Am. Midl. Nat. 151:369–377

The Distribution of Fox Squirrel (Sciurus niger) Leaf Nests within Forest Fragments in Central Indiana

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ABSTRACT.—We examined the abundance and placement of leaf nests by fox squirrels in six urban woodlots in central Indiana ranging in size from 1.06 to 8.28 ha. Four of the woodlots were disturbed, or subject to extensive human impact, whereas the remaining two were nature preserves. We counted all leaf nests present in each woodlot and recorded nest tree characteristics. We then conducted a quantitative vegetation analysis of trees present and estimated percentages of herbaceous and shrub cover along a minimum of two 100 m transects at each site. Fox squirrels showed a preference to build nests in certain species of trees. However, preference for nest tree species was not consistent across sites. Fox squirrels preferred to build nests in large trees with vines in the canopy at all sites. Characteristics of nests and nest trees did not differ among sites, but nest density was greater in the disturbed sites compared to the nature preserve sites. The nature preserve sites differed from the disturbed sites only with regard to the amount of shrub and herbaceous cover; shrub cover was greater and herbaceous cover was less at the disturbed sites. Results of this study suggest that fox squirrels are flexible with regard to nest tree species used and that the choice of a nest tree is dependent, in part, on tree size and the presence of vines. Further, a higher density of leaf nests in disturbed woodlots suggests that habitat disturbance and fragmentation due to urbanization may not have detrimental effects on the abundance and persistence of fox squirrels.

INTRODUCTION

Human activity has led to the disturbance, reduction and fragmentation of natural habitats worldwide. Clearing of land for agricultural purposes and subsequently converting land from agricultural to urban use has permanently altered the characteristics of many natural landscapes in North America (Turner *et al.*, 2001). The effects of habitat disturbance and fragmentation on the biota are wide ranging. Habitat fragmentation can result in population declines and local extinction events for many species as viable habitat patches become smaller, more isolated and more exposed due to increased edge boundaries (Turner *et al.*, 2001). Species vary with regard to their sensitivity to habitat fragmentation and disturbance. For example, large-bodied species with large home ranges may be more adversely affected by habitat fragmentation than smaller-bodied species (Belovsky, 1987; Bennett, 1987). Further, species with specific habitat requirements, and those favoring interior habitats, will be more vulnerable to habitat fragmentation and disturbance than species with broad habitat tolerances (Saunders *et al.*, 1991).

Investigation of habitat use and preferences among species has long been a focal point of ecologists. Historically, the characterization of habitat requirements and preferences has been derived from studies conducted in relatively undisturbed habitats specifically chosen to model natural habitats prior to human influence (Lord *et al.*, 2003). Effective species management practices in an age of dwindling natural, undisturbed habitats, however,

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necessitate that populations embedded within urban and agricultural landscapes be examined.

Fox squirrels (*Sciurus niger*) are common inhabitants of urban and suburban areas throughout eastern North America (Steele and Koprowski, 2001) and they are known to frequent small fragmented woodlots and areas disturbed for agriculture (Baumgartner, 1943; Taylor, 1974; Mumford and Whitaker, 1982). Researchers have examined many aspects of fox squirrel ecology including the demographics, social behavior and spatial dynamics of populations inhabiting a suburban park (Armitage and Harris, 1982; Koprowski, 1991, 1996) and of fox squirrels inhabiting fragmented habitat patches within an agricultural landscape (Sheperd and Swihart, 1995; Swihart and Nupp, 1998). Characteristics of leaf nest location by fox squirrels have also received attention (Baumgartner, 1943; Sanderson *et al.*, 1980; Edwards and Guynn, 1995); however, no one to our knowledge has done so for populations inhabiting fragmented woodlots within an urban landscape (defined for the purposes of this study as a human populated landscape transected by numerous roadways and dominated by residential and nonagricultural commercial properties). Examination of leaf nests is of particular importance because of the relative ease with which nests can be observed and because leaf nest abundance may be used to estimate squirrel population density in an area (Don, 1985; Wauters and Dhondt, 1988; but *see* Uhlig, 1956). Thus, monitoring the location and abundance of squirrel leaf nests in woodlots may be useful for determining the impact of urbanization on squirrel population size (or density).

The objective of this study was to characterize the nest locations of fox squirrels inhabiting fragmented woodlots within an urban landscape. Our specific goals were to: (1) characterize the placement of leaf nests with regard to tree species, height and diameter at breast height; (2) determine if fox squirrels prefer to nest in trees of a specific species or size; (3) calculate the density of leaf nests per woodlot; and (4) determine whether the abundance and placement of nests is dependent on woodlot size, level of disturbance or overall vegetative characteristics of the woodlot. By examining leaf-nest placement across woodlots of varying size and level of disturbance, we hope to shed light on how urbanization and habitat fragmentation are influencing fox squirrel ecology.

METHODS

Study area.—Our study was conducted from February to June 2003 in six woodlots located in the city of Indianapolis, Marion County, Indiana. The woodlots ranged in size from 1.1 to 8.3 ha and they varied in shape and, consequently, the amount of edge habitat they contained. We attempted to survey woodlots with clear boundaries. In most cases the boundaries were delineated by an abrupt end to the woods and a transition into a grassy field or a major roadway. In other cases the boundaries were delineated by a river or wide stream that was most likely impassable to squirrels. We considered the edge of each woodlot to be a buffer strip 10 m in width around the boundary of the wooded area. The woodlots were comprised of deciduous trees with a canopy dominated primarily by maple (*Acer* spp.), oak (*Quercus* spp.), elm (*Ulmus* spp.), ash (*Fraxinus* spp.), hickory (*Carya* spp.) and hackberry (*Celtis occidentalis*). The understory and the herbaceous ground cover varied among the six sites.

Five of the six woodlots were located in or adjacent to residential areas with mature trees and all woodlots were subject to regular foot traffic by humans, dogs and, in some cases, cats. We characterized four of the woodlots as "disturbed" because they had indicators of extensive human impact. The disturbed woodlots known as Crown Hill, East Canal, West Canal and White River contained an abundance of invasive plant species such as garlic mustard (*Alliaria petiolata*), winter creeper (*Euonymous fortunei*) and a dense understory of

Amur honeysuckle (*Lonicera maackii*). Non-native trees, including Siberian elm (*Ulmus pumila*), tree-of-heaven (*Ailanthus altissima*) and Norway maple (*A. platanoides*), were also found in the East and West Canal woodlots. Additionally, the East Canal, West Canal and White River woodlots were located on the banks of the Central Canal and the White River. The high ratio of edge to interior due to the linear shape of these woodlots combined with high levels of human activity on trails within the woodlots and along the Central Canal made these areas more susceptible to disturbance. The remaining two woodlots, known as Marott Park and Spring Pond, were state nature preserves and, thus, were subject to management strategies to eliminate invasive species and to minimize human impact. These sites were characterized by a diverse herbaceous layer including many ephemeral spring wildflowers and few to no occurrences of invasive shrubs such as Amur honeysuckle. Both the Marott Park and Spring Pond woodlots were contiguous with wooded areas that were not part of the nature preserve and were subject to greater human impact.

The fox squirrel was the dominant tree squirrel species found in each of the woodlots examined. Fox squirrels were observed on numerous occasions in each woodlot. The Eastern gray squirrel (*Sciurus carolinensis*), a sympatric congener of fox squirrels found throughout Indiana, is also known to use leaf nests for shelter (Mumford and Whitaker, 1982; Koprowski, 1994a). The Eastern gray squirrel, however, is decreasing in number in the northern half of the state and is rare in Marion County (Mumford and Whitaker, 1982). We observed only one Eastern gray squirrel throughout the course of this study. The American red squirrel (*Tamiasciurus hudsonicus*) is also found throughout the state and is known to build leaf nests (Mumford and Whitaker, 1982). Red squirrels were observed infrequently throughout the study perhaps because they prefer coniferous to mixed hardwood forests (Gurnell, 1983). Also, leaf nests constructed by red squirrels tend to be smaller and more compact than those of *Sciurus* and they are mostly present in conifers (Mumford and Whitaker, 1982) Thus, we were confident that the leaf nests observed in this study were built and used primarily by fox squirrels.

Leaf nest survey.—We surveyed each of the six woodlots for the location and density of leaf nests from February to April 2003. We attempted to locate all leaf nests by walking straight transects approximately 15 m apart through each woodlot. Leaf nests were considered derelict and were not included in the study if light could be seen through the nest when viewed from below (*see* Don, 1985). We recorded the species, diameter at breast height (1.5 m from the ground; dbh) and height of each nest tree. We also recorded the nest height and the position of the nest in the tree—in the crown, along the trunk or on a side branch. Tree and nest height were measured using an optical reading clinometer (Suunto PM-5) equipped with a percent and degree scale. We also examined each nest tree for the presence of vines consisting mostly of poison ivy (*Toxicodendron radicans*), Virginia creeper (*Panthenocissus quinquefolia*) and grape (*Vitis* spp.).

Vegetation survey.—We returned to each of the six woodlots from May to June 2003 to characterize the vegetation. A minimum of two 100 m transects were surveyed in each woodlot, one was placed in the center of the woodlot and another was set parallel to and 5 m in from the edge of the woodlot. We were unable to survey an internal transect at the East Canal site, however, because the wooded area was very narrow and the entire area fell within the 10 m edge buffer. Also, we surveyed two internal transects and one edge transect at the larger Crown Hill and Marott Park sites.

We conducted point-quarter sampling of trees ($\geq$10 cm dbh) at 10 points, one located every 10 m, along each transect (Brower *et al.*, 1990). We recorded the species, dbh, point-to-plant distance and the presence or absence of vines for each tree sampled. We did not record the presence or absence of leaf nests in the trees surveyed at this time because we were unable to reliably see into the canopy as the trees were fully leafed. We also characterized the density of the herbaceous ground cover and shrub layer in five 10 m^2 plots along each transect. The plots (each 2.24 × 4.47 m) were located every 20 m along the transect. We estimated by consensus the percentage of each plot that was covered by herbaceous plants and shrubs.

ANALYSIS

Vegetation survey.—We characterized the vegetation of each woodlot by calculating the mean dbh of the trees, the total density of trees (per hectare), the total number of tree species present, the relative density of each tree species at each site, the relative coverage and relative frequency for each species at each site and the importance value for each tree species by site. We also calculated the percentage of trees sampled at each site that had vines growing in the canopy and the mean percentage of herbaceous cover and shrub cover at each site. Data from interior and edge transects at each site were combined for these calculations. We compared the mean percentage of herbaceous cover, shrub cover and vines present between the disturbed and nature preserve sites using separate Student's *t*-tests. All percentages were arcsine transformed for analysis. We also compared tree dbh between disturbed and nature preserve sites using a Student's *t*-test. The dbh values were log transformed to correct for deviations from normality.

Leaf nest survey.—We calculated the mean dbh and mean tree height of nest trees and mean nest height for each site and for all sites combined. We used chi-square goodness-of-fit tests to determine if nests were found in trees in accordance to the relative densities of each tree species at each site. Similarly, the percentage of nests found in trees with vines at each site was compared to the average percentage of trees observed with vines at each site using a chi-square goodness-of-fit test. Tree species were combined for these analyses when necessary to maintain expected values ≥ 5 for 80% of the categories (Neave and Worthington, 1988). We used a two-way analysis of variance general linear model to test whether the dbh of nest trees differed from the dbh of trees sampled with the point-quarter method at each site. The dbh values were log transformed to correct for deviations from normality and significant factor effects were tested using Tukey post-hoc simultaneous tests. Further, we compared mean dbh of nest trees, mean height of nest trees, mean nest height and mean distance of nests from the top of the nest tree between the disturbed and nature preserve sites using separate Student's *t*-tests.

The total area (ha) of each woodlot was determined using a 2002 aerial black and white photograph of Marion County, Indiana. The aerial view was georeferenced and examined using ArcGIS software (ESRI version 8.2). The density of leaf nests per ha was then calculated for each woodlot. We compared mean leaf nest density per hectare between the disturbed and nature preserve sites using a Student's *t*-test.

All statistical analyses were conducted using Minitab software (Release 13 for Windows). Statistical significance was determined at $\alpha = 0.05$.

RESULTS

Vegetation survey.—There was nearly a two-fold difference in the number of tree species observed and the total tree density among sites (Table 1). The variation in the number of tree species observed was a function of the area surveyed; the highest and lowest species counts were observed at the largest and smallest sites respectively (Pearson's correlation coefficient: $r = 0.841$, $df = 4$, $P < 0.05$). Sugar maples had the greatest importance value at the Crown Hill, East Canal and Spring Pond sites. The tree species with the highest

TABLE 1.—Summary of vegetative characteristics of six woodlots. Trees were surveyed using the point-quarter method along a 100 m transect and herbaceous and shrub cover were surveyed through plot sampling. CH, Crown-Hill; EC, East Canal; WC, West Canal; WR, White River; MP, Marott Park; SP, Spring Pond; D, disturbed site; NP, nature preserve site; TD, total density; dbh, diameter at breast height

Site	D/NP	Area of site (ha)	# of tree species observed	TD (# trees/ha)	Dbh (cm) Mean	Dbh (cm) SD	Mean % trees with vines	Mean % herbaceous cover	Mean % shrub cover
CH	D	8.28	20	361.66	27.5	20.79	34.75	26.4	38.0
EC	D	2.34	17	672.03	28.5	24.38	6.25	0.3	57.5
WC	D	3.97	14	411.98	28.0	18.19	47.50	28.7	64.1
WR	D	1.06	12	628.13	26.0	16.66	48.75	1.4	77.9
MP	NP	6.85	18	541.67	25.2	16.94	15.00	58.0	20.7
SP	NP	4.39	16	407.50	29.4	16.62	8.75	55.5	28.0

importance values at the West Canal, White River and Marott Park sites were hackberry, boxelder and black maple, respectively.

Disturbed sites did not statistically differ from nature preserve sites with regard to the percentage of trees with vines in their canopies ($t = 2.18$, df = 3, P = 0.117), total density of trees per ha ($t = 0.43$, df = 3, P = 0.697) or tree size based on tree dbh ($t = 0.03$, df = 440, P = 0.980). Disturbed and nature preserve sites did differ significantly with regard to the amount of herbaceous and shrub cover (Table 1). Shrub cover was significantly greater at the disturbed sites ($t = 3.62$, df = 3, P = 0.036) and herbaceous cover was significantly greater at the nature preserve sites ($t = 5.76$, df = 3, P = 0.010).

Leaf nest survey.—Leaf nests were found in large trees (mean dbh = 39.7 cm, SD = 21.33; mean height = 21.1 m, SD = 7.64) and were located high in the trees (mean nest height = 15.6 m, SD = 5.63) at all sites. No nests were found below a height of 3.3 m above the ground. The density of leaf nests observed among the woodlots ranged from 2.73 to 8.82 per ha (Table 2). Nest density was significantly greater at disturbed sites compared to nature

TABLE 2.—Characteristics of leaf nests and leaf-nest trees in the six woodlots. Numbers in parentheses represent counts. EC—East Canal; WC—West Canal; WR—White River; CH—Crown Hill; MP—Marott Park; SP—Spring Pond; dbh—diameter at breast height

Site	# of nests	Nest density (per ha)	dbh (cm) Mean	dbh (cm) SD	Nest tree height (m) Mean	Nest tree height (m) SD	Nest height (m) Mean	Nest height (m) SD	Distance of nest from tree top (m) Mean	Distance of nest from tree top (m) SD	Two most common nest tree species
CH	55	6.52	38.4	15.55	22.5	7.04	16.5	5.84	6.0	4.58	*Bitternut Hickory (12) Sugar Maple (10)
EC	16	6.84	30.7	10.17	18.9	5.42	15.6	4.94	3.5	1.62	*Hackberry (5) Sugar Maple (3)
WC	35	8.82	46.9	27.9	20.5	9.3	14.0	5.62	6.6	4.64	Boxelder (10) *White Ash (8)
WR	8	7.55	40.7	18.55	21.1	11.09	14.8	6.07	6.3	7.67	Boxelder (3) Hackberry (2)
MP	31	4.53	31.5	18.22	19.3	6.41	14.6	4.62	4.6	4.63	*Sugar Maple (15) Hackberry (7)
SP	13	2.73	53.4	29.60	23.8	6.73	18.2	6.80	5.6	3.98	Bitternut Hickory (3) Beech (2)

* Indicates tree species that were used in greater numbers than expected

TABLE 3.—Chi-square goodness-of-fit results comparing nest locations by tree species to tree availability in six woodlots. Degrees of freedom (df) reflect the grouping of some data categories where the expected values were less than 5. CH, Crown Hill; EC, East Canal; WC, West Canal; WR, White River; MP, Marott Park; SP, Spring Pond

Site	# of tree species used	X^2 value	df	P value
CH	18	33.46	6	<0.001
EC	8	22.66	2	<0.001
WC	10	57.24	4	<0.001
WR	5	0.59	2	0.790
MP	8	27.49	2	<0.001
SP	8	33.91	1	<0.001

preserve sites ($t = 4.03$, df = 4, P = 0.016). There were no significant differences in nest tree dbh ($t = 0.39$, df = 4, P = 0.716), nest tree height ($t = 0.45$, df = 4, P = 0.679), nest height ($t = 0.89$, df = 4, P = 0.422) or distance of nests to the top of the nest tree ($t = 0.44$, df = 4, P = 0.684) between disturbed and nature preserve sites.

Chi-square results indicate that leaf nests were found in trees with vines in numbers significantly greater than expected ($X^2 = 117.2$, df = 5, $P < 0.001$) at both nature preserve and disturbed sites. Leaf nests were also found in a variety of tree species at each woodlot with sugar maple and hackberry being the most common nest trees overall (Table 2). The number of tree species harboring nests ranged from 5 species at the White River site to 18 species at the Crown Hill site (Table 3). The location of leaf nests was independent of the relative densities of trees at all sites except for the White River site (Table 3). A lack of significance at this site may be due to small sample size. At each site leaf nests were often found in one or two tree species at a frequency much greater than expected and the preferred tree species were not consistent among sites. For example, sugar maple trees were not used as nest trees at the White River site although available, and they were underutilized at the Crown Hill, East Canal and Spring Pond sites. However, sugar maple trees were used as nest trees at a greater than expected frequency at the Marott Park site (Table 2). Analysis of variance results indicate that the average size of nest trees with regard to dbh was greater than the average tree size available (F = 53.75, df = 1, 708, $P < 0.001$). No significant differences in tree size based on dbh were found among sites except that the trees at Spring Pond were significantly larger than those sampled at Marott Park ($t = 3.466$, P = 0.0070).

DISCUSSION

Leaf nests of fox squirrels in this study were not located in trees based on tree species availability which suggests that fox squirrels preferred to build nests in specific tree species. However, the preferred nest tree species varied among woodlots in this study (Table 2). In a previous study of fox squirrels in Ohio, Baumgartner (1943) observed nests most frequently in oak trees, but tree availability data were not collected, thus, a preference for oak trees could not be clearly demonstrated. Hickories, white oaks, scarlet oaks and beech were selected as nest trees more often than expected, based on availability, by fox squirrels living in several sites in Ohio, West Virginia and Illinois (Sanderson *et al.*, 1980). In the current study, oaks and hickories were observed along transects at all but the White River and West Canal sites. Oaks were not selected as nest trees significantly more than expected when they were present. Bitternut hickories (*Cayra cordiformis*) were the most frequently selected nest trees at the Crown Hill and Spring Pond sites and were used significantly more than expected at the Crown Hill site ($X^2 = 15.6$, df = 1, $P < 0.001$). Thus, the location of leaf nests in this study does not support the conclusions of previous studies that fox squirrels prefer to nest in oaks. We suggest that the variation in nest tree selection among sites indicates that criteria in addition to nest tree species likely influence leaf nest placement and that fox squirrels show considerable plasticity in their preference for nest-tree species.

Fox squirrels built nests in trees that were larger, as indicated by dbh, than the average trees available at each site. Edwards and Guynn (1995) similarly found that fox squirrel in Central Georgia chose trees greater than 60 cm dbh more often than expected. The average dbh of trees did not vary significantly among sites in the current study except that Spring Pond trees were larger than those sampled at Marott Park. Interestingly, leaf nest density was greater at Marott Park than at the Spring Pond site.

The presence of vines in the tree canopy appeared to be an important factor influencing nest tree choice at all sites except the Spring Pond and West Canal sites. At the remaining four sites, fox squirrel nests were observed more often than expected in nest trees associated with vines. In many cases, we observed that the leaf nests were constructed such that they were partially anchored by the vines. The higher than expected percentage of leaf nests in trees with vines agrees with the findings of a previous study where the presence of vines considerably increased the odds that a tree would contain a leaf nest (Sanderson *et al.*, 1980). Baumgartner (1943) found that leaf nests lasted longer when supported by vines (but *see* Sanderson *et al.*, 1980).

The vegetative characteristics of the six woodlots surveyed in this study varied considerably. There were no consistent differences among disturbed and nature preserve sites with regard to tree size, tree density, presence of vines or tree species composition. The disturbed and nature preserve sites differed significantly only with regard to shrub and herbaceous cover—shrub cover was higher and herbaceous cover lower at the disturbed sites compared to the nature preserve sites. The higher leaf nest density at the disturbed sites suggests that fox squirrels prefer to nest in woodlots with a dense shrub layer. Fox squirrels are less arboreal than other closely related species of tree squirrels (Dueser *et al.*, 1988; Steele and Koprowski, 2001). The shrub layer may provide protective cover from aerial predators when the squirrels are on the ground. The finding of greater leaf nest density in woodlots with a dense understory is in contrast to other studies that indicate that fox squirrels prefer more open woodlots with little understory while gray squirrels prefer larger stands with a dense understory (Madson, 1964; Taylor, 1974). It is possible that the positive relationship between shrub cover and nest density in the current study is not a causal one (*see* Brown and Batzli, 1984). With the exception of the Crown Hill site, all of the disturbed sites were linear in shape with a high ratio of edge to interior area. The high shrub cover may be indicative of the large edge area of the linear woodlots. Fox squirrels are known to prefer to nest along forest edges (Baumgartner, 1943; Nixon *et al.*, 1984; Dueser *et al.*, 1988; Steele and Koprowski, 2001); thus, a high density of leaf nests in the disturbed sites may be a consequence of the greater edge available rather than the shrub density. Further detailed study of the spatial distribution of leaf nests within woodlots of varying size and shape is necessary to substantiate this hypothesis. Also, it is well documented that the density and species composition of seed producing trees in an area is positively correlated to long-term squirrel densities (Gurnell, 1983). Previous researchers have suggested that nest placement by *Sciurus* spp. was determined in part by the nearness of preferred seed producing trees (Nixon and Hansen, 1987). A greater than expected number of nests in bitternut hickory trees, a preferred seed producing tree of fox squirrels (Koprowski, 1994b), suggests that this may be the case in the current study. It is also conceivable that nest density in this study was dependent, in part, on the nearness of birdfeeders located in nearby residential areas; fox squirrels are known to frequently feed at birdfeeders (Steele and Koprowski, 2001). We did not map the location of each leaf nest with regard to the location of potential seed-producing trees preferred by squirrels or neighborhood birdfeeders, however. This would be necessary to fully elucidate the influence of seed-producing trees and birdfeeders on leaf nest density.

The results of this study support the contention that fox squirrels have broad habitat tolerances that allow them to adapt well to forest fragmentation and disturbance (Sheperd and Swihart, 1995; Swihart and Nupp, 1998). The higher nest densities in disturbed woodlots compared to nature preserve sites suggest that the effects of urbanization may in fact have a positive impact on fox squirrel abundance. The mechanism explaining the ability of fox squirrels to thrive in disturbed fragmented urban woodlots was not examined in this study. Swihart and Nupp (1998), however, suggest that the well-developed dispersal ability and the low dispersal mortality relative to other tree squirrels as well as the ability to use agricultural crops may explain the success of fox squirrels in agriculturally fragmented landscapes. Additional examination of fox squirrel movement patterns between woodlots and leaf nest density in woodlots of varying sizes and levels of isolation is necessary to determine if this explanation holds for fox squirrels inhabiting an urban landscape.

Acknowledgments.—We thank T. Nupp and an anonymous reviewer for helpful comments on this manuscript. We also thank S. N. Gashti and R. R. Amodeo for their help with data collection in the field and Butler University, Crown Hill Cemetery and Indianapolis Parks and Recreation for allowing access to woodlots. Funding for this project was provided by the Department of Biological Sciences at Butler University and a Faculty Fellowship awarded to C. M. Salsbury by the Holcomb Awards Committee at Butler University.

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SUBMITTED 17 JULY 2003 ACCEPTED 10 NOVEMBER 2003