 1800s and early 1900s (Litvaitis 1993). However, most of these abandoned farmlands matured into closed-canopy forests (circa 1960), and populations of New England cottontails and other taxa quickly retracted. Currently, populations of cottontails are small, disjunct, and span approximately 20% of the area this species occupied historically (Litvaitis and Litvaitis 1996). In response to this decline, the Northeastern Nongame Technical Committee has listed

the New England cottontail as a priority species for additional restoration efforts and several national organizations have petitioned the United States Fish and Wildlife Service to list this species as threatened or endangered (M. Amaral, United States Fish and Wildlife Service, Concord, N.H., personal communication).

In the Mid-Atlantic and Interior Southeast, Appalachian cottontails (*S. obscurus*, previously considered southern populations of *S. transitionalis*, see Chapman et al. 1992) occupy a variety of early successional forests with dense shrubs (especially *Rubus*) or mature stands with a dense understory of rhododendron (*Rhododendron maximum*), mountain laurel (*Kalmia latifolia*), or blueberries (*Vaccinium*) at high elevations (ca. 700–900 m above sea level, Sommer 1997). In western Maryland, for example, Appalachian cottontails selected sites within 2 m of dense understory vegetation and avoided sites with sparse understory cover (Sommer 1997). Although only limited research has been conducted on the historic and current abundance of this species, populations have declined (Merritt 1987) in response to habitat fragmentation and suppression of wildfires (Chapman and Morgan 1973, Sommer 1997). Remaining populations are currently restricted to large blocks of continuous forests where human land uses are limited (Chapman and Stauffer 1981, Chapman et al. 1992).

Eastern cottontails (*S. floridanus*) occupy the largest geographic range of any cottontail (Chapman et al. 1982) and are adapted to exploit a variety of habitats, including those modified by contemporary land uses (Smith and Litvaitis 2000). Nevertheless, this species also has responded to changes in land use. Initially, clearing forests for agriculture resulted in an interspersed of fields, brushy edges of pastures, and woodlots that provided eastern cottontails with abundant food and cover, and populations expanded (Chapman and Morgan 1973). However, subsequent changes in agricultural practices (especially in the Midwest) have reversed this trend. For example, farming practices in Illinois have shifted to large fields that are dedicated to single crops, and idle areas and hedge rows have been cleared (Vance 1976, Mankin and Warner 1999a). Populations of eastern cottontails there declined by >70% from 1956 to 1978 in response to these changes (Mankin and Warner 1999a). Although eastern cottontails are able to persist in these intensively farmed areas, they are substantially restricted to small portions of the landscape where suitable cover is available (Mankin and Warner 1999b). Remaining shelterbelts and other woody vegetation associated with farmsteads provide the only cover, which is critical to cottontail survival in winter (Mankin and Warner 1999b).

I have highlighted responses of lagomorphs to losses of early successional forests and shrub-dominated habitat because these species obviously depend on these habitats. Additionally, lagomorphs are significant components in many biotic communities, and changes in abundance of these herbivores influence other trophic levels (e.g., Wagner 1981, Boutin et al. 1995). For example, rabbits or hares are the major prey of bobcats (*Lynx rufus*) throughout the range of this carnivore (Larivière and Walton 1997). The decline of New England cottontail populations resulted in functional and numeric responses among bobcats in the Northeast (Litvaitis 1993). Specifically, cottontail remains were found in 43% of the bobcat carcasses that were submitted for bounty payment during 1951–1954 in New Hampshire. This dropped to an occurrence of only 10% in carcasses collected during 1961–1965, the period when second-growth forests were no longer suitable for New England cottontails (Litvaitis 1993). Likewise, average annual harvests of bobcats by trappers and hunters in New Hampshire dropped from 350 in 1951–1954 to only 36 during 1965–1969 (Litvaitis 1993). Abundance of bobcats in New Hampshire apparently has not rebounded despite closed hunting and trapping seasons for >15 years (E. Orff, New Hampshire Fish and Game, Durham, N.H., personal communication).

Facultative or opportunistic users of early successional forests

Most mammals that occupy eastern forests utilize resources from 2 or more habitats on a daily or seasonal basis (DeGraaf and Yamasaki 2001). For example, black bears (*Ursus americanus*) utilize numerous seral stages in response to the seasonal distribution of food (Pelton 1982). In spring, grasses, forbs, and buds are important foods. These are abundant in wetlands, forests openings, and regenerating stands (Landers et al. 1979, Pelton 1982). These same areas also contain soft mast-producing shrubs (e.g., *Rubus*, *Vaccinium*, and *Gaylussacia*) that are consumed by bears in summer (Brody and Stone 1987). Depending on the forest type and geographic region, bears may not depend on regenerating stands in spring and summer because foods used in these seasons are found in older stands or other habitats (e.g., Lander et al. 1979). Clark et al. (1994), for example, reported that transmitter-equipped bears in Arkansas used regenerating stands less than expected even though these sites had abundant seasonal foods.

In late summer and autumn, bears move to mature stands of oak (*Quercus* spp.), hickory (*Carya* spp.), black gum (*Nyssa sylvatica*), or beech (*Fagus americana*), where they consume the hard mast or seeds of these trees (Landers et al. 1979, Pelton 1982). Although spring and

summer foods maintain bears during these seasons, the high concentration of carbohydrates and fats in hard mast have an obvious influence on bear survival and reproduction (Rogers 1976). As a result, mature forest stands are more influential than regenerating stands in affecting productivity of a local bear population (Figure 1b).

Bats also utilize a variety of habitats and forest size-classes (Barclay and Brigham 1996, Pierson 1998). In the Northeast, little brown bats (*Myotis lucifugus*) forage in a variety of habitats (e.g., over bodies of water and forest trails) and roost in mature forests or human-built structures (Anthony and Kunz 1977, Krusic et al. 1996). In one predominantly forested landscape, little brown bats were detected foraging in regenerating stands more often than any other seral stage (Figure 1c, Krusic et al. 1996). Foraging bats may indeed congregate in regenerating stands, but insect abundance in these stands is no greater than in older stands (Grindal and Bringham 1998). Roosting sites may be more limiting than foraging habitat to little brown bats and other forest-dwelling bats (Pierson 1998).

It is apparent that bears and bats utilize early successional habitats, but the resources sought by both taxa in young forests are available in other seral stages or non-forested habitats. As a result, we should not expect an obvious numeric response to the decline in early successional habitats by either species. Responses by other opportunistic users of these habitats may differ. White-tailed deer (*Odocoileus virginianus*) utilize early successional forests, and these areas often provide more forage than older forest age-classes (Harlow 1984: Figure 112). Deer can respond to the availability of these habitats at local and regional scales (Harlow 1984). Following widespread timber harvesting in the Great Lakes region, deer populations increased from approximately 2–4/km² to about 14/km² (Alverson et al. 1988). Notwithstanding this response, deer should not be considered early successional obligates. This generalist species is even more responsive to human-dominated landscapes. For example, deer densities have exceeded 50/km² in portions of Pennsylvania where woodlots, pastures, and croplands combined to provide deer with an abundance of forage and cover (Palmer et al. 1997).

Limitations of early successional habitats in contemporary landscapes

As mid-succession forests throughout the East mature, natural forces will eventually generate disturbances in which understory vegetation can develop. However, it likely will be a century or longer before these stands reach a size- and age-class distribution where disturbances

create openings on a regular basis (Borman and Likens 1979). Most of these openings will be small, several hectares or less (Lorimer 2001). In pre-colonial landscapes, such openings were important habitats for disturbance-dependent mammals. The matrix that now comprises many eastern landscapes, however, is very different from historic conditions (including agricultural fields, suburbs, industrial parks, and extensive networks of powerlines and roads). Small disturbed patches may no longer function as suitable habitat in these altered environments. The current condition of New England cottontails and bobcats illustrates this point.

New England cottontails that occupy small (<3-ha) patches of habitat encounter food shortages during winter (Villafuerte et al. 1997). In response, cottontails in small patches frequently forage away from escape cover and are killed by predators at approximately twice the rate as cottontails on large patches where per-capita food resources are more abundant (Barbour and Litvaitis 1993, Villafuerte et al. 1997). It may seem counter to previous comments on the decline of bobcats to suggest that predation can be influential in limiting cottontails. Generalist predators (especially coyotes [*Canis latrans*] and foxes [*Vulpes vulpes*]) that are capable of exploiting a variety of habitats and prey, however, have replaced bobcats as the major proximate mortality factor of cottontails (Barbour and Litvaitis 1993, Smith and Litvaitis 2000). Populations of these predators have increased in response to converting forests to other land uses (Oehler and Litvaitis 1996). Thus, as cottontail populations have declined in response to habitat loss, their predators have increased. Survival rates of cottontails in small patches are so low that these patches function as demographic sinks (Barbour and Litvaitis 1993, Brown and Litvaitis 1995, Villafuerte et al. 1997). As a result, the pattern of local extinction and subsequent recolonization that likely characterized populations of New England cottontails in pre-Columbian landscapes is no longer viable. Few individuals disperse from small patches of habitat (Barbour and Litvaitis 1993), and those that do encounter habitats with limited cover where they are vulnerable to intense predation (Brown and Litvaitis 1995). Present-day populations of New England cottontails, therefore, are dependent on large patches of habitat close to each other to assure long-term survival (Litvaitis and Villafuerte 1996).

Bobcats also are at risk in some eastern forests. Home-range size of bobcats was correlated with local abundance of lagomorphs (Litvaitis et al. 1986). As a result, scarce or widely disjunct prey populations may result in frequent road crossings by bobcats, making them vulnerable to vehicle collisions and other sources of

mortality. Collisions with vehicles were the second most frequent cause of mortality among a group of transmitter-equipped bobcats in Maine (20% of all mortalities, Litvaitis et al. 1987) and likely affect regional distributions of this carnivore (*sensu* Fuller et al. 1992). These observations indicate that efforts to benefit mammals may vary according to the degree that regional land uses have modified forest continuity.

Managing early successional habitats to benefit forest mammals

Perhaps a logical first step in considering how to respond to reductions in early successional habitats would be to define an appropriate benchmark or baseline for comparison. If we could decide on the “normal” abundance of these habitats, then we should be able to respond to a shortfall or overabundance rather than simply react to changes. Such a discussion would be especially relevant when considering how to manage habitats where the influences of contemporary human populations are limited or can be controlled and where disturbance regimes can operate to recreate baseline conditions.

Management in landscapes with limited human activity

In regions where forests remain largely intact, the resumption of natural disturbances may eventually generate sufficient habitats to sustain populations of early successional mammals. Public lands, especially national forests, may be large enough to avoid concerns of generalist predators and networks of paved highways. As a starting point, the amount of early successional habitat could be based on historic (pre-Columbian) levels of disturbance. This will obviously vary by forest type and region (e.g., Lorimer 1977, Ware et al. 1993). Management activities (including even-aged timber management) could then be used to complement existing spatial and temporal scales of disturbance. The level of human intervention would be based on the degree that natural disturbances are affecting forest age-class distribution relative to baseline conditions. In mid-successional forests, human intervention may be essential in providing sufficient habitat for decades until natural disturbances are sufficiently frequent.

Regardless of the specific manipulations used (e.g., Thompson and DeGraaf 2001), management activities will require public support, which is currently lacking. Public opposition to activities that create and maintain early successional habitats (especially clearcutting) is responsible for the obvious reluctance by the United States Forest Service to achieve its mandated objectives

of providing these habitats on several eastern forests (Litvaitis et al. 1999). The recent decision to list Canada lynx (*Lynx canadensis*) as a threatened species (Nordstrom et al. 2000), however, should stimulate new discussions regarding habitat management on northeastern and north-central forests. The United States Fish and Wildlife Service and United States Forest Service recently developed a lynx conservation agreement (United States Forest Service Agreement #00-MU-11015600-013) that requires the Forest Service to promote the conservation of lynx habitat on national forests within the historic range of lynx. Because the demography of lynx is closely associated with abundance of snowshoe hares (Ruggiero et al. 2000), application of even-aged timber management may increase (from near nonexistent levels on some forests) to assure an adequate prey base. Concern for populations of other species (especially migratory songbirds, Hunter et al. 2001) may prompt similar discussions in other regions.

Although the creation of early successional habitats in much of the East has been associated with even-aged timber management, this is not essential in some areas, especially on xeric sites. Disturbance-dependent habitats also include pitch pine (*Pinus rigida*) and scrub oak (*Quercus ilicifolia*) barrens. These habitats have been degraded and reduced substantially throughout the eastern United States in response to various land uses and the suppression of wildfires (Motzkin et al. 1999). Restoration of these communities can provide substantial habitat but will require more than simply cutting existing vegetation (Niemuth and Boyce 1998). Once located, candidate sites should be prioritized based on several criteria, including land-use history and the ability to reinstate burning regimes. Sites that have never been plowed may support more diverse communities (Motzkin et al. 1999) and should be favored.

Management in human-dominated landscapes

In regions where the continuity of forests has been disrupted by intense human activity, innovations in habitat management will be needed to provide suitable habitat. Here, natural disturbance patterns (i.e., many small and few large disturbances) may not provide a useful template because of the limitations imposed by a fragmented landscape. Diverse land uses, small average land holdings, and frequent turnover in land ownerships also will present challenges to manipulating forest habitats (Brooks and Birch 1988).

In landscapes substantially modified by suburban-urban developments with a dense network of roads, it may be most effective to dedicate moderate (>10-ha) to large (>25-ha) tracts to serve as "core habitats." These

tracts could support populations of small herbivores that would be less susceptible to the limitations of the surrounding landscape matrix and large enough to withstand short-term perturbations. Clustering core habitats (within several kilometers of each other) and positioning them adjacent to existing land uses that include early habitats (especially powerline corridors [Askins 1994]) would facilitate exchanges among populations of small mammals and other vertebrates associated with early successional habitats (Kjoss and Litvaitis 2001). Powerline corridors may function as dispersal corridors that link 2 or more clusters of habitat within a township, thus promoting regional security. Maintaining clusters away from paved roads also would maximize their suitability to wide-ranging carnivores (Litvaitis et al. 1996). If suitable public lands are not available to serve as core habitats, conservation easements may be necessary to assure long-term commitment. Maintaining these habitats with timber harvests may not be cost-effective. Mowing and selective use of herbicides (Thompson and DeGraaf 2001) may be the most practical alternatives to prevent an overstory canopy from developing. If management schedules permit, including these sites in the regular maintenance of adjacent powerline corridors would reduce costs.

In agricultural areas, development of new federal set-aside programs has the potential to provide additional habitats. In recent decades, programs such as the Conservation Reserve Program (CRP) have diverted considerable lands from production agriculture back to native habitats (Warner et al. 2000). Most of these programs were directed toward grasslands, and the benefits to wildlife in these habitats were substantial (Reynolds et al. 1994). Although CRP contracts lasted 10 years, most agreements (e.g., Payment-In-Kind and Acreage Conservation Reserve) were short-term (often annual). Such arrangements have limited effects on improving habitat (Warner et al. 2000) and would do nothing to enhance early successional forests. If these programs are re-established, modifications of contract length and the variety of habitats eligible for enrollment could substantially restore habitats with native shrubs and trees to areas of the Midwest.

Obviously, the scenarios just described are hypothetical, but they do suggest that it is possible to provide suitable early successional habitats in substantially modified ecosystems. Such efforts would substantially improve the status of mammals and other wildlife dependent on these habitats.

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