

The response of tree squirrels to fragmentation: a review and synthesis

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Abstract

Habitat fragmentation is often considered a major threat to biodiversity; however, our understanding of how fragmentation impacts populations is poor. Identifying appropriate models for such studies is difficult. Tree squirrels are dependent on mature forests for food, cover and nests; these are habitats that are being fragmented rapidly and that are easily defined by humans. Squirrels represent excellent models for study of fragmentation. The literature on tree squirrels was reviewed to glean data on density and home-range size in forest fragments. Sufficient data were available on four species (*Sciurus carolinensis*, *S. niger*, *S. vulgaris*, *Tamiasciurus hudsonicus*). Density was negatively related to fragment size for *S. carolinensis* and *S. niger* and marginally so for *T. hudsonicus*. *Sciurus vulgaris* did not exhibit this relationship. Home-range size was analysed for three species of *Sciurus* and was positively related to forest fragment size for *S. carolinensis* and *S. niger*. Again, only *S. vulgaris* did not to show this relationship. *Sciurus vulgaris* is rarely found in small forest fragments and is believed to be especially sensitive to fragmentation; other tree squirrels appear to be sensitive to fragmentation in more subtle ways. Home range compaction provides a mechanism by which densities may increase in small fragments. The demographic consequences resultant from the high densities of squirrels found in small woodlots are not known but may explain the forest damage, avian nest predation and reduced diversity often cited to occur in woodland fragments.

INTRODUCTION

Habitat fragmentation is often considered one of the greatest threats to conservation of biodiversity and is a principal cause of endangerment (Czech & Krausman, 1997; Lawler *et al.*, 2002; Kerr & Chilar, 2004). Consequences of fragmentation for abiotic and biotic components of ecosystems are varied (for reviews, see Yahner, 1988; Tscharntke *et al.*, 2002). Most major ecosystems have been fragmented through anthropogenic activities in the last 200 years; however, forested ecosystems have undergone excessively high levels of fragmentation (Nixon, Havera & Hansen, 1978; Middleton & Merriam, 1983; Harris, 1984; Nixon & Hansen, 1987; Sheperd & Swihart, 1995; Verbeylen, De Bruyn & Matthysen, 2003). Genetic variation is often, but not always, lost with habitat fragmentation (Awise, Neigel & Arnold, 1984; Wauters *et al.*, 1994b; Frankham, 1997; Eldridge *et al.*, 1999; Small, Stone & Cook, 2003). Biodiversity can also be lost (Laurance, 1990; Andren, 1994; Nupp & Swihart, 1996; Lomolino & Perault, 2000, 2001; McShea *et al.*, 2003) as some species are unable to persist in small fragments; however, the response of

natural populations to fragments of different sizes is not well known.

In a meta-analysis of density and area relationships, Conner, Courtney & Yoder (2000) found that for many taxa, densities are positively correlated with island size; however, mammals did not show this relationship. The sign of the relationship between density and patch size is often quite variable between studies and taxa (Bowers & Matter, 1997; Bender, Contreras & Fahrig, 1998; Debinski & Holt, 2000; Krauss, Steffan-Dewenter & Tscharntke, 2003). Island biogeographical models relate species diversity to population level processes and attributes such as dispersal and local extinction (Bowman, Cappuccino & Fahrig, 2002), which suggests that demography might differ on the basis of site characteristics. Island populations of small mammals differ from mainland populations in a number of demographic parameters (for a review, see Gliwicz, 1980; Adler & Levins, 1994). Densities of small mammals tend to be higher (Jewell, 1966; Sullivan, 1977; Tamarin, 1977; Bujalska, 1985) and more stable (Sullivan, 1977; Tamarin, 1977; Bujalska, 1985) on islands. Reproductive output is typically lower in island populations due to reduced litter size and/or increased age of first reproduction (Tamarin, 1978; Bujalska, 1985; Stamps & Buechner, 1985). Survival is also often higher in island versus mainland

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populations (Tamarin, 1977; Adler & Levins, 1994). Collectively the differences between island and mainland populations have been termed the 'island population syndrome' (Adler & Levins, 1994). Whether islands of habitat have demographic characteristics similar to oceanic islands is not well known. Given that demographic parameters are important to our understanding of the response of organisms to fragmentation (Krohne, 1997), knowledge of how species respond to fragments of different size is required.

Tree squirrels (*Sciurus* and *Tamiasciurus*) may provide excellent models to assess the potential consequences of habitat fragmentation. Tree squirrels are obligates of mature forests (Gurnell, 1987; Steele & Koprowski, 2001) that depend heavily on mature trees for nests (Baumgartner, 1939; Wauters & Dhondt, 1990; Halloran & Bekoff, 1994; Young, Greer & Six, 2002) and food (Thompson & Thompson, 1980; Korschgen, 1981; Gurnell, 1987; Koprowski, 1991, 1994a, 1994b; Koprowski & Corse, 2001; Steele & Koprowski, 2001). As a result, habitat fragments are relatively easily defined by humans at a scale that is probably meaningful to the organism. Furthermore, large leaf nests (Bouffard & Hein, 1978; Don, 1981), body size (Gurnell, 1987; Steele & Koprowski, 2001), diurnal activity (Hicks, 1949; Horwich, 1972; Thompson, 1977; Wauters, Swinnen & Dhondt, 1992), moderate home-range sizes (Koprowski, 1998) and relative ease of trapping (Gurnell & Pepper, 1994) make tree squirrels conspicuous for the estimation of density, assessment of home-range size and determination of presence/absence in a forest fragment. Due in large part to these characteristics, several species of tree squirrel have been studied frequently enough in a diversity of habitat patches that a data set of sufficient size exists to enable comparative studies. Finally, most tree squirrels are of precarious conservation status in at least some portion of their range (Koprowski & Steele, 1998) with eight out of nine species of holarctic *Sciurus* and two out of three species of *Tamiasciurus* receiving some form of legal protection. Assessing the impacts of forest fragmentation on this group is thus quite timely. Previous studies of individual species in a local area have suggested that home-range size or density may be related to woodlot size (fox squirrels, *Sciurus niger*: Baumgartner, 1943; Sheperd & Swihart, 1995; eastern grey squirrels, *S. carolinensis*: Erossy, 1973; Don, 1983; Fisher & Merriam, 2000; red squirrels, *Tamiasciurus hudsonicus*: Bayne & Hobson, 2000). Herein, a comparative generalised individuals–area relationship (Gaston & Matter, 2002) approach will be used across species and geographical areas to assess the response of tree squirrel density and home-range size to forest fragmentation.

METHODS

Data were gleaned from published literature, theses and dissertations on red squirrels, fox squirrels, eastern grey squirrels and Eurasian red squirrel (*S. vulgaris*: common

names after Wilson & Cole, 2000). To be included, a value was required to meet the following criteria:

- (1) Area of the woodlot or forest in which study occurred must be clearly defined. Often study area was well-defined, however, size of forest patch in which the study area was placed was not described by the authors.
- (2) Forest fragment could not be described as the result of recent felling of trees.
- (3) Home ranges were determined from radiotelemetry, observations, or extensive live trapping and represented 95% or 100% minimum convex polygon (MCP) estimates.
- (4) Sex-specific home ranges must be provided.
- (5) Densities of squirrels were determined from extensive live trapping efforts.

Study sites are only represented once in each of the analyses. Forests >1000 ha were assigned a value of 1000 ha, the largest fragment size considered in the analyses. Because *Tamiasciurus hudsonicus* defend territories throughout most of their range (Smith, 1968; Gurnell, 1987; Steele, 1998), while the species of *Sciurus* are home-range species, space-use data were only analysed for *Sciurus*. A meta-analysis could not be conducted due to the lack of appropriate detail to determine effect sizes in subsets of the sources.

RESULTS

The density of the four most commonly researched tree squirrels (*Sciurus carolinensis*, $n = 10$; *S. niger*, $n = 14$; *S. vulgaris*, $n = 22$; *Tamiasciurus hudsonicus*, $n = 10$) is negatively related to woodlot size; the tendency for density to increase in small fragments is strong when data for all species are combined ($F_{1,55} = 38.70$, $P < 0.0001$, $R^2 = 0.468$). To be certain that data from large continuous forests were not significantly changing the relationship, all data for forests ≥ 1000 ha were removed and density:woodlot size was re-analysed; the relationship remained strongly negative ($F_{1,41} = 18.06$, $P < 0.001$, $R^2 = 0.311$). When density and woodlot area data were analysed for species individually (Fig. 1), a strong negative relationship was detected for *S. carolinensis* ($F_{1,9} = 70.38$, $P < 0.0001$, $R^2 = 0.898$) and *S. niger* ($F_{1,13} = 127.97$, $P < 0.0001$, $R^2 = 0.914$), a moderately negative relationship was found for *T. hudsonicus* ($F_{1,9} = 3.21$, $P = 0.111$, $R^2 = 0.286$), and no relationship for *S. vulgaris* ($F_{1,21} = 1.22$, $P = 0.281$, $R^2 = 0.0525$). *Sciurus vulgaris* was rarely found in small woodlots and appears to require continuous forests or high levels of food supplementation or habitat connectivity to persist in fragmented environs (Celada *et al.*, 1994; Magris & Gurnell, 2002; Verbeylen *et al.*, 2003).

Home-range sizes of all species (*Sciurus carolinensis*, $n = 11$; *S. niger*, $n = 9$; *S. vulgaris*, $n = 12$) were positively related to woodlot size for both males ($F_{1,33} = 37.90$, $P < 0.0001$, $R^2 = 0.542$) and females

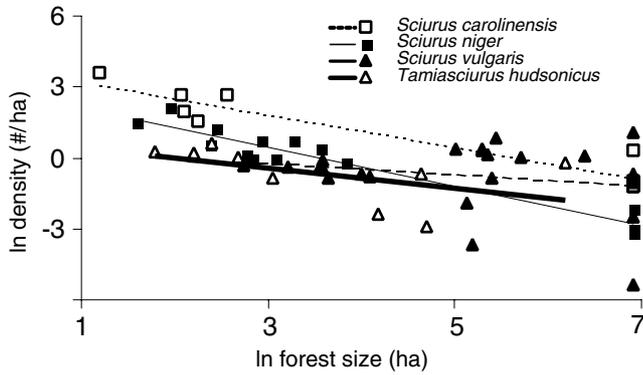


Fig. 1 Species-specific relationships between squirrel density and forest fragment size. Lines determined by simple linear regression. Data are from: Williams, 1936; Baumgartner, 1939, 1943; Moore, 1957; Flyger, 1960; Brink, 1964; Cordes, 1965; Taylor, 1966; Smith, 1967; Wood, 1967; Mosby, 1969; Barkalow, Hamilton & Soots, 1970; Geeslin, 1970; Kemp & Keith, 1970; Cordes & Barkalow, 1972; Silva, 1972; Erossy, 1973; McCloskey, 1975; Adams, 1976; Whitehead, 1976; Fancy, 1981; Manski, Van Druff & Flyger, 1981; Nixon, Havera & Hansen, 1984; Herkert, 1985; Koprowski, 1985; Wauters & Dhondt, 1985, 1992; Sullivan & Moses, 1986; Weigl *et al.*, 1989; Kantola & Humphrey, 1990; Andren & Delin, 1994; Wauters *et al.*, 1994a,b, 2001; Shuttlesworth, 1996; Halliwell, 1997; Münch, 1998; Delin & Andren, 1999; Smith, 1999; Cagnin *et al.*, 2000; Cartmel, 2000; Magris & Gurnell, 2002.

($F_{1,33} = 36.43$, $P < 0.0001$, $R^2 = 0.532$). Removal of woodlots ≥ 1000 ha did not influence the relationship for either males ($F_{1,18} = 18.64$, $P < 0.0005$, $R^2 = 0.523$) or females ($F_{1,18} = 27.36$, $P < 0.0001$, $R^2 = 0.617$). When species were examined independently (Fig. 2), a strong positive relationship between home-range size and woodlot area was noted for *S. carolinensis* males ($F_{1,8} = 9.33$, $P < 0.019$, $R^2 = 0.571$) and females ($F_{1,8} = 16.67$, $P < 0.0047$, $R^2 = 0.704$), for *S. niger* males ($F_{1,7} = 52.76$, $P < 0.0004$, $R^2 = 0.898$) and females ($F_{1,7} = 116.70$, $P < 0.0001$, $R^2 = 0.951$), but not for either male ($F_{1,11} = 1.19$, $P = 0.301$, $R^2 = 0.106$) or female ($F_{1,11} = 0.045$, $P = 0.837$, $R^2 = 0.004$) *S. vulgaris*.

DISCUSSION

Densities and home-range dynamics of tree squirrels appear to be influenced by fragmentation. Gaston & Matter (2002) suggest that the negative relationship between densities and areas can be an artifact of methods of estimation of density and area. This does not appear to be the case for tree squirrels. Compaction of home ranges, as typically determined from methods independent from trapping such as observation or radiotelemetry, appears to provide a mechanism for increases in density in small woodlots. The negative relationship between density and woodlot area appears to correspond to a positive relationship between home-range size and woodlot area.

Previous researchers have noted similar relationships in tree squirrels while working in local areas. Home

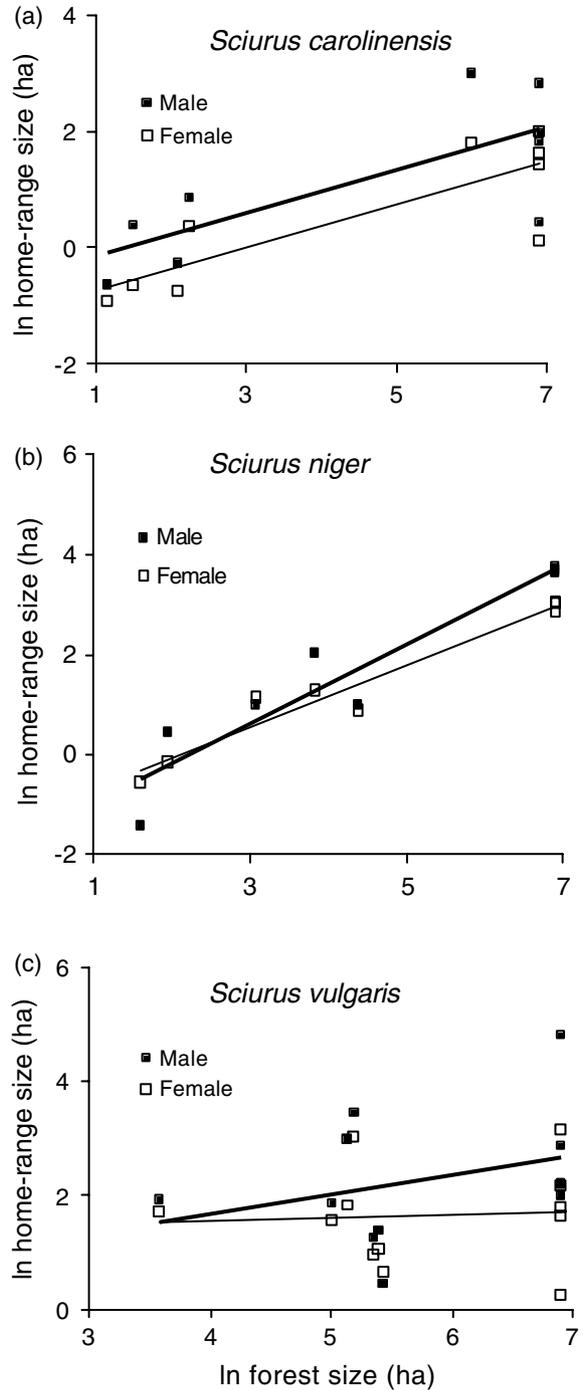


Fig. 2 Species-specific home-range size of male and female tree squirrels and forest fragment size. Lines determined by simple linear regression. (a) *Sciurus carolinensis*, (b) *Sciurus niger*, (c) *Sciurus vulgaris*. Data are from: Robinson & McCowan, 1954; Flyger, 1960; Cordes, 1965; Taylor, 1966; Geeslin, 1970; Cordes & Barkalow, 1972; Silva, 1972; Erossy, 1973; Doebel & McGinnes, 1974; McCloskey, 1975; Adams, 1976; Benson, 1980; Wauters & Dhondt, 1985, 1992; Weigl *et al.*, 1989; Kantola & Humphrey, 1990; Andren & Delin, 1994; Wauters *et al.*, 1994a, 2001; Sheperd & Swihart, 1995; Shuttlesworth, 1996; Halliwell, 1997; Münch, 1998; Smith, 1999; Cartmel, 2000; Conner, 2000; Nupp & Swihart, 2000.

ranges of fox squirrels (Baumgartner, 1943) and eastern grey squirrels (Erossy, 1973) were suggested to be

positively related to woodlot size. Empirical support for this was found in fragmented forests in agricultural regions of Indiana (Sheperd & Swihart, 1995). Densities were also noted to be higher in fragmented landscapes relative to continuous forests for red squirrels (Bayne & Hobson, 2000) and eastern grey squirrels (Fisher & Merriam, 2000). The strong negative relationship between density and woodlot size suggests upon extrapolation that extraordinarily large continuous forests would have densities of zero and forested areas approaching zero would have the highest squirrel densities. Clearly, a critical habitat patch size is required for persistence in tree squirrels and it appears that this size may vary between species (Fisher & Merriam, 2000; Verbeylen *et al.*, 2003).

How can higher densities of squirrels be maintained in isolated woodlots? Many mammalian predators are negatively impacted by fragmentation and use small fragments less frequently than large fragments (Virgos, Telleria & Santos, 2002). Reduced predation pressure might enable higher densities of tree squirrels to accumulate within small fragments. High densities of squirrels in small woodlots might also suggest that areas with increased edge provide higher quality habitat than large continuous forests. Density can be a misleading indicator of habitat quality (Van Horne, 1983). Because woodlots included in this study were not the result of recent fragmentation events, densities were not likely to be in a transitory or non-equilibrium state. Although the relationship between density and area varies greatly between and among taxa, such a negative relationship has been reported for a variety of other mammal species (Nupp & Swihart, 1996; Bowers & Matter, 1997; Connor *et al.*, 2000). Some ecosystems appear to subsidise higher population densities through increased productivity (Andersen & Wait, 2001). Forest fragments may be able to 'subsidise' high densities of tree squirrels due to higher productivity, including increased tree growth (Murcia, 1995; Mourelle, Kellman & Kwon, 2001; Asbjornsen, Vogt & Ashton, 2004) and increased production of tree seeds (Johns, 1988; Herrera *et al.*, 1994; Healy, 1997; Healy, Lewis & Boose, 1999; Greene *et al.*, 2002; Guariguata & Saenz, 2002) at forest edges. Small fragments with high edge:area ratios may be more productive than large fragments, enabling densities to be maintained at higher levels, at least until other changes in community structure occur (Yahner, 1988; Murcia, 1995).

Why does *Sciurus vulgaris* not demonstrate the same response to fragmentation as other tree squirrels? First, data on Eurasian red squirrels in small fragments are sorely lacking, in part due to the continued decline of this species in many areas of their range in Europe (Wauters *et al.*, 1994b; Verbeylen *et al.*, 2003). Furthermore, Eurasian red squirrels typically are not found in isolated woodlots (Verboom & van Apeldoorn, 1990; Celada *et al.*, 1994). In some localities, home ranges of *S. vulgaris* are larger in small woodlots (Wauters, Casale & Dhondt, 1994a) probably because individuals rely on numerous fragments in an archipelago of patches (Delin & Andren, 1999; Verbeylen *et al.*, 2003). Alternatively, on the Island

of Jersey, Eurasian red squirrels are able to persist entirely within small to moderate woodlots with increased densities found in forest fragments where supplemental food is provided (Magris & Gurnell, 2002). These studies suggest that *Sciurus vulgaris* may be able to persist in fragmented environments where patches are of high quality or where densities can be subsidised by the use of multiple fragments or supplemental food. Eurasian red squirrels appear to be particularly sensitive to forest fragmentation. Other species of tree squirrel were also sensitive to fragmentation but in apparently more subtle ways that demonstrated a modest level of area sensitivity permitting their persistence in smaller fragments than Eurasian red squirrels.

Eastern grey squirrels were introduced and spread throughout much of the range of Eurasian red squirrels in the United Kingdom (Gurnell, 1987). The spread of eastern grey squirrels has been attributed to a plethora of causes (Gurnell, 1987; Rushton *et al.*, 1997; Gurnell *et al.*, 2001; Lurz *et al.*, 2001). Part of the success of the alien squirrels may be the ability to persist in a heavily fragmented landscape (Petit, Howard & Stuart, 2004). Concern over the spread of eastern grey squirrels across continental Europe from introductions in Italy (Lurz *et al.*, 2001; Bertolino & Genovesi, 2003) is appropriate, especially given that the European continent is considered to have the most highly fragmented forests in the world (Wade *et al.*, 2003). The few studies that report the persistence of Eurasian red squirrels in small fragments of forest were conducted in localities where alien eastern grey squirrels do not yet occur (Wauters *et al.*, 1994a; Delin & Andren, 1999; Magris & Gurnell, 2002; Verbeylen *et al.*, 2003). The present review of the literature suggests that eastern grey squirrels are found in much smaller fragments and in higher densities in small and moderate fragments than Eurasian red squirrels. As a result, habitat fragments probably serve as plentiful sources of eastern grey squirrels along colonising fronts. In addition, decreased sensitivity of eastern grey squirrels to fragmentation also suggests that habitat fragments could provide demographic and genetic rescue when populations of the alien are exterminated or lost (Tallmon, Luikart & Waples, 2004). Efforts to maintain allotopy between these two species clearly are justified; however, this can create a conservation dilemma. Efforts to increase forested lands are underway and have led to a 9% increase in woodlands but with only modest decreases in fragmentation (Petit, Howard & Stuart, 2004). The ghosts of fragmentation past may be difficult to overcome.

Increases in density and compaction of home ranges in tree squirrels that occur with fragmentation suggest the potential for changes in social and mating systems. Density is frequently associated with changes in social organisation and space use (Lott, 1991; Travis, Slobodchikoff & Keim, 1995; Kjellander *et al.*, 2004). Increased interaction rates (Zenuto, Vassallo & Busch, 2002), increased wounding (Boonstra & Boag, 1992; Zenuto *et al.*, 2002; Macdonald *et al.*, 2004), increased weight loss (Macdonald *et al.*, 2002) and reduced frequency or age of first reproduction (Wolff, Schaubert &

Edge, 1997; Rodel *et al.*, 2004) can occur in high density populations. In tree squirrels, home-range size is negatively related to density (Don, 1983) and communal nesting is frequent in small urban woodlots (Taylor, 1969; Koprowski, 1996). The propensity of female eastern grey squirrels to remain in their natal areas to form overlapping generations of kin as well as to nest in large groups (Koprowski, 1996) may further explain the ability of the alien species to invade and displace the solitary native Eurasian red squirrels (Gurnell *et al.*, 2001). Behavioural changes associated with fragmentation are suggested to be important (Yahner & Mahan, 1997).

High densities and behavioural differences in response to fragmentation of habitat may have unforeseen and negative community-level consequences. Damage to trees, such as bark stripping and girdling, increases with increasing density of eastern grey squirrels in the United Kingdom (Kenward & Parish, 1986). *Sciurus* and *Tamiasciurus* are known predators of avian eggs and nestlings (Gurnell, 1987; Steele, 1998; Koprowski, 1994a,b). Higher levels of nest predation are often, but not always, reported in forest fragments (For reviews, see Robinson *et al.*, 1995; Chalfoun, Thompson & Ratnaswamy, 2002; Thompson *et al.*, 2002). Although the high nest predation rates are often attributed to edge effects, numerous alternative hypotheses exist (for a review, see Lariviere, 2003). Increased nest predation due to tree squirrels is reported in forest fragments (Yahner, 1988; Bayne & Hobson, 1997, 1998, 2000). Such unforeseen community-level consequences emphasise the potential cascade of effects that can occur due to habitat fragmentation.

Finally, the response of other species of tree squirrels to forest fragmentation is not known. Despite the fact that the status of 10 out of 12 species of holarctic *Sciurus* and *Tamiasciurus* is of conservation concern, it was only possible to glean enough data on four of these species to assess their sensitivity to fragmentation. Data on the response of species outside the holarctic regions, such as in tropical forests where trends in fragmentation are on the increase (Wade *et al.*, 2003), are not available. Although tree squirrels have been suggested as potential indicators of forest health (Steele & Koprowski, 2001; Kremsater *et al.*, 2003), ecological publications are available for only about 13% of known species (unpublished results). My findings suggest that response to habitat fragmentation may differ in important ways even among closely related species. The ramifications of this differential sensitivity are poorly known.

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