BREEDING SUCCESS OF PIED FLYCATCHERS IN ARTIFICIAL FOREST EDGES: THE EFFECT OF A SUBOPTIMALLY SHAPED FORAGING AREA

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ABSTRACT.—We conducted an experimental study of nest-site selection and breeding success of Pied Flycatchers (*Ficedula hypoleuca*) in artificial forest edges. The nest-site selection experiment revealed a clear pattern in the order of occupancy of nest boxes by males: boxes situated at the edge between the forest stand and the clearcut were consistently avoided by the earliest-arriving males, which preferentially selected boxes 50 to 100 m from the edge. We also wanted to assess the possible fitness consequences associated with the observed nest location by moving randomly selected breeding pairs to a new location with respect to distance from the edge. The body mass of offspring was lower in nests moved to the edge than in nests moved into the interior of the forest stand. Body mass may be correlated with the lower feeding rate observed at edge nests compared with interior nests. We present evidence that pairs nesting at the extreme edge were forced to use suboptimal foraging areas (i.e. a semicircle of habitat), whereas interior pairs had a complete circle of suitable habitat in which to forage. Pied Flycatchers did not use clearcuts for foraging. Birds may try to compensate for suboptimal foraging area by increasing their food-search efficiency, or they may try to enlarge their foraging area by increasing its radius. Both strategies may increase the energy consumption of adults and the time spent searching for food, which may, in turn, decrease feeding frequency. However, we found no support for increased energy consumption. Nest-predation rate, food availability, and survival of parents were not associated with the distance of the nest from the edge. Our results indicate a harmful edge effect from forest fragmentation for Pied Flycatchers because offspring mass is related to fitness through brood survival to the next breeding season. *Received 15 December 1997, accepted 31 October 1998.*

CLEARCUTS IN MATURE FOREST reduce forest patch size and increase the extent of forest edge (e.g. Forman and Godron 1986, Gustafson and Parker 1992, Hansson et al. 1995). Habitat edges are assumed to be good breeding areas for birds because of their high diversity of vegetation and increased food supply (e.g. Leopold 1933, Helle and Muona 1985, Hansson 1994, Jokimäki et al. 1998). Nest-site selection is a critical component of reproduction and is presumed to have evolved in relation to factors such as predation and resource availability. Detrimental effects on reproduction in birds have occurred because of increased nest predation and nest parasitism (e.g. Gates and Gysel 1978, Wilcove 1985) and lower food abundance (Burke and Nol 1998) in small patches and near forest edges. Moreover, the foraging

areas of territorial birds along the edge of forest patches are non-circular if the habitat in the surrounding matrix is unsuitable for foraging. Evidence suggests that breeding at the forest edge is disadvantageous because of the non-optimal shape of the foraging area, which may increase the costs involved in the search for food and thereby affect nest-site selection and reproductive success (Kuitunen and Mäkinen 1993).

Natural selection is expected to favor individuals whose territories have characteristics that minimize metabolic costs and maximize individual fitness (i.e. optimal foraging theory; Charnov 1976, Pyke et al. 1977, Pyke 1979). Resource availability and defense costs are assumed to be the main factors that determine optimal territory size (Hixon 1980, Schoener 1983). Models also assume that the shape of the territory should be optimal, but relatively few studies have examined this issue (but see Getty 1981, Eason 1992).

Central-place foragers are animals that carry

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TABLE 1. Density and % cover of vegetation at edge and interior areas. Values are $\bar{x} \pm 1$ SE. Numbers following tree-layer variables denote different height categories ($1 = 2$ to 5 m, $2 = 6$ to 10 m, $3 > 10$ m). The number of plots sampled in each site is 40.

Variable	Edge	Interior	P[a]
Junipers (stems per m²)	0.02 ± 0.01	0.01 ± 0.01	0.121
Spruce shrubs (stems per m²)	0.08 ± 0.02	0.03 ± 0.01	0.006
Pine shrubs (stems per m²)	0.07 ± 0.02	0.06 ± 0.02	0.255
Deciduous shrubs (stems per m²)	0.02 ± 0.01	0.00 ± 0.00	0.016
Spruces (stems per m²)	0.09 ± 0.01	0.06 ± 0.01	0.010
Pines (stems per m²)	0.08 ± 0.01	0.06 ± 0.01	0.375
Deciduous trees (stems per m²)	0.03 ± 0.01	0.02 ± 0.01	0.792
Dwarf shrubs (%)	43.27 ± 3.21	43.85 ± 2.56	0.802
Bare soil (%)	0.60 ± 0.25	2.20 ± 0.90	0.137
Shrubs total (stems per m²)	0.19 ± 0.04	0.01 ± 0.03	<0.001
Tree layer 1 (stems per m²)	0.09 ± 0.01	0.04 ± 0.01	0.003
Tree layer 2 (stems per m²)	0.06 ± 0.01	0.04 ± 0.01	0.224
Tree layer 3 (stems per m²)	0.05 ± 0.01	0.06 ± 0.01	0.409
Trees total (stems per m²)	0.19 ± 0.02	0.14 ± 0.01	0.008

[a] Wilcoxon matched-pairs signed-rank test.

resources back to a particular site, e.g. birds carrying food to their nests (Orians and Pearson 1979). If a forager is an energy maximizer (Schoener 1971, Pyke et al. 1977), it should try to maximize the amount of food delivered per unit time to the central place by adopting a territory size and shape that will minimize both the time needed to find a prey patch and the distance from the patch back to the central place. Models generally predict that the optimal territory shape for a central-place forager should be round (Pyke et al. 1977, Pyke 1979). Territories and foraging areas of suboptimal shape are thus expected to be more costly, but this assumption has never been tested (Morrison 1978, Hixon 1980, Andersson 1981).

The Pied Flycatcher (*Ficedula hypoleuca*) is a migratory passerine and a secondary cavity nester that to some extent prefers tracts of mature forest (Virkkala et al. 1994). We used experiments to study nest-site selection and breeding success of Pied Flycatchers in artificial forest edges. In the first experiment, we set up nest boxes at different distances from the forest edge to find out how individuals select nest sites in relation to the forest edge. In the second experiment, we wanted to clarify the possible benefits and costs in terms of breeding success associated with nests close to the forest edge. This was done by moving randomly selected pairs of Pied Flycatchers to locations closer and farther from the forest edge.

STUDY AREA AND METHODS

The study was conducted in Meltaus, Finland (67°N, 25°E) in 1993 and 1996. The mature forests in the study area are dominated by Scotch pine (*Pinus sylvestris*) intermixed with birch (*Betula* spp.) and Norway spruce (*Picea abies*). The landscape is heavily fragmented by large clearcuts and open mires. We restricted our sites to artificial forest edges created by clearcuts of recent origin (ca. 5 to 10 years old). These clearcuts had no vegetation taller than 1.0 m and were covered with herbs, grass, bare soil, and planted pine seedlings. Most of the variables used to describe vegetation structure were similar between the forest edge and the interior of the stands (Table 1).

Nest-site selection experiment.—In 1993, we studied how breeding Pied Flycatchers distributed themselves relative to the forest edge. We used nest boxes to standardize the availability, distribution, and quality of nest sites. All of the boxes were the same size (height 250 mm, width 100 mm, entrance diameter 35 mm) and were placed on trees at a height of 1.5 m, the entrance hole facing toward the clearcut. The study was conducted in 28 forest patches (≥5 ha) that bordered open areas. Nest boxes were placed along transects extending from the forest edge to the forest interior. One transect, containing an average of six nest boxes (range 5 to 8) set 50 m apart, was created in each stand. The first nest box of each transect was placed directly on the edge (i.e. 0 m to edge) between the forest and the open area.

Nest boxes were checked daily to observe the arrival date of the parents. Each transect was monitored to collect information on the occupancy by males according to distance from the forest edge. Male Pied Flycatchers arrive at the breeding grounds

TABLE 2. Breeding success of Pied Flycatcher pairs experimentally moved to the edge and to the interior. Values are $\bar{x} \pm 1$ SE, with n in parentheses.

Variable	Edge	Interior	P
Laying date	37.00 ± 0.66 (30)	36.00 ± 0.61 (31)	0.653[a]
Clutch size	5.88 ± 0.17 (33)	5.85 ± 0.15 (33)	0.882[a]
Number of nestlings	5.42 ± 0.23 (33)	5.39 ± 0.18 (33)	0.899[a]
Number of fledglings	5.30 ± 0.22 (33)	5.24 ± 0.20 (33)	0.790[a]
Mass of fledglings (g)	13.99 ± 0.16 (33)	14.35 ± 0.13 (33)	0.028[a]
Hatching success (%)	91.10 ± 2.91 (33)	90.86 ± 2.60 (33)	0.975[b]
Fledgling success (%)	89.80 ± 3.07 (33)	90.10 ± 2.95 (33)	0.972[b]
Feeding rate (trips / 30 min)	12.44 ± 0.98 (16)	17.75 ± 1.09 (16)	0.008[b]
Males	5.63 ± 0.83 (16)	7.75 ± 0.83 (16)	0.054[b]
Females	6.69 ± 0.79 (16)	9.94 ± 1.17 (16)	0.021[b]

[a] Paired t-test.
[b] Wilcoxon matched-pairs signed-rank test.

ahead of the females, usually so that older (i.e. perhaps more experienced) individuals arrive before yearlings (Lundberg and Alatalo 1992). Thus, early males had the advantage in taking possession of any nest box along the transects. The date when a singing male was observed for the first time at a nest box was used as the arrival date for that male. The "first-arrived male" was defined as the one that settled before other males along a transect and occupied a site by confining its singing activity to a particular nest box.

Nest-site relocation experiment.—We assumed that the best sites would be occupied first by high-quality individuals. Egg laying also starts earlier in high-quality territories, which may affect reproductive output. Therefore, we could not compare breeding success among sites directly because the quality of territories may have been correlated with the quality of territory owners. To remove the effects of breeding time and parental quality on breeding success, we divided the parents randomly into two homogenous groups with respect to arrival time and pair formation. We then relocated the pairs to new sites with respect to distance from the forest edge. The experiment was conducted in 1993 and 1996 partly at the same sites used in the first experiment by erecting nest boxes 50 m apart along transects parallel to the forest-clearcut edge at an initial distance of 50 m from the edge. Nest boxes were checked daily for newly arrived singing males and newly paired females. Whenever two pairs were formed simultaneously and the females started nest building, we randomly assigned one pair to be moved toward the edge and the other to me moved toward the interior. Occupied boxes were moved gradually (10 m per day) during the nest-building period, which usually takes 5 to 11 days, toward the forest edge while the other boxes in the interior group were moved deeper toward the center of the stand. Moving was stopped when the edge box was located directly on the forest-clearcut edge and the interior box was located 100 m from the edge. Thus, each nest box was moved 50 m

from its original site. In this experiment, we used the results of the nest-site selection experiment to determine which distances from the forest edge were avoided and which were favored as nesting sites by Pied Flycatchers. In this way, we ensured that the experimental relocation distances were appropriate.

Clutch size, as well as the number of nestlings and fledglings, were counted in each nest. Fledglings were weighed to the nearest 0.1 g at the age of 13 days, when they were ready to leave the nest. We also monitored nest-predation rate and adult survival during the breeding season.

Bird capture.—All adult birds used in the experiments were captured at the end of the nestling period using traps placed inside nest boxes. Females also were captured and weighed during the hatching period to determine their mass change during brood rearing. Each captured bird was given an individually numbered aluminum leg band. We also determined the age (adult vs. yearling; Karlsson et al. 1986), sex, body mass, wing length (straightened chord), tail length, and tarsus length of each individual.

Feeding behavior.—We observed the feeding rates of nestlings at 32 nests (16 edge nests and 16 interior nests) used in the relocation experiment using a telescope (20×) and binoculars (8×) from a blind. The blind was located at the distance of approximately 50 m from each nest on the left or right side of the nest. Each nest was observed when the nestlings were 9 to 11 days old during 30 min in the afternoon in good weather. We considered a foraging trip to begin when a bird left its nest box and to end when it returned to the box with food. The distribution of the feeding trips for each sex is presented in Table 2.

Pied Flycatchers flew up to 100 m or more from their nests in search of food. We measured the use of space by the parents according to the directions from which they transported prey items to their nestlings. Observations were classified into one of three main directions from the nest box: (1) "behind" (birds collected food from the habitat behind the box), (2)

"side" (birds used the habitat to the right or left side of the box), and (3) "front" (birds used the habitat in front of the box). For edge-nesting birds, "front" corresponded to the clearcut adjacent to the nest, and "side" corresponded to the area along the border between the forest and the clearcut.

Prey availability.—We estimated the quality of nest sites by collecting invertebrate samples with a sweep net (net diameter 35 cm) using a standardized method. The samples were collected within the forest stands (50 m and 100 m from the edge), at the edge (0 m), and in the adjacent clearcut (50 m and 100 m from the edge). Within forest stands, samples were collected at the same sites where the relocation experiment was conducted. Five samples (10 sweeps per sample) were taken per site in the forest, one each from the ground layer, from a deciduous and a coniferous bush, and from the lower branches of a deciduous tree and a coniferous tree. In the clearcut area, only ground-layer samples were collected. Ground-layer samples were taken by walking along the transect for 10 m and at every second step sweeping the net once in a semicircle as close to the ground as possible. All samples were collected at the beginning of July (which is the middle of the nestling period) in the afternoon when the vegetation was dry.

Invertebrates were identified by order and classified into three size classes according to body length (<0.5 cm, 0.5 to 1.0 cm, and >1.0 cm) using a microscope. Six taxonomic classes (Araneae, Coleoptera, Diptera, Homoptera, Hymenoptera, and Lepidoptera larvae) were used in the study. These groups form the main food items for adult and nestling Pied Flycatchers during the breeding season (Lundberg and Alatalo 1992).

Vegetation description.—Vegetation characteristics were recorded at 80 randomly selected circular plots (radius = 3.0 m, area = 28.27 m^2) in both the edge (0 m) and the interior (100 m). Within each circle, we recorded the numbers of pines, spruces, and deciduous trees by height class (2 to 5 m, 6 to 10 m, and >10 m). In the shrub layer, we counted the number of junipers, coniferous shrubs, and deciduous shrubs (<2 m). We also recorded the percentage cover of dwarf shrubs and of bare soil in the field layer.

Statistical analyses.—We used two-sample and paired *t*-tests, the Wilcoxon matched-pairs signed-rank test, the χ^2 test with Yates' correction, and one-way ANOVA in the comparisons; pairwise tests were done using Tukey's HSD. Use of space by birds around the nest was analyzed using Friedman's one-way ANOVA. All of the statistical tests were two-tailed and were performed using SYSTAT (1992).

RESULTS

Nest-site selection experiment.—The distribution of nest-site selection by the earliest-arriv-
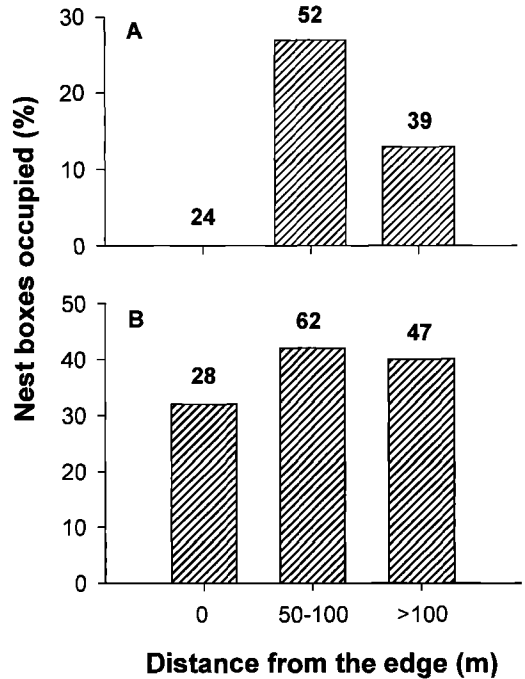

FIG. 1. Proportion of nest boxes occupied by (A) first-arriving and (B) later-arriving male Pied Flycatchers relative to distance of the box from the forest-clearcut edge. The earlier males clearly preferred boxes away from the edge habitat. Numbers above columns indicate the number of nest boxes available in each distance class.

ing males was uneven with respect to distance from the forest edge. The first males showed a clear preference for nest boxes farther away (50 to 100 m) from the edge (χ^2 = 9.22, df = 2, P = 0.01; Fig. 1A). However, later-arriving males occupied the boxes at the edge once the interior sites had been occupied (Fig. 1B). Using distance categories of 0 m, 50 to 100 m, and >100 m, the age distribution of territory-holding males and females was independent of the distance from the forest edge (% adult vs. yearling males, χ^2 = 2.32, df = 2, P = 0.31; % adult vs. yearling females, χ^2 = 4.86, df = 2, P = 0.09). The morphological characteristics of males and females were not correlated with the distance of their nest boxes from the forest edge (Spearman rank correlation, P > 0.05, data not shown).

Nest-site relocation experiment.—Within the edge group, 4 out of 37 females rejected their nest box during the nest transfer and disappeared, probably to breed elsewhere, whereas

none of the 37 females in the interior group did so ($\chi^2 = 2.38$, df = 1, $P = 0.12$). Neither arrival date (males, paired $t = 0.76$, df = 24, $P = 0.46$; females, paired $t = 0.63$, df = 22, $P = 0.54$), age distribution (males, $\chi^2 = 0.00$, df = 1, $P = 1.0$; females, $\chi^2 = 0.57$, df = 1, $P = 0.45$), nor morphological characteristics (two-sample t-test, $P > 0.05$, data not shown) of the birds differed between the treatment groups.

The body mass of females did not differ between edge and interior groups during the hatching period (paired $t = 0.49$, df = 31, $P = 0.63$) nor during the fledgling period (paired $t = 0.02$, df = 29, $P = 0.98$). Mass loss by females during the nestling period did not differ significantly between treatment groups (edge, $\bar{x} = 1.76 \pm$ SE of 0.11 g; interior, $\bar{x} = 1.64 \pm 0.11$ g; paired $t = 0.52$, df = 28, $P = 0.61$). Body mass of fledglings at 13 days of age was lower in the edge group than in the interior group (Table 2). We observed no nest predation or mortality of breeding adults during the two experiments.

Pied Flycatchers in the edge group fed their nestlings less frequently than pairs in the interior group (Table 2). The pairs at the edge consistently avoided the clearcut (i.e. "front") when searching for food (Friedman's ANOVA, $\chi^2 = 19.34$, df = 2, $P < 0.001$; Fig. 2A). In contrast, the pairs in the forest interior captured prey rather evenly from all directions around the nest box, indicating that they used the habitat surrounding the nest equally for foraging (Friedman's ANOVA, $\chi^2 = 1.0$, df = 2, $P = 0.61$; Fig. 2B). The number of invertebrates differed between the clearcut and the interior, but not between the forest edge and the interior, with large invertebrates (>1.0 cm) being more abundant in the clearcut than in the interior. The total number of invertebrates sampled did not differ significantly among the edge, interior, and clearcut (Table 3).

DISCUSSION

The first males to arrive avoided nest boxes at the forest-clearcut edge, but there was no difference in occupancy of boxes located 50 to 100 m from the edge versus >100 m from the edge, suggesting that the extreme edge was the zone that was most strongly avoided by males. However, some later-arriving males occupied nest sites at this extreme edge. Also, during the transfer of nest boxes, desertion of nests oc-
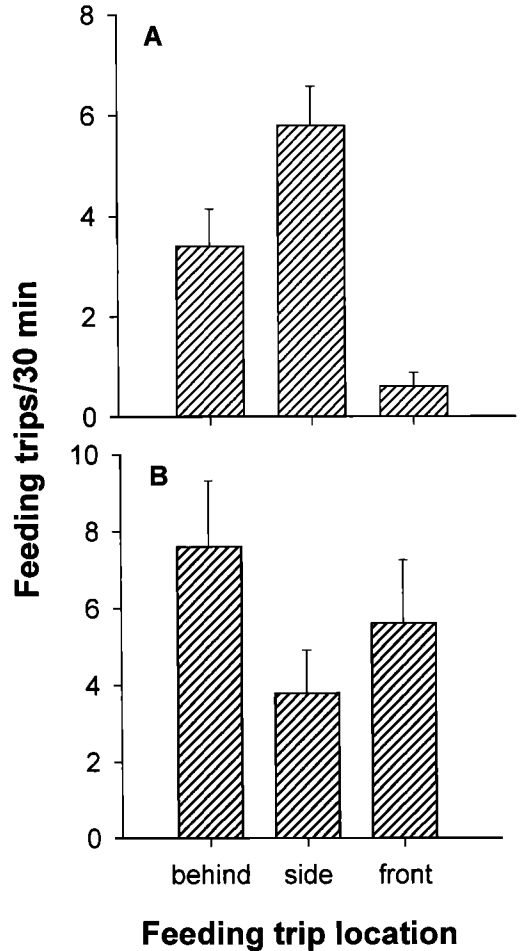

FIG. 2. Use of space surrounding the nest by foraging Pied Flycatchers that nested in boxes (A) at the forest edge and (B) within the forest interior. Values are $\bar{x} \pm$ SE of the number of feeding trips made in each direction from the nest. Pairs nesting at the forest-clearcut edge consistently avoided foraging in the clearcut located in front of their boxes. Statistically significant differences (Wilcoxon tests) in (A): "front" versus "side" ($z = 3.37$, $P = 0.001$); "front" versus "behind" ($z = 3.19$, $P = 0.001$).

curred only among females belonging to the edge group. This suggests that neither males nor females favor nest boxes close to the forest edge. Based on the nest-site relocation experiment, the body mass of offspring in nests at the edge was lower than that of offspring from nests within the interior, probably because feeding rates were lower at edge nests.

The size and the shape of foraging areas are predicted to be such that they fulfill the daily

TABLE 3. Number of individuals sampled ($\bar{x} \pm$ SE) and size classes of invertebrates in clearcut, edge, and interior habitats during the nestling period of the Pied Flycathcer; n denotes the number of plots sampled in each site.

Order/size class	Clearcut ($n = 29$)	Edge ($n = 15$)	Interior ($n = 30$)	ANOVA[a]	t-test[b]
Araneae	1.21 ± 0.28	2.93 ± 0.52	4.63 ± 0.60	<0.001[c]	0.123
Coleoptera	3.17 ± 0.45	3.87 ± 1.08	3.87 ± 0.59	0.701	0.518
Diptera	21.52 ± 1.82	28.00 ± 5.09	40.77 ± 6.16	0.284	0.476
Homoptera	5.14 ± 1.09	2.60 ± 1.29	1.43 ± 0.31	0.003[d]	0.438
Hymenoptera	4.62 ± 0.60	4.93 ± 1.06	7.67 ± 0.87	0.028[d]	0.068
Lepidoptera	1.93 ± 0.81	0.60 ± 0.19	1.03 ± 0.21	0.606	0.234
Class (<0.5 cm)	28.24 ± 2.17	36.93 ± 6.24	51.07 ± 6.83	0.123	0.331
Class (0.5 to 1.0 cm)	9.10 ± 1.32	8.20 ± 1.25	12.47 ± 1.48	0.165	0.128
Class (>1.0 cm)	1.55 ± 0.32	0.13 ± 0.09	0.43 ± 0.11	<0.001[c]	0.093
Total	13.00 ± 1.48	15.09 ± 3.16	21.32 ± 3.25	0.575	0.332

[a] *P*-values from one-way ANOVA among habitats.
[b] *P*-values from *t*-test comparing edge versus interior habitats.
[c] Clearcut significantly different ($P < 0.05$) from edge and interior habitats based on Tukey's HSD test.
[d] Clearcut significantly different ($P < 0.05$) from interior habitat based on Tukey's HSD test.

energy requirements of the birds and minimize their metabolic costs while searching for food (Pyke et al. 1977, Hixon 1980, Andersson 1981). In our study area, the shape of foraging areas used by Pied Flycatchers is determined by the availability of suitable forest habitat, because this species does not forage in cleared areas. Thus, foraging areas in the interior appeared to be circular, whereas those at the edge were semicircular according to the birds' habitat use surrounding the nest boxes. Pied Flycatchers forage mainly outside a very small defended breeding territory (i.e. nest hole and its immediate surroundings), and foraging areas may even overlap with those of neighboring pairs (Lundberg and Alatalo 1992, E. Huhta pers. obs.). By selecting nest sites away from the edge, males may be avoiding harmful fitness consequences that could result from their foraging areas being reduced to semicircles. If the availability of food is positively correlated with the size of the foraging area, a consequence of a small foraging area would be reduced food supply for the nestlings.

While searching for food, an individual should adopt a distance between the food patch and the central place that will minimize the distance to the patch and maximize the rate of food gain (Morrison 1978, Pyke 1984). Individuals living at the forest-clearcut edge may try to compensate for their suboptimal foraging area by increasing the radius of their foraging area to obtain the same amount of food that would be available within a circular area. However, as the distance between the food patch and the central place increases, the energetic costs of transporting food to the central place will increase accordingly. This is explained by the observation that for a semicircle to encompass the same area as that covered by a full circle, the radius of the semicircle must be approximately 1.5 times larger than that of the full circle. An increase in the distance flown would be very costly for small passerines such as Pied Flycatchers because parents feed nestlings very frequently, about once every two minutes (Lundberg and Alatalo 1992, this study). In addition, the increased time spent transporting prey to nestlings may limit the time that parents have available for feeding and maintaining themselves, thus making adults more vulnerable to predation during the nestling period.

Mass loss by females during brood rearing did not differ significantly between treatment groups. This suggests that increased energy consumption did not exist in the edge group. One possible explanation for this is that the parents in the edge group adjusted their feeding efforts to a level that did not lower their future fitness (i.e. the probability of surviving to the next breeding season). Fitness and reproductive success are assumed to increase linearly with the average net rate of energy gain (Hixon 1980, Schoener 1983). Individuals that forage efficiently are predicted to have higher reproductive success and fitness than individuals that forage inefficiently. Although we found no differences in brood size, lower body mass of fledglings has important fitness con-

sequences because body mass can be positively correlated with postfledgling survival among passerines (e.g. Lindén et al. 1992). Our results suggest that late-arriving Pied Flycatchers suffer fitness costs because they are forced to take possession of lower-quality nest sites that produce offspring with lower body mass.

Other explanations for the reduced feeding rate can be presented. Differences in prey abundance and quality may affect feeding rates through searching and handling times (Charnov 1976). The low feeding frequency among birds nesting at the edge may indicate lower food availability, which makes it difficult for parents to find adequate amounts of food. However, in our study, the size distribution and total number of invertebrates did not differ between edge and interior areas. On the other hand, if prey densities did not vary with distance away from the nest, larger prey items or larger loads should be returned by the forager to compensate for longer travel distances (Orians and Pearson 1979, Stephens and Krebs 1986). Unfortunately, we have no data on the quality or quantity of food provided to nestlings.

In the breeding area, Pied Flycatchers catch food mainly from the ground and on trees, and less often in the air (von Haartman 1954, Alatalo and Alatalo 1979). Denser layers of bushes and young trees at the edge may increase the energy requirements of parents and impede their movements in search of food. Furthermore, short flights are energetically more expensive than long ones because of the high costs associated with takeoffs and landings (Tatner and Bryant 1986, Carlson and Moreno 1992). We cannot fully justify this assumption, but it is obvious that at the edge, the possible influence of denser vegetation on food searching is of minor importance because edge birds mainly foraged in the interior parts of the forest surrounding their nest boxes.

An alternative explanation for the avoidance of extreme edges is nest predation (see Holt and Martin 1997). The edge effect may increase nest predation on passerines (e.g. Gates and Gysel 1978, Wilcove 1985, Robinson et al. 1995). Pied Flycatchers may avoid the extreme edge as a breeding site because their nest sites may be more visible there than in the interior, which could increase the risk of nest predation. Also, predation risk for the parents may differ be-

tween edge and interior sites. However, neither nest predation rate nor adult survival was associated with the distance of nests from the edge (see also Huhta et al. 1998).

Our study raises the issue of what kind of fitness effects result from birds breeding at forest edges. Our experimental evidence suggests that artificial edges affect the reproductive success of individuals, especially those that are forced to occupy territories at the extreme edge of the forest. This was probably due to the lower feeding rate that resulted from the suboptimal shape of the foraging area, which we suggest is a proximate reason for the lower mass of nestlings at the forest edge. Conditions similar to those we found for Pied Flycatchers at the forest edge commonly will arise in other habitat margins, e.g. along shorelines and stream banks as well as near man-made features such as powerline corridors and roadsides (Forman and Godron 1986). In this sense, the reduced body mass of young birds in nests at forest edges can be seen as a harmful consequence of habitat fragmentation.

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