ORNIS SVECICA 3:59-68, 1993 https://doi.org/10.34080/os.v3.23044

Differences in bird habitat quality between plantations of Scots and Lodgepole Pine measured in terms of Pied Flycatcher *Ficedula hypoleuca* breeding success

KJELL SJÖBERG, ROGER PETTERSSON & OLA ATLEGRIM

Abstract

The breeding density and reproductive performance of Pied Flycatchers *Ficedula hypoleuca* inhabiting nest boxes were studied in ca. 20-year-old plantations in Sweden of two pine species: the native Scots Pine *Pinus sylvestris* and the introduced North American Lodgepole Pine *P. contorta*. The analyses are based on data from 35 nest boxes placed within each of three Scots Pine and three Lodgepole Pine plantations. The plantations were distributed pairwise at each of three different sites. During the 4-year study (1989-1992), a total of 126 and 107 clutches were found in Scots and Lodgepole plantations, respectively. There was no significant difference in number of breeding pairs between the two types of pine plantations. However, reproductive success, as regards number of nestlings, tended to be higher in Scots than Lodgepole Pine habitats, and clutch size was significantly larger in Scots Pine plantations. Flycatcher food abundance in the trees was indexed by measuring insect larval droppings under pines during the nestling period in 1989. There were no significant differences in number of droppings between the habitat types. Although the Pied Flycatcher clutch size was higher in the Scots Pine habitats, it did not result in a higher number or weight of nestlings. Our results indicate that this was due to a high within-habitat and between-site variation in flycatcher breeding success. The reasons for these variations are discussed.

Kjell Sjöberg, Roger Pettersson & Ola Atlegrim. Department of Animal Ecology, Swedish University of Agricultural Sciences, S-901 83 Umeå, Sweden

Received 15 December 1992, Accepted 7 May 1993, Edited by T. Pärt

Introduction

The Lodgepole Pine *Pinus contorta* was commercially introduced into Swedish forestry during the end of the 1960's (Hagner 1985). About 540 000 ha of Swedish forest land is now planted with this North American species. In some areas it constitutes more than 10% of all coniferous trees (Skogsstyrelsen/Swedish Forestry Board 1992). Since Lodgepole Pine is currently the third most common of the managed coniferous species in Sweden, many forest animals are now faced with a new type of habitat. This fact has raised concerns regarding the ability of animals adapted to the original forests to cope with this change in habitat type. Invertebrate biomass is generally lower on an introduced tree species than on native ones (Southwood 1977). This relationship also seems to apply to the introduced Lodgepole Pine in Sweden and the habitat it creates (Kardell *et al.* 1989, Sjöberg 1989, Sjöberg & Pettersson, unpubl. data), although some invertebrate species, e.g. the Pine-flower Weevil *Anthonomus phyllocola,* have adapted well to the new host (Pettersson 1992).

Mean clutch size in the Pied Flycatcher *Ficedula hypoleuca* has been reported to differ between habitats (for review, see Gezelius *et al.* 1984, Lundberg & Alatalo 1992). This difference has been attributed to variation in breeding density (e.g. Curio 1959, Lundberg *et al.* 1981, but see also Järvinen & Tast 1980), laying date, adult size and age, female weight, and frequency of polygyny. However, all of these factors might be related to habitat quality (e.g.

food abundance). For example, differences in the clutch size of birds, the mean weight of young, population density, etc., are normally higher in deciduous forest than in coniferous forest (Alatalo & Lundberg, 1984a, Alatalo *et al.* 1985, Lundberg & Alatalo 1992). Consequently, if differences in food abundance also occur between different types of coniferous forest, one would expect to find corresponding habitat-related differences in the breeding success of the Pied Flycatcher.

It seems reasonable to assume that the food availability for insectivorous birds is lower in introduced Lodgepole Pine compared to native Scots Pine *P. sylvestris* (cf. Southwood 1977). If this is the case, Lodgepole Pine plantations should have a lower habitat quality and the reproductive performance of the Pied Flycatcher should be lower than in plantations of Scots Pine. To test this we compared the average reproductive performance of the Pied Flycatcher over a 4-year period in equally-aged plantations of Lodgepole and Scots Pine at three sites. In both types of plantations nest boxes were available in excess. We also indexed one aspect of habitat quality for the flycatchers, namely the abundance of potential food items, by measuring the number of insect larval droppings (cf. Morris 1949, Tenow & Larsson 1987) from the pine trees at three sites during one of the study years.

Study area

The pine plantations are situated in central Sweden, between 61° and 63° north latitude. They were all planted between 1970 and 1972, and arranged in such a way that a *sylvestris* and a *contorta* plantation were situated side by side, creating similar conditions with regard to soil and climate, thus enabling paired comparisons. Each of the plantations was about 20 ha in size. The trees in the Scots Pine plantations are now about 8 m high, the fast-growing Lodgepole Pine about 10 m. The Lodgepole Pine allows less light to reach the ground, which may influence the field and bottom layer of vegetation, and thus potentially the abundance of insects.

Three sites, each with a pair of plantations, were selected to index insect larvae abundance. These sites, together with an additional pair of plantations of similar kind, were used to study the reproductive success of the Pied Flycatcher. However, at one of these sites Pied Flycatchers did not start to breed until 1992 (only two nest boxes occupied), and this site (which corresponds to experimental plantation 14, belonging to "Svenska Cellulosa Aktiebolaget", SCA) was therefore not included in the analysis.

Although the plantations were similar regarding the above-mentioned conditions, there were some differences: At site 1 most deciduous bushes had been removed, thus the proportion of this vegetation type, which consisted mainly of birch *Betula spp.*, was lower there than in the other plantations. At site 2 there were some wetter patches, particularly in the Lodgepole plantation, where seedling survival had been poor. This site also had a higher proportion of deciduous trees, particularly birch, than the other sites. Site 3 differed in that the pine seedlings were planted close to each other along two rows, but with comparatively long distance to the next pair of rows (Sites 1, 2 and 3 correspond to SCA's experimental plantations 2, 12 and 19, respectively.). Of the larval dropping sites, I and II corresponds to nest box sites 1 and 2.

Material and methods

In each of the six plantation stands 35 wooden nest boxes with an entrance diameter of 30 mm were distributed over the central part of the area, 50 m apart from each other, during spring 1989, well before the arrival of the Pied Flycatcher. The nest boxes were checked twice per breeding season: at the first inspection the clutch size was recorded, and at the second inspection, conducted just before fledging, the nestlings were counted and weighed. However, in 1992 the nest boxes were visited only once (when we weighed the nestlings) and this year's clutch size was estimated by adding the number of nestlings and infertile eggs in the nest. The age of nestlings when weighed differed somewhat between years, owing to variation in start of breeding, which we were not able to totally compensate for when estimating the proper time for weighting the nestlings. They were weighed on a digital balance to the nearest 0.1 g.

In total ten clutches were deserted. Of these four clutches consisted of clutches with only one or two cold eggs. These were regarded more as breeding attempts, and hence excluded from the statistical analysis. Six deserted clutches with an apparantly normal number of eggs were, however, included.

Insect larval droppings were used as an indirect measure of insect larvae abundance in the plantations (cf. Morris 1949, Tenow & Larsson 1987). In each of the stands ten square pieces of masonite (25x25 cm) were covered with a thin layer of a glue (Hernia 4286) and placed on a stick about 1 m above ground and 1 m from the trunk of a pine tree. The plates were distributed systematically throughout the plantation by placing them 50 m apart in lines. They were set out on 20 and 21 June 1989. The plates were brought into the laboratory after two weeks and the number of larval droppings were counted. We separated droppings from the following species/species groups: the Pine-flower Weevil *Anthonomus phyllocola,* and caterpillars of Lepidoptera and sawflies (Hymenoptera: Symphyta). Droppings from orders with very small insects, such as Psocoptera and Aphidoidea, were not counted.

Statistical analysis

The aim of this study was to test if there exists a general difference in habitat quality between 20-year-old plantations of *P. sylvestris* and *P. contorta.* Thus, taken this approach, differences for single years may exist, but if there is a general difference this should be detectable as a higher average value of the pied flycatcher reproductive success over a longer period of years. Otherwhise one habitat is not superior to the other in the long run. We therefore calculated annual means for the Lodgepole and Scots Pine plantations, respectively, at each site, giving four year-values for each habitat at each site. Since we wanted to test the *general* effect of habitat quality and to avoid pseudoreplication (sensu Hurlbert 1984), we then calculated the average value of these four annual mean values for each habitat at each site, giving a total of six values for the whole data set. These six values were then used to analyse the general effect of habitat quality using a randomized block ANOVA with the factors habitat and site, where site was considered as a block effect.

The same randomized block ANOVA was used to test the general effect of habitat (Lodgepole and Scots Pine) on the abundance of larval droppings. This analysis was based on mean values for each habitat at each site (total N = 6).

All analyses were conducted with the SAS statistical package. For the analysis of variance the assumption of homoscedasticity was tested by plotting residual values against both factors and predicted values. We used the Shapiro-Wilk's test to check the assumption of normality. In the dropping analysis, the sawfly larvae *Anthonomus* and "total number" of droppings were log-transformed before analysis (Zar 1984). When a significant effect of site was found, we assessed differences between sites using the Tukey test (alpha = 0.05, df = 2).

Results

The Pied Flycatcher

If differences in habitat quality exists between the Scots and Lodgepole Pine plantations, habitat should significantly explain variation in reproductive success of Pied Flycatchers. The total number of breeding pairs of Pied Flycatcher within the three sites during the period 1989-1992 was 126 and 107 in Scots Pine and Lodgepole Pine, respectively (Table 1). Habitat did not significantly explain the variation in the number of breeding birds, i.e. the breeding density of Pied Flycatcher (Table 2, Fig. 1a). However, habitat had a significant effect on the mean number of eggs in the clutch (Table 2). Although the mean number of eggs in the clutch varied considerably between sites for each habitat type, the clutches were larger in the Scots Pine habitat than in the habitat of Lodgepole Pine (Fig. 1b). This relationship between the habitats was evident for most of the years at each site (Table 3). Also the factor site contributed significantly to explain variation in clutch size (Ta-

Table 1. Mean weight (±1 S.E.) of Pied Flycatcher nestlings, number of unhatched clutches, number of deserted broods and number of broods which had left the nest boxes by the time of weighing, in plantations of Scots Pine and Lodgepole Pine, respectively. N=Number of weighed clutches.

Medelvärden för kullvikt och dess spridningsmått (± 1 S.E.), antal ännu ej utkläckta kullar (No. unh.), antal övergivna kullar (No. des.) och antal utflugna kullar (No. left).

	Pinus sylvestris						*Pinus contorta*					
Year	N	Weight	S.E.	No. unh.	No. des.	No. left	N	Weight	S.E.	No. unh.	No. des.	No. left
1989	14	12.9	0.8	1	0	0	16	13.2	0.8	1	0	1
1990	21	13.4	0.3	0	0	7	25	13.2	0.3	0	1	6
1991	38	9.1	0.6	3	3	0	22	10.7	0.6	3	3	0
1992	35	11.5	0.6	3	1	0	27	13.0	0.5	2	0	0

Table 2. Summary of randomized block ANOVA:s for the breeding success of Pied Flycatchers in the two habitats, Lodgepole Pine and Scots Pine plantations. Site was analyzed as a block effect.

Sammanfattning av ANOVA upplagd som ett randomiserat blockförsök för olika häckningsvariabler hos svartvit flugsnappare i planteringar av contortatall och tall.

	$MS_{habitat}$	df	p	MS_{site}	df	p	MS_{error}	df	R^2
No. of breeding pairs *Antal häckande par*	3.760	1	0.590	2.542	2	0.785	9.292	2	0.322
Clutch size *Kullstorlek*	0.079	1	0.009	0.105	2	0.006	0.001	2	0.995
No. of hatched eggs *Antal kläckta ägg*	0.051	1	0.418	0.135	2	0.270	0.050	2	0.763
No. of fledglings *Antal ungar*	0.092	1	0.159	0.123	2	0.134	0.019	2	0.899
Total weight of brood *Kullens totalvikt*	2.266	1	0.800	62.203	2	0.304	27.151	2	0.700
Mean brood weight *Kullens medelvikt*	0.274	1	0.548	0.212	2	0.716	0.534	2	0.395

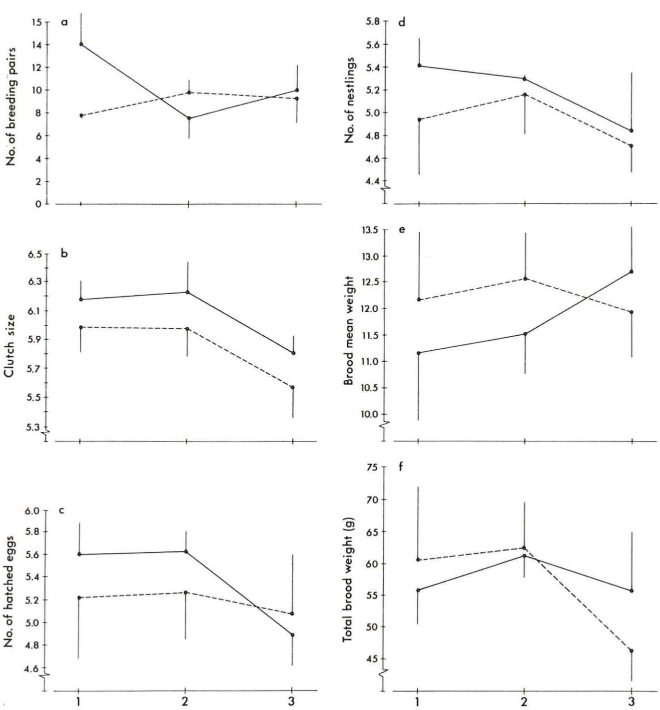

Fig. 1. Clutch size and reproductive success of the Pied Flycather utilizing nest boxes placed in plantations of *Pinus sylvestris* (solid line) and *P. contorta* (broken line) from three different sites/localities in central Sweden. Each data point is based on mean year values for each plantation during the years 1989-1992; the vertical line represents one S.E. of the mean. Site 1 corresponds to SCA's experimental plantation 2, site 2 to plantation 12 and site 3 to plantation 19. a) number of breeding pairs, b) mean clutch size, c) mean number of hatched eggs, d) mean number of nestlings, e) mean brood weights in gram, and f) mean of total brood weights in gram.

Kullstorlek och häckningsframgång hos svartvit flugsnappare i planteringar av tall (heldragen linje) och contortatall (streckad linje) från tre olika lokaler i södra Norrland. Varje punkt består av ett medelvärde från varje plantering från åren 1989-1992 (N=4). Den vertikala linjen visar medelvärdets spridning (± 1 S.E.). Lokal 1 är SCA:s försöksplantering nr 2, lokal 2 försöksplantering nr 12 och lokal 3 försöksplantering nr 19. a) antal häckningar, b) antal ägg i kullen, c) antalet kläckta ägg, d) antal ungar i kullen, e) medelvikten hos kullen i gram, och f) medelvärdet av den totala kullvikten i gram.

Table 3. Mean values (± 1 S.E.) of clutch sizes during the study period 1989-1992. N=233.
Medelvärden för kullstorlekar och spridningsmått (± 1. S.E.) under perioden 1989-1992.

	Pinus sylvestris			*Pinus contorta*		
Year	Site 1	Site 2	Site 3	Site 1	Site 2	Site 3
1989	6.0±0.3	5.7±0.3	5.8±0.9	6.3±0.4	5.8±0.4	5.3±0.3
1990	6.5±0.2	6.4±0.2	5.9±0.2	6.3±0.3	6.4±0.3	6.2±0.2
1991	6.0±0.2	6.7±0.3	6.1±0.2	5.6±0.2	6.2±0.3	5.3±0.2
1992	6.1±0.1	6.2±0.4	5.5±0.3	5.8±0.3	5.6±0.4	5.5±0.3

ble 2), and site 3 had significantly lower mean clutch size compared to both site 1 and 2 (Fig. 1b).

There was a tendency, although non-significant, for a higher average number of nestlings during the four year period in the Scots Pine habitat as compared to the Lodgepole Pine habitat (Fig. 1d, Table 2). Other breeding success parameters, i.e. number of hatched eggs, brood mean weight and total brood weight, were not associated with habitat type (Table 2). These variables also showed a high within-habitat variation as well as a high variation between sites (Fig. 1c, e and f).

Pied Flycatchers started to breed earlier during the second year (1990), and thus some broods had already left the nest boxes at the time of weighing. In that year, the number of such broods was about equally distributed between the Scots Pine and Lodgepole Pine stands (7 vs 6; Table 1). On the other hand, the spring of 1991 was unusually late, and in each of the pine plantation types, three clutches had still not hatched by the time that the birds were weighed. In 1992, three and two clutches, respectively, had not yet hatched (Table 1). Thus, we did not find any evidence for within-year differences in the time of breeding between the two pine habitats.

No predation on nestlings was observed during the study. In 1990, however, dead nestlings were found in two of the nest boxes in the Lodgepole Pine plantations. Consequently, predation on adult birds outside the nest boxes could not be excluded. This could also be the case for those clutches considered as deserted. However, in one nest box (in a Lodgepole Pine plantation in 1990) even the female was found dead, together with her brood, which might also indicate food shortage. In 1991, three clutches in each plantation type were deserted (Table 1).

Similar proportions of male Pied Flycatchers were present at the nest boxes in the two pine habitat types. In 1992, males were present at 53% of the nest boxes with broods in the *P. sylvestris* plantations, and at 71% in the *P. contorta* plantations. The difference was not statistically significant ($T = 1.29$, $p = 0.325$, $df = 2$, paired t-test on arcsin-transformed values, see Zar 1984).

Larval droppings

Droppings from the Pine-flower Weevil and sawfly larvae dominated while lepidoptera larvae droppings were rare. However, habitat had no significant effect on the number of droppings from these insects or on the total number of droppings (Table 4). Except for site I the *contorta* plantations tended to have higher number of droppings (Fig. 2). The Scots Pine plantations showed a low within-habitat variation, while the opposite was true for the Lodgepole Pine plantations (site III tended to have higher number of droppings, Fig. 2).

Discussion

A female Pied Flycatcher apparently selects a male depending on the quality of the nest site he offers, whereas the characteristics of the male itself seems to be of secondary importance (Askenmo 1984, Alatalo *et al.* 1986, Slagsvold 1986). The Pied Flycatcher defends the nest box area (von Haartman 1956, Harvey *et al.* 1988), but not the feeding area around the box. Still, a flycatcher is likely to forage close to its nest site, where it collects food items from the air, branches or trunks of trees, or from the field- and bottom-layer vegetation (e.g. von Haartman 1954, Alatalo & Alatalo 1979, Atlegrim 1992). Since flycatchers are not likely to forage very far from the nest site, differences in food abundance between different habitat types should be reflected in habitat-related variation in breeding phenology and reproductive performance. Sometimes, however, the flycatchers fly to more distant areas to forage (pers. obs.). Thus, such a bird species may not be the most suitable one for testing habitat quality (for example, biomass of available invertebrate food)

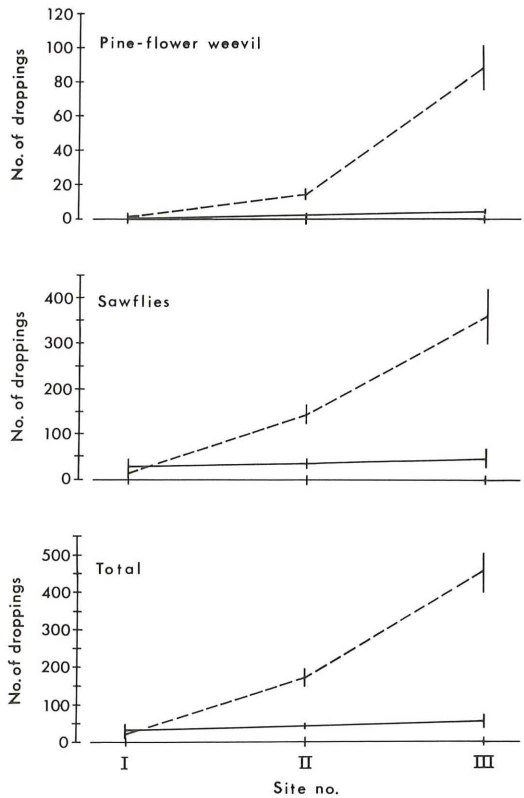

Fig. 2. Mean number of droppings from larvae of Pine-flower Weevil, sawflies and total (also including a small number of droppings from Lepidoptera larvae) on plates placed under trees in plantations of *Pinus sylvestris* (solid line) and *P. contortra* (broken line). Mean values from ten plates in each stand; the vertical line represent one S.E. of the mean. Sites I and II corresponds to SCA's experimental plantations 2 and 12, i.e. no. 1 and 2 in Fig. 1, while site III corresponds to experimental plantation no. 14.

Medelvärdet av antalet spillningar från tallblomvivel, växtstekellarver och totalt (d v s spillning från tallblomvivel och växtstekellarver samt ett fåtal spillningar från mätarlarver) som hamnat på plattor försedda med lim placerade under träd i planteringar med tall (heldragen linje) och contortatall (streckad linje). Medelvärden, samt spridningsmått (± 1 S.E.) från tio plattor i varje plantering. Lokal I och II motsvarar nummer 1 och 2 i Fig. 1, d v s SCA:s försöksplanteringar nummer 2 och 12, medan lokal III motsvarar försöksplantering nummer 14.

Table 4. Summary of randomized block ANOVA:s for mean number of insect larvae droppings in the two habitats, Lodgepole Pine and Scots pine plantations. Site was analyzed as a block effect. All variables except the mean number of Lepidoptera droppings were log-transformed according to log (y+1) before entering analysis (c.f. Zar 1984).

Sammanfattning av ANOVA upplagd som ett randomiserat blockförsök för medelvärden av insektsspillning från larver i planteringar av contortatall och tall. Lokal analyserades som en blockeffekt. Alla variabler utom medelvärdet av spillning från Lepidoptera logtransformerades enligt log(y+1) innan analysen utfördes (jfr. Zar 1984).

	$MS_{habitat}$	df	p	MS_{site}	df	p	MS_{error}	df	R2
Lepidoptera *Fjärilar*	18.03	1	0.234	14.06	2	0.310	6.33	2	0.78
Symphyta *Växtsteklar*	1.12	1	0.415	0.81	2	0.374	1.08	2	0.69
Anthonomus *Tallblomvivel*	4.21	1	0.133	3.21	2	0.179	0.70	2	0.88
Total *Summa*	1.60	1	0.307	1.57	2	0.354	0.86	2	0.73

within a particular habitat type. Nevertheless, if the birds regularly collect food at some distance from the defended territory, it should result in a higher energetic cost, compared with birds collecting food in the vicinity of the nest boxes (unless the former select more valuable food; cf. Lifjeld & Slagsvold 1988).

Alatalo *et al.* (1985) regarded food abundance to be one of the most important habitat selection criteria used by Pied Flycatchers. Their strongest evidence supporting this view is that even when the number of nest cavities is not limiting, breeding density is markedly lower in coniferous than in deciduous forest. When nest boxes are provided in excess, the population increases up to a limit which is probably determined by the food supply (Alatalo *et al.* 1985).

In our four-year study period, the clutch size was significantly affected by habitat type. Larger clutches, was found in the Scots Pine plantations (Table 2, Fig. 1b). The most probable reason for this is a difference in food abundance between the habitats. Invertebrate biomass is generally lower on introduced tree species than on native ones (Southwood 1977), but in our study the number of droppings from insect larvae collected during the nestling period did not differ between habitats (Table 2, Fig. 2). Note, however, that only two of the sites where dropping data was collected are congruent with the three sites where bird breeding success was studied. Even if there had been a significant effect of habitat on number of larval droppings, it is not probable that the dominant larvae (*Anthonomus phyllocola*) are available for the Pied Flycathers as they live more or less hidden in the pine flowers. Further, the second most common insect larvae group, the sawflies, defend themselves against enemies by synchronized movements and by producing oral effluents (Björkman 1991, p. 9; see also Hanski 1987), and is probably also of low value to the birds.

Our indirect measure of habitat quality with respect to food availability only included measures of insect larvae living in the pine trees. It can not be excluded that differences still exists between the two habitats if there are differences in density of deciduous trees, insect availability in the air, the field and/or ground layer. There is some evidence that this may be the case (Kardell *et al.* 1989, Sjöberg 1989, Danell & Sjöberg 1993, Sjöberg & Pettersson, unpubl. data).

The larger clutch size and the assumed higher food abundance in Scots Pine plantations lead to the expectation of a higher reproductive success in this habitat compared to Lodgepole Pine plantations. Contrary to expectation, habitat quality did not have any effect on the number of hatched eggs, the number of nestlings, the mean brood weight or the total brood weight (Table 2, Fig. 1c-f). The reason for this may be that there exist a difference in habitat quality just during the egg laying period, but not during the Pied Flycatcher nesting period. However, our results indicate that a high within-habitat variation and high variation between sites for bird reproduction parameters may be the reason for lack of a significant effect of habitat quality for these parameters (see Fig. 1c-f).

Beside habitat, site also contributed significantly to explain variation in clutch size and site 3 had significantly lower clutch sizes compared to both site 1 and 2 (Fig. 1b). Although sites did not differ significantly, there was a tendency for lower number of hatched eggs, number of nestlings and total brood weight, but higher mean brood weight at site 3 (Fig. 1c-f). Such a pattern may be explained on the basis of the low clutch sizes at site 3. However, the low breeding success at site 3 may also be explained by a more harsh climate, i.e. more close to the mountain range, and a lower abundance of deciduous bushes compared to site 1 and 2, which could be important with respect to food availability (se above). It ought to be noted though, that the mean clutch sizes in both pine plantation types in our study are generally of the size which could be expected for Pied Flycatcher broods in the region. For example, in the vicinity of Uppsala, i.e. south of our sites, the clutch size in coniferous forest was 6.3 eggs (Lundberg & Alatalo 1992), while in spruce plantations in Scania in southern Sweden, Källander *et al.* (1987) found the mean clutch size to be 6.16, and Gezelius *et al.* (1984) 6.58. In a spruce forest in Norway the mean clutch size (pooled data) during a five-year period was 5.55-5.97 eggs, compared with 6.0-6.5 and 5.8-6.3 for clutches in the Scots Pine and Lodgepole Pine plantations, respectively, in our study. Beside depending on nest box type (Slagsvold 1987), clutch size varies condiderably between years, along latitude gradients and between habitat types (e.g. Järvinen & Väisänen 1984, Järvinen 1989, Lundberg & Alatalo 1992).

Divergence at site three also causes a high within-habitat variation. For example, the higher number of hatched eggs in the Scots Pine plantation at site 1 and 2 is changed at site 3 (Fig. 1c). The diverging habitat pattern at site 3 may be interpreted in the same way as for site 3 divergence above. However, note that the Pied Flycathcers in the Scots Pine plantations have a high loss at hatching, and almost no losses between hatching and fledgling stage. Contrary to this, losses in the Lodgepole Pine plantations is more evenly distributed among the egg, hatching and fledgling stages.

The breeding success data can be summarized as follows: Mean clutch size was higher in the Scots Pine plantations, and this may indicate higher habitat quality than in the plantations of the introduced Lodgepole Pine. Between-site variation was probably dependent on differences in the planting techniqe, thinning operations and occurrence of wet patches causing site differences in tree density, light conditions, abundance of deciduous trees, moisture conditions, etc., which may have influenced food availability for the Pied Flycatchers. Differences in climate may also to some extent explain the variation in breeding results between different sites. Also the within-habitat variation was probably influenced by light conditions, abundance of deciduous trees, etc., but could even to some extent have been influenced by differences in breeding density between different stands (cf. Askenmo 1973, 1977, Alatalo & Lundberg 1984a, 1989), which also could be explained by the same habitat quality factors.

References

Alatalo, R. V. & Alatalo, R. H. 1979. Resource partitioning among a flycatcher guild in Finland. *Oikos* 33: 46-54.

Alatalo, R. V. & Lundberg, A. 1984a. Density-dependence in breeding success of the pied flycatcher *(Ficedula hypoleuca). J. Anim. Ecol.* 53: 969-978.

Alatalo, R. & Lundberg, A. 1984b. Polyterritorial polygyny in the pied flycatcher *Ficedula hypoleuca* - evidence for the deception hypothesis. *Ann. Zool. Fennici* 21: 217-228.

Alatalo, R. & Lundberg, A. 1989. Clutch size of the pied flycatcher *(Ficedula hypoleuca)* - an experiment. *Ornis Fennica* 66: 15-23.

Alatalo, R. V., Lundberg, A. & Ulfstrand, S. 1985. Habitat selection in the pied flycatcher *Ficedula hypoleuca*. Pp. 59-83 in Cody, M. (ed.), *Habitat selection in birds*. Academic Press, New York.

Alatalo, R. V., Lundberg, A. & Glynn, C. 1986. Female pied flycatchers choose territory quality and not male characteristics. *Nature* 323: 152-153.

Askenmo, C. 1973. Nestling weight and its relation to season and brood-size in the Pied flycatcher *Ficedula hypoleuca* (Pallas). *Ornis Scand.* 4: 25-31.

Askenmo, C. 1977. Effects of addition and removal of nestlings on nestling weight, nestling survival, and female weight loss in the pied flycatcher *Ficedula hypoleuca* (Pallas). *Ornis Scand.* 8: 1-8.

Askenmo, C. E. H. 1984. Polygyny and nest site selection in the pied flycatcher. *Anim. Behav.* 32: 972-980.

Atlegrim, O. 1992. Mechanisms regulating bird predation on a herbivorous larva guild in boreal coniferous forests. *Ecography* 15: 19-24.

Björkman, C. 1991. *Interactions between a pine sawfly, its host and natural enemies as mediated by plant chemicals.* PhD thesis, Uppsala 1991.

Curio, E. 1959. Verhaltensstudien am Trauerschnäpper. *Zeitschr. Tierphychol. Beiheft* 3: 1-118.

Danell, K. & Sjöberg, K. 1993. Wildlife and lodgepole pine plantations - a review of present knowledge in Scandinavia. Pp. 24-37 in *Proceedings of Pinus contorta - from untamed forest to domesticated crop* (Lindgren, D. ed.). Meeting of IUFRO WP 2.02.06 and Frans Kempe Symposium, Umeå, August 24-28, 1992. Department of Forest Genetics and Plant Physiology, Swedish University of Agricultural Sciences, Report 11, 1993.

Gezelius, L., Grahn, M., Källander, H. & Karlsson, J. 1984. Habitat-related differences in clutch size of the pied flycatcher *Ficedula hypoleuca. Ann. Zool. Fennici* 21: 209-212.

Haartman, L. von 1954. Der Trauerfliegenschnäpper. III. Die Nahrungsbiologie. *Acta Zool. Fennica* 83: 1-96.

Haartman, L. von 1956. Territory in the pied flycatcher *Muscicapa hypoleuca. Ibis* 98: 460-475.

Hagner, S. O. A. 1985. Lodgepole pine management in Sweden. A strategy for higher yield. Pp. 211-217 in *Proceedings of Lodgepole pine. The species and its management* (Baumgartner, D. M., Krebill, R. G., Arnott, J. T. & Weetman, G. F., editors), May 8-10, 1984 Spokane, Washington, USA and repeated May 14-16, 1984 Vancouver, British Columbia, Canada.

Hanski, I. 1987. Pine sawfly population dynamics: patterns, processes, problems. *Oikos* 50: 327-335.

Harvey, P. H., Stenning, M. J. & Campbell, B. 1988. Factors influencing reproductive success in the pied flycatcher. Pp. 189-200 in *Reproductive success. Studies of individual variation in contrasting breeding systems* (Clutton-Brock, T. H. ed.). University of Chicago Press, Chicago and London.

Hurlbert, S. M. 1984. Pseudoreplication and the design of ecological field experiments. *Ecol. Monogr.* 54: 187-211.

Järvinen, A. 1989. Clutch-size variation in the pied flycatcher *Ficedula hypoleuca. Ibis:* 131: 572-577.

Järvinen, A. & Tast, J. 1980. Regulation of subarctic populations of small rodents and box-nesting passerines (In Finnish with Engl. summary). *Luonnon Tutkija* 84: 26-30.

Järvinen, A. & Väisänen, R. A. 1984. Reproduction of pied flycathcers *Ficedula hypoleuca* in good and bad breeding seasons in a northern marginal area. *Auk* 101: 439-450.

Kardell, L., Boström, U. & Holmer, M. 1989. *Några synpunkter på contortatallens betydelse för markfauna och fågelliv.* Sveriges lantbruksuniversitet. Institutionen för skoglig landskapsvård. Report No. 43.

Källander, H., Karlsson, J., Rosenlund, N. & Svensson, S. 1987. Clutch-size and breeding success of the pied flycatcher *Ficedula hypoleuca* in two contrasting habitats in South Sweden. *Acta Regiae Soc. Sci. Litt. Gothoburgensis. Zoologica* 14: 76-83.

Lifjeld, J. T. &. Slagsvold, T. 1988. Effects of energy cost on the optimal diet: an experiment with pied flycatchers *Ficedula hypoleuca* feeding nestlings. *Ornis Scand.* 19: 111-118.

Lundberg, A. & Alatalo, R. V. 1992. *The pied flycatcher.* T & A D Poyser, London.

Lundberg, A., Alatalo, R. V., Carlson, A. & Ulfstrand, S. 1981. Biometry, habitat distribution and breeding success in the pied flycatcher *Ficedula hypoleuca. Ornis Scand.* 12: 68-79.

Morris, R. F. 1949. *Frass-drop measurement in studies of the European spruce sawfly.* Univ. of Michigan School of Forestry and Conservation. Bulletin No. 12.

Pettersson, R. B. 1992. (The pine flower weevil - the character species of lodgepole pine forests). *Ent. Tidskr.* 113 (3): 37-38. (In Swedish with Engl. summary.)

Sjöberg, K. 1989. Skogsbrukets effekter på faunan - med exempel från contorta- och gransumpskogar. *Sveriges Skogsvårdsförbunds Tidskrift* 2-89: 25-31 (In Swedish).

Skogsstyrelsen 1992. *Contortatallen i Sverige - en lägesrapport.* Skogsstyrelsens contortautredning. 226 pp.

Slagsvold, T. 1986. Nest site settlement by the pied flycatcher: does the female choose her mate for the quality of his house or himself? *Ornis Scand.* 17: 210-220.

Slagsvold, T. 1987. Nest site preference and clutch size in the pied flycatcher *Ficedula hypoleuca. Ornis Scand.* 18: 189-197.

Southwood, T. R. E. 1977. The stability of the trophic milieu, its influence on the evolution of behaviour and of responsiveness to trophic signals. *Coll. Int. C.N.R.S.* 265:471-493.

Tenow, O. & Larsson, S. 1987. Consumption by needle-eating insects on Scots pine in relation to season and stand age. *Holarctic Ecology* 10: 249-260.

Zar, J. H. 1984. *Biostatistical analysis.* Prentice-Hall, Inc., Englewood Cliffs, New Jersey, USA.

Sammanfattning

Skillnader i biotopkvalitet mellan planteringar av contortatall och vanlig tall mätt som häckningsframgång hos svartvit flugsnappare.

Den till Sverige införda nordamerikanska contortatallen började planteras i större omfattning i slutet av 1960-talet och början av 70-talet. Planteringarna är i stort sett geografiskt begränsade till Norrland och upptar där numera en areal omfattande totalt ca 540.000 ha. Vi har undersökt den svartvita flugsnapparens häckningsframgång i ca 20 år gamla planteringar av contortatall *Pinus contorta* med motsvarande planteringar av inhemsk tall *P. sylvestris*. I varje plantering, som var och en omfattar ca 20 ha, har vi placerat ut 35 holkar, där diametern på ingångshålet är 30 mm. I samtliga planteringar finns ett överskott på holkar. Studierna har utförts inom fyra av skogsbolaget SCA:s försöksplanteringar. Där har contortatall och inhemsk tall planterats i samma område, vid samma tillfälle och under så lika förhållanden som möjligt. Dessa parvisa försöksplanteringar, där alltså planteringar med contortatall och tall ligger sida vid sida, har utnyttjats för våra jämförande häckningsstudier. Totalt har vi använt oss av 8 planteringar; 4 med contortatall och 4 med vanlig tall. Träden är ca 8 meter höga i tallplanteringarna, och ca 10 m i de mera snabbväxande contortaplanteringarna. Genom sin snabba tillväxt sluter sig contortaplanteringarna tidigare än tallbestånden, vilket i sin tur påverkar ljusförhållanden och därmed även vegetationssammansättningen i fält- och bottenskikt. Detta, liksom förekomst av lövträd (främst björk), d v s om planteringarna är lövröjda eller inte (och hur noggrant och konsekvent de i så fall är röjda), påverkar förekomsten av potentiella födodjur för insektsätande fåglar såsom den svartvita flugsnapparen.

Häckningsresultatet har insamlats under perioden 1989-1992, alltså fyra år. Utgångspunkten för denna häckningsstudie har varit att få ett svar på frågan om det föreligger generella skillnader i häckningsframgång hos svartvita flugsnappare mellan ca 20-åriga planteringar av contorta och vanlig tall. I den statistiska analysen har vid därför använt oss av häckningsresultatens medelvärden för de fyra studieåren och vi har således i stort sett bortsett från den skillnad mellan habitaten som kan ha funnits enskilda år. Medelvärdet för den svartvita flugsnapparens häckningsframgång över de fyra studieåren analyserades för respektive plantering (totalt N=6) som ett randomiserat blockförsök med hjälp av en 2-vägs variansanalys (ANOVA), med faktorerna habitat (habitatkvalitet) och lokal (block-faktor).

Under ett av studieåren, 1989, mätte vi indirekt förekomsten av potentiella födoorganismers förekomst i tallkronorna genom att kvantifiera antalet spillningar från insektslarver. Spillningen föll ner på limförsedda plattor. Dessa var placerade under träd i planteringarna i två veckor. Insamlingsperioden sammanföll i tid med den period då fåglarna matade sina ungar. Resultaten av denna delstudie blev att inga statistiskt signifikanta skillnader mellan habitaten kunde urskiljas i antalet spillningar från fjärilslarver, växtstekellarver, eller från tallblomvivelns larver, ej heller i det totala antalet spillningar. (Fig. 2, Tabell 4).

Vår slutsats är att det i denna studie endast i ett avseende förelåg en generell, statistiskt signifikant skillnad i flugsnapparens häckningsresultat mellan vanlig tall och contorta. Kullstorleken var högre i vanliga tallplanteringar jämfört med contorta-planteringar (Fig. 1, Tabell 2). Däremot var inte antalet ungar, eller ungarnas medelvikt, skilda åt i de två typerna av plantering (Fig. 1, Tabell 2). Slutresultatet blev således att i slutet av häckningssäsongen förelåg ingen statistiskt signifikant skillnad mellan habitaten med avseende på flugsnapparnas häckningsframgång. Skillnader i förekomst av t ex lövträd och fuktstråk i planteringarna tycks ha väl så stor påverkan på häckningsresultatet som tallarten som sådan. Reservation bör dock göras för att vi ännu inte har möjlighet att mäta kvaliteten i äldre bestånd av contortatall, ej heller i senare tall-generationers påverkan på övrig vegetation i planteringarna, som i sin tur påverkar insekts-förekomst, och därmed potentiell fågelföda.

Acknowledgements

We would like to thank Jonas Lundberg for skilful assistance in the field, Lennart Bondesson for valuable statistical discussions and assistance, and Svenska Cellulosa Aktiebolaget (SCA) for allowing us to use their experimental pine plantations for our field experiments. John P. Ball and Per Persson gave valuable comments on an earlier version of this manuscript. Financial support was provided by the Swedish Environmental Protection Agency, SSFf (Stiftelsen Skogsbrukets Forskningsfond) and Bo Rydins Stiftelse för Vetenskaplig Forskning.