Published paper

Griesser, M., Nystrand, M., Eggers, S. and Ekman, J. (2007) *Impact of forestry practices on fitness correlates and population productivity in an open-nesting bird species.* Conservation Biology, 21 (3). pp. 767-774. ISSN 0888-8892

Impact of forestry practices on fitness correlates and population productivity in an open-nesting bird species

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Word count: 5683 words

Running head: Forestry effects on Siberian Jays

Keywords: population viability, habitat fragmentation, thinning, clear-cutting, Siberian Jay, *Perisoreus infaustus*

Abstract

In the boreal forests of Fennoscandia, over 99% of the forest area has been altered by forestry practices, which has created forests of differing age structures and stand characteristics than primary forest stands. Although many researchers have investigated how forestry affects species abundance, few have assessed how forestry affects fitness correlates of species living in altered habitats, and this has negatively affected management efforts. We experimentally addressed the effect of standard forestry practices on fitness correlates of an open-nesting, long-lived bird species typical to boreal forests of Eurasia, the Siberian Jay (*Perisoreus infaustus* L.). Using a before-after comparison of reproductive data on the level of territories, we found that standard forestry practices had a strong negative effect on the breeding success of jays. Both partial thinning of territories and partial clearcutting of territories reduced future breeding success by a factor of 0.35. Forestry practices reduced territory occupancy. Thus, over the 15 years of the study the productivity of the affected population declined over 50% as a result of territory abandonment and reduced breeding success. Results of previous studies on Siberian Jays suggest that the strong effect of forest thinning on fitness is explained by the fact that most common predators of nests and adults are visually oriented, and thinning makes prey and nests more visible to predators. The consequences of thinning we observed are likely to apply to a wide range of species that rely on understory to provide visual protection from predators. Thus, our results are important for the development of effective conservation management protocols and for the refinement of thinning practices.

INTRODUCTION

Among the habitat types with the most rapid alteration rates are forests in the tropical and subtropical regions, where more than 60% of the natural habitats have been altered during the last 50 years (Whitemore & Sayer 1992). However, habitat alterations in the temperate zones have occurred over much longer time periods and, thus, a much larger proportion of these habitats are altered (Meyer & Turner 1992). In the boreal forests of northern Europe, forestry has affected almost all forest patches during the last 200 years, leaving behind as little as 1% of primary forest (Linder & Östlund 1998).

Forestry in Fennoscandia is intense and large scaled. A commercial growth cycle takes around 80 to 120 years (Loman 2005) and involves a number of steps. Following harvesting (i.e., clearcutting), forests are regenerated almost exclusively by planting pine seedlings (*Pinus* spp.), which is the tree species of greatest commercial importance in this region. During a growth cycle, forests are thinned three times: first after about 25 years, then after 40 years, and finally at about 60 to 80 years. The purpose of thinning is to remove trees of poorer quality from the stand to increase growth of the remaining crop (Hamilton 1982). Hence, this procedure removes most of the understory (all vegetation under the tree canopy). As a result, the forest becomes more open and the view is less obstructed. Such practices clearly affect forests on a local level by changing tree diversity, age structure, and visual properties of the habitat. In addition, on a landscape level, forestry affects patch connectivity and landscape structure (Hansson 1992; Linder & Östlund 1998).

It is widely claimed that structural changes of forests are responsible for the loss in species abundance and diversity in a wide range of taxonomic groups (e.g., Harris 1984; Helle & Järvinen 1986; Gärdenfors 2000). A number of large-scale correlative studies support this hypothesis and demonstrate a link between habitat alteration and species abundance (Harris & Reed 2002; Hausmann et al. 2005). These studies are the basis for current management concepts that largely focus on protecting the few remaining primary patches and creating dispersal corridors between these patches (Mönkkönen 1999; Aune et al. 2005). However, current management guidelines are likely to be insufficient, and potentially misguiding (Spence 2001), because almost all forests today are affected by forestry, whereas the majority of the research has focused on patches unaffected by forestry. Moreover, the effect of modern forestry practices on actual fitness components in single species remains unclear (Sallabanks et al. 2000; Marzluff et al. 2000); thus, a causal understanding of the effect of forestry is complicated and management implications to date remain vague (Mönkkönen 1999).

We investigated the impact of standard forestry practices on reproduction and survival of an open-nesting bird species that is typical of boreal forests throughout Eurasia, the Siberian Jay (*Perisoreus infaustus*, L.). This non-migratory species lives in small groups formed around the breeding pair (Ekman et al. 1994, 2002). Jays breed once per year and build a new nest for every breeding attempt (mean clutch size = 3.9 ± 0.1; Eggers et al. 2006). Nest predation in this species is high; only 46% of all nests are successful (Eggers et al. 2005a). The main cause of reproductive failure is nest predation and corvid species are the most important nest predators. Together, they have been found to be responsible for 86% of all nest predation events where the predator could be identified (Eggers et al. 2005a). Corvids hunt with visual cues (Eggers et al. 2005a) and hence, the habitat structure around the breeding site directly affects nest predation rates (Ekman et al. 2001; Eggers et al. 2005b). We specifically tested the effect of standard forestry practices on breeding success, territory occupancy, and population productivity. In the study area, forest patches have been thinned and clearcut continuously throughout the last 15 years, creating patches of different openness and structure. This allowed us to use forestry practices as a “natural” experiment to investigate the effect of habitat changes with a before-after comparison, focusing on the effects of forest thinning on fitness correlates of Siberian Jays in particular. We hypothesized that thinning reduces the breeding success of birds breeding on affected territories because the habitat becomes more open and thus, nests are more exposed to visual predators. To assess the magnitude of thinning effects on breeding success, we compared thinned territories with partially cut territories and unmanaged territories. We also tested if, as a result of their lower productivity, partially cut and thinned territories were abandoned more often than unmanaged territories. Thus, we expected population productivity to be lower in the managed part of the study site compared to the unmanaged part of the study site.

METHODS

Study site and population

The study was conducted between 1989 and 2004 in a natural population of Siberian Jays, near Arvidsjaur, northern Sweden (65°40’ N, 19°0’ E). The number of studied territories increased throughout the study period from 3 to 54 territories (mean annual number of studied territories ± SE = 24.3 ± 4.69; 413 territory years in total). Since the start of the study, all individuals in the study population have been individually color banded and blood samples have been taken from all individuals (100 µL of blood from the alar vein) for molecular sex determination (Griffiths et al. 1998).

The vegetation at the study site is representative of forest of the boreal zone of Fennoscandia with the dominant species being Scots pine (*Pinus sylvestris* L.) and Norway spruce (*Picea abies* L.) (hereafter referred to as pine and spruce respectively; Ahti et al. 1968). Deciduous trees such as birch (*Betula pubescens* Erh.), aspen (*Populus tremula* L.), and willow (*Salix* spp.) are naturally less abundant. Our study site consists of two adjacent parts characterized by two distinct forest structures. The southern part of the study site consisted of clearcuts, plantations, and a variety of patches managed to different degrees, with a few, small, remnant patches of pristine forest (n = 37 territories). In contrast, the northern part (n = 17 territories) consisted almost exclusively of pristine forest that was unaffected by forestry for at least 200 years. Here, the landscape consisted of a natural mosaic of forests, marshes, and watercourses. We classified all territories according to if they had been affected by forestry during the study period. “Unmanaged territories” included all territories located in pristine forest and those territories in the managed part of the study site that had only been affected by forest management before the onset of this study. We use the term forest management to describe both thinning and clear-cutting. “Managed territories” included all territories that had been subject to forest management during the course of the study. Hence, the territories from the managed area could be used to measure the effect of forestry on fitness correlates of Siberian Jays, while using unmanaged territories as a control.

Forestry at the study site

Before the start of this study (between 1960 and 1988), 25.6% of the managed study site (64 km^2) was clearcut and replanted with pine (*Pinus* spp.). Because of the harsh climate in the region, regrowth in these plantations is slow; today the stands are still only a few meters high. During the time of this study, six forest patches (affecting seven territories) within the study site were commercially thinned (mean ± SE = 0.21 ± 0.03 km^2, total area 1.31 km^2), resulting in removal of the entire understory (small spruces, deciduous trees). Nine patches were clearcut (mean ± SE = 0.17 ± 0.05 km^2, total area 2.01 km^2), which affected 11 territories.

Breeding success

We used three different methods to assess breeding success in each territory. We assessed the breeding success in most territories and years directly by finding nests with the help of radio-tagged breeders. All nestlings were banded 1 to 2 weeks before fledging (n = 277 broods). In the cases in which we were unable to find the nest, breeding success was determined with two alternative methods. We visited groups shortly before juvenile dispersal in June and caught juveniles with mist nets (n = 27 broods). Alternatively, we determined breeding success in autumn by checking the presence of retained offspring (n = 66 broods). In the majority of groups that have successful reproduction, at least one of the offspring will delay dispersal and remain in the parental territory, where they stay until next breeding season or longer (Ekman et al. 2002; Kokko & Ekman 2002). By assessing aggressive interactions between breeders and juveniles on feeding sites in autumn, it is possible to determine accurately relatedness between individuals in a group (see Griesser 2003 for detailed description).

To compare the breeding success of different territories, we calculated a nesting success index (NSI) (Ekman et al. 2001). The NSI consists of the sum of differences over years between the actual nesting success within a given territory and year (0 = failure, 1 = success) and the average nesting success in the entire population the same year. Thus, NSI can be used for direct comparison of the reproductive success among territories because it gives a centered measure of breeding success of a given territory relative to the other territories in the study population.

To assess the effect of forestry practices on breeding success, we calculated a separate NSI before and after the territories were affected by forestry. Because our aim was to measure direct effects of forestry on breeding success, we only included years during which a territory was occupied in the calculations. The use of the NSI to assess relative nesting success is more robust than using the number of fledglings produced because it allowed us to include territories where nests had not been found but where successful reproduction could be confirmed by observations before juvenile dispersal or through the presence of retained offspring. In addition, use of the NSI instead of the number of produced fledglings was a more conservative measure because Siberian Jays have a lower clutch size in more open nest sites than in denser nest sites (Eggers et al. 2006). We only included territories where we had data on reproductive success for at least 4 years (*n* unmanaged territories excluded = 8; *n* managed territories excluded = 2). Two pairs moved their breeding territories in response to forestry, and these two territories were therefore excluded from the analyses.

Effect of breeder quality

In 9 of the 14 territories affected by forestry, at least one member of the same breeding pair occupied the territory before and after habitat alteration. Thus, reproductive data from these territories offered the possibility to assess whether any change in productivity before and after the treatment was due to the change in habitat structure. Alternatively, individuals with a high reproductive output could abandon managed territories and be replaced by individuals with a lower reproductive output. We tested for the effect of breeder quality by comparing the average breeding success and the average number of offspring produced before and after forest management. Whenever possible, we included reproductive data from females to control for maternal effects ($n = 7$ territories) while in two territories, only the male breeder was the same before and after the territory was altered by forest management.

Number of high-quality offspring produced

To assess the effect of forestry practices on productivity of individual territories in the study population, we assessed the number of retained offspring present on the studied territories each autumn (see above for assessment of relatedness). Retained offspring are those individuals that ultimately occupy high-quality territories and thus contribute most to the productivity of the study population (Ekman et al. 1999, 2001). Thus, the number of retained offspring present in a territory in autumn is a good measure of the number of high-quality offspring produced in a territory.

Territory occupancy, breeder dispersal, and population productivity

We collected data on group composition at least twice a year: during the breeding season (March - May) and in late autumn (September – October) after juvenile dispersal. This observational scheme allowed us to assess territory occupancy and most breeding dispersal events (i.e., change of territory by an already established breeder), with the exception of those breeders that dispersed but died before being resighted in their new territory (Ekman et al. 2001; Kokko & Ekman 2002). We assessed the effect of forestry on the productivity of the whole study population by comparing the average number of retained offspring produced in the managed study population with the production of retained offspring in the pristine habitat.

Statistical analyses

We used SAS 9.1 (SAS institute, Cary, North Carolina) and Genstat 8.2 (VSN International, Herts, United Kingdom) to analyze the data. To assess the effect of forestry on the breeding success of each territory, we used repeated measures general linear models (GLM) in SAS and compared the average NSI before and after forestry. We did preplanned comparisons of within-group differences by investigating differences in least square means. As a control, we assessed any changes in NSI in territories that were not affected by forestry by splitting all unmanaged territories in equal halves and calculating the mean NSI for both halves. This allowed us to control for temporal changes in breeding success over the study period. We used the same model to compare the productivity of retained offspring before and after forestry management. Changes in breeding success on territories, where the same breeder was present before and after the management, were compared with a nonparametric comparison for paired data (Wilcoxon matched-pair test). To assess the effect of forestry on territory occupancy, we used a generalized linear mixed model (GLMM) in Genstat. We tested whether territory occupancy in a given year depended on the related management practice in that territory (i.e., partially cut, thinned, or unmanaged) on the current NSI, controlling for territory identity and year by fitting them as random factors (binomial error distribution and logit link). With a similar model, we analyzed how time since a territory had been subjected to forestry practices affected territory occupancy (Poisson error distribution and logarithm link). The effect of habitat quality on reoccupation of abandoned territories was tested with a GLM (binomial error distribution and logit link).

RESULTS

Breeding success and productivity of high quality offspring

Forest management strongly affected the NSI (Table 1a, Fig. 1). Pairs living on territories that were affected by forestry had a significantly lower breeding success after management (0.35 lower NSI, which is roughly equivalent to 3.5 fewer successful broods over 10 years). However, the reduction in nesting success was independent of the management method, and the NSI was reduced equally much in thinned as in partially cut territories (least squares means difference: estimate = -0.13, SE = 0.14, $t_{79.2} = -0.86$, $p = 0.38$). Also, the size of the managed patches had no effect on the change in the NSI (size managed patch: df = 1; $F = 1.29$, $p = 0.26$), despite the fact that the individual sizes varied substantially (range 2.0- 33.8 ha; mean ± SE = 15.6 ± 2.5). As expected, the reduction in breeding success as a consequence of forest management also resulted in lower production of high-quality offspring (Table 1b, Fig. 2). The production of retained offspring in both partially thinned and partially clearcut territories was significantly lower after the habitat had been altered due to forestry. This decrease was also independent of the management method (thinning vs. partial cutting: least squares means difference: estimate = -0.03, SE = 0.22, $t_{85.8} = -0.15$, $p = 0.88$).

The reduction in breeding success was unlikely to be a result of a change in breeder quality. Forestry practices significantly reduced both the average breeding success (Wilcoxon matched pair test: Z= -2.04; p = 0.042) and the mean number of fledglings produced when using a within-individual comparison on those territories where we had data of breeders before and after their territory was affected (Wilcoxon matched pair test: Z= -2.10; p = 0.035). These patterns remained when we included only female breeders in the analyses (Wilcoxon matched pair test: mean breeding success: Z = -1.89; p = 0.058; mean number of fledglings: Z = -1.99; p = 0.046).

Effect of forestry on territory occupancy and population productivity

Territories that were partially thinned or partially clearcut remained unoccupied significantly more often than unmanaged territories (GLMM binomial distribution; logit link: Wald χ^2 = 8.88, p = 0.003; including year and territory as random factors). In addition, territories with a generally lower NSI remained unoccupied more often than territories with a generally higher NSI (Wald χ^2 = 11.06, p = 0.004). The NSI was not only related to patterns of territory abandonment, but was also related to the likelihood of a territory being reoccupied. Empty territories with a high NSI were significantly more often reoccupied than empty territories with a low NSI (GLM: effect of NSI t_1 = 2.24, p = 0.025). Furthermore, there was a time lag in the response to forestry practices. The majority of managed territories remained occupied some years after management before they were finally abandoned (Fig. 3). This was an effect of the original territory owner remaining on the territory following forest management before moving to a neighbor territory or dying: Four territories were never reoccupied after the death of both breeders, on 9 territories a breeder dispersed from the territory after the death of the partner and four pairs dispersed together after a territory became available in the neighborhood. All the dispersal of breeders aimed at improving NSI and breeders only moved to a new territory if the NSI there was higher than in their former territory (t_{50} = - 4.09; p < 0.0001).

As demonstrated above, forestry affected both breeding success and territory occupancy, factors that both contribute to the total population productivity. Thus, as expected, there was a significant decrease in productivity of the entire population (including unmanaged, managed, and abandoned territories) in the managed area; the average annual number of retained offspring (n = 34 territories) decreased by more than 50% from 21.80 to 9.18 offspring over the course of the study (χ^2 = 7.31; df = 1; p < 0.01). In contrast, the productivity of the study population in the pristine habitat (n = 17 territories) did not change during the same time period (nonsignificant increase from 8.17 to 10.00; χ^2 = 0.41; df = 1).

DISCUSSION

Our results demonstrate a strong effect of forestry-induced habitat alteration on breeding success, territory occupancy, and the total productivity of offspring in a population of Siberian Jays. Thinning, a standard forestry measure, had an especially devastating effect on breeding success and territory occupancy and thus on population productivity. Our study design allowed for a straightforward assessment of the consequences of forestry practices. Most previous researchers that have investigated the effects of habitat change on species abundance or species diversity have used a correlative approach (Trzcinski et al. 1999; Villard et al. 1999) and were unable to conclusively address the mechanisms that link forestry practices to population declines (e.g., Drapeau & Leduc 2000; Marzluff et al. 2000; Lampila et al. 2005). Consistent with our results, of the few other studies that have investigated experimentally the effect of forest structure on fitness components, all found a strong link between habitat correlates and fitness parameters (Suorsa et al. 2003, 2005). Suorsa et al. (2003) demonstrated that habitat patch size and forest volume surrounding the nests of Eurasian Treecreepers (*Certhia familiaris* L.) affected offspring condition. Treecreepers were unable to find enough food in small patches that contained few large trees, resulting in higher levels of physiological stress indicators. Based on these findings, Suorsa et al. (2005) were able to predict a critical threshold of timber volume (>152 m^3/ha) for successful reproduction.

We found strong effects of forest thinning and partial clearcutting, despite the fact that thinning only removes around 3% of the total timber volume (Loman 2005). Results of previous studies on Siberian Jays offer further understanding to the causal link between thinning and its consequence on various aspects of fitness. A recent experimental study on Siberian Jays investigated the perceived predation risk around the nest by exposing breeders to predator playbacks before the onset of breeding (Eggers et al. 2006). The results showed a strong link between habitat structure and predator avoidance, where Jays reacted to a perceived increase in the presence of predators by choosing denser nest sites and laying smaller clutches (Eggers et al. 2006). Because the main nest predators of Siberian Jays locate their prey visually (Carrion Crow [*Corvus corone* L.], Raven [*Corvus corax* L.], Eurasian Jay [*Garrulus glandarius* L.]; Ekman et al. 2001, Eggers et al. 2005a,b), dense habitat structure around the nest increases the probability of successful breeding. However, habitat structure interacts with predator abundance, and Siberian Jays can nest successfully in open habitat if the predator abundance is low (Eggers et al. 2005a). Forest structure is also a major determinant of yearling survival during their first winter, with individuals living in more open forest having a substantially higher risk of being taken by Goshawks (*Accipiter gentilis*), a visually oriented predator (Griesser & Ekman 2004; Griesser et al. 2006). Combined, the results of these studies indicate that an open forest structure adversely affects both reproduction and survival of Siberian Jays and suggest that thinning may ultimately endanger population size and viability (Eggers et al. 2005a).

Forestry practices had a negative effect on the occupation of territory by Siberian Jays. A reduction in territory quality through forestry practices caused breeders to abandon their territories, thereby reducing the productivity in the entire population. This pattern agrees with theoretical predictions stating that individuals should prefer environments that assure high survival and reproductive success (Fretwell & Lucas 1970; Orians & Wittenberger 1991) and abandon low-quality territories (Ekman et al. 2001). Based on these theoretical predictions, all occupied territories should be of good quality (Sergio & Newton 2003). In some Siberian Jay territories, however, territories are occupied continuously despite not having produced a single offspring for over 11 years (Ekman et al. 2001). Thus, using territory occupancy as a proxy to assess habitat quality may provide insufficient or even faulty information on breeding habitat quality.

The mechanism that links forest structure to the population productivity of Siberian Jays highlights the need for effective tools to assess habitat quality. Many researchers have used habitat structure data from digital maps (e.g., Suorsa et al. 2003, 2005) or very coarse-scale data on management history (Drapeau et al. 2000; Fort & Otter 2004; see Sallabanks et al. 2000 for review) to estimate the effects of habitat alteration on fitness components. Vegetation maps are generally generated at a coarse scale and may often lack the detailed information required to detect small changes in the forest structure. Without knowledge about the fine-grained structure of the forest, it may be difficult to assess the ecological value and the consequences of smaller-scale alterations on fitness components. Our results clearly highlight the negative effects of such fine-grained habitat alteration such as thinning. In Fennoscandia it is recommended that boreal forests be thinned at least 2-3 times per growth cycle (Hamilton 1982). These thinning procedures, however, are so far not considered in the forest certification guidelines of the Forest Steward Council (FSC), whose role is to create guidelines for sustainable forestry practices. Based on the effects of forest thinning demonstrated in this study, we believe that it is important to reassess standard management guidelines in order for forest certification to be biologically meaningful.

ACKNOWLEDGEMENTS

We thank F. and M. Lindgren for sharing their knowledge about the Jays and G. and I. Pavval for their hospitality at Lappugglan. D. Dowling, J. Faaborg, B. Hatchwell, J. Marzluff and A. Russell gave valuable comments on different versions of the manuscript. This study was supported by the Swedish Research Council (J.E), Formas (J.E.), the Swedish Environmental Protection Agency (J.E.), Stiftelsen för Zoologisk forskning (M.G.), C. F. Lilljewalchs resestipendium (M.G.), Stiftelsen Alvins fonds för fågelskydd (M.G., M.N.), Hiertas Minnesfonds (M.G.), Kungl. Skogs- och Lantbruksakademien (M.G.), Helge Ax:son Johnson Stiftlesen (M.N.) and the Swiss National Science Foundation (M.G.).

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Table 1. Repeated measures general linear models on a) the effect of forestry practices on the NSI (nesting success index) in territories located in managed and unmanaged forests; b) the effect of forestry practices on productivity of Siberian jays, measured as the number of retained offspring present.

a)

	df	*F*	*p*
Fixed effects			
Area	1.38	3.15	0.084
Before vs. after	1.39	12.34	0.0011
Management	2.38	3.90	0.029
Before vs. after * management	2.39	6.51	0.0036

Differences of least square means (before after comparisons)

Management	*estimate*	*SE*	*df*	*t*	*p*
None	0.079	0.05	41	-0.55	0.58
Thinned	0.36	0.15	41	2.38	0.022
Partially cut	0.47	0.12	41	3.99	0.0003

b)

	df	*F*	*p*
Fixed effects			
Area	1.47	0.89	0.35
Before vs. after	1.48	18.25	<0.0001
Management	2.48	2.57	0.087

Before vs. after *management	2.48	3.82	0.029

Differences of least square means (before after comparison)

Management	*estimate*	*SE*	*d.f.*	*t*	*p*
Unmanaged	0.10	0.08	48	1.18	0.24
Thinned	0.55	0.20	48	2.75	0.0083
Partially cut	0.47	0.15	48	3.19	0.0025

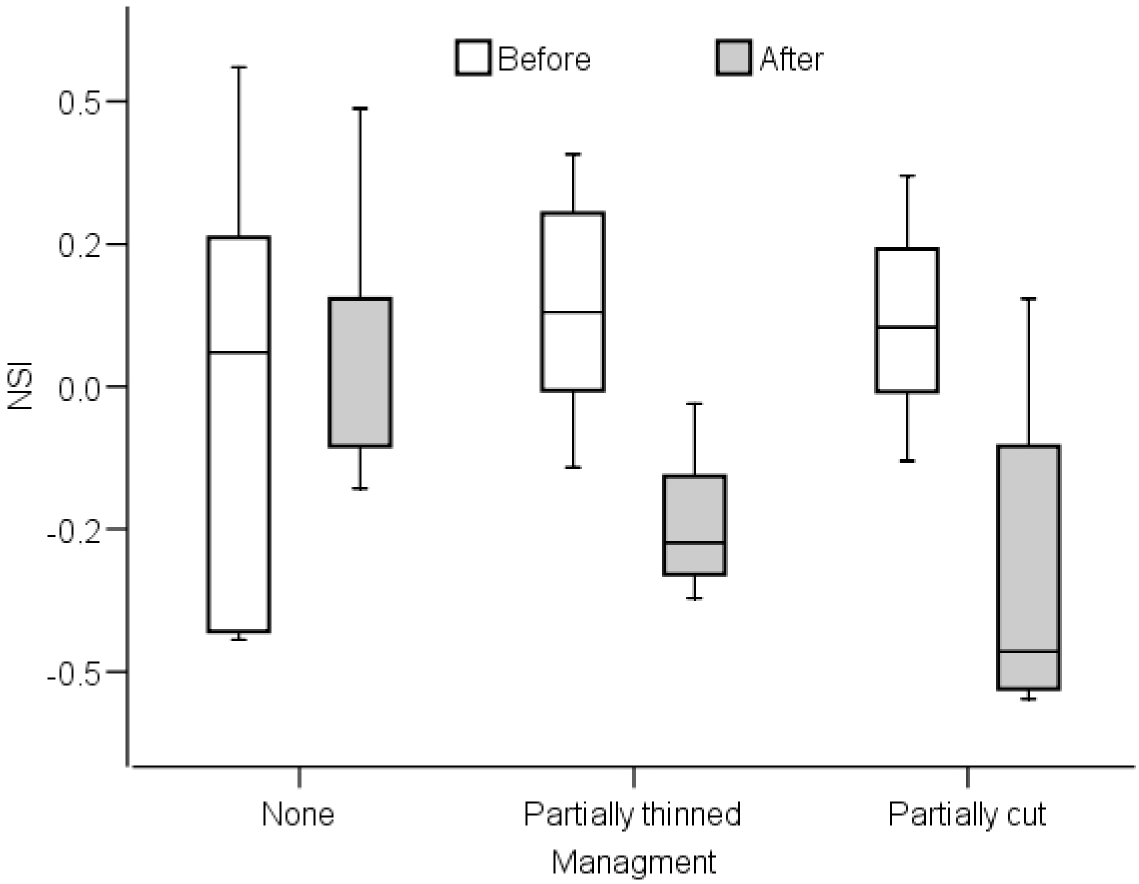
Figure legends

Figure 1. Effect of forestry practices (before and after) on nesting success index (NSI) (mean ± SE) of Siberian jays. Unmanaged territories were split in equal halves (see methods). The central line in all box plots shows the mean, the outer box the 25 and 75% quartiles, and the vertical lines the minimum and maximum values.

Figure 2. Annual number of retained Siberian Jay offspring produced per territory (mean ± SE) on unmanaged, thinned, and partially cut territories before and after management. Unmanaged territories were split in equal halves (see methods).

Figure 3. Effect of time since forest management on territory occupancy by Siberian Jays (Generalized Linear Mixed Model: Poisson distribution; logarithm link; years since management: Wald statistic$_1$ = 21.97, 4.69, $p < 0.0001$; NSI (nesting success index): Wald statistic$_1$ = 11.71, $p < 0.0001$; controlling for year and territory).

Figure 1.



Before
After
0.5
0.2
0.0
-0.2
-0.5
NSI
None
Partially thinned
Partially cut
Managment

Figure 2.

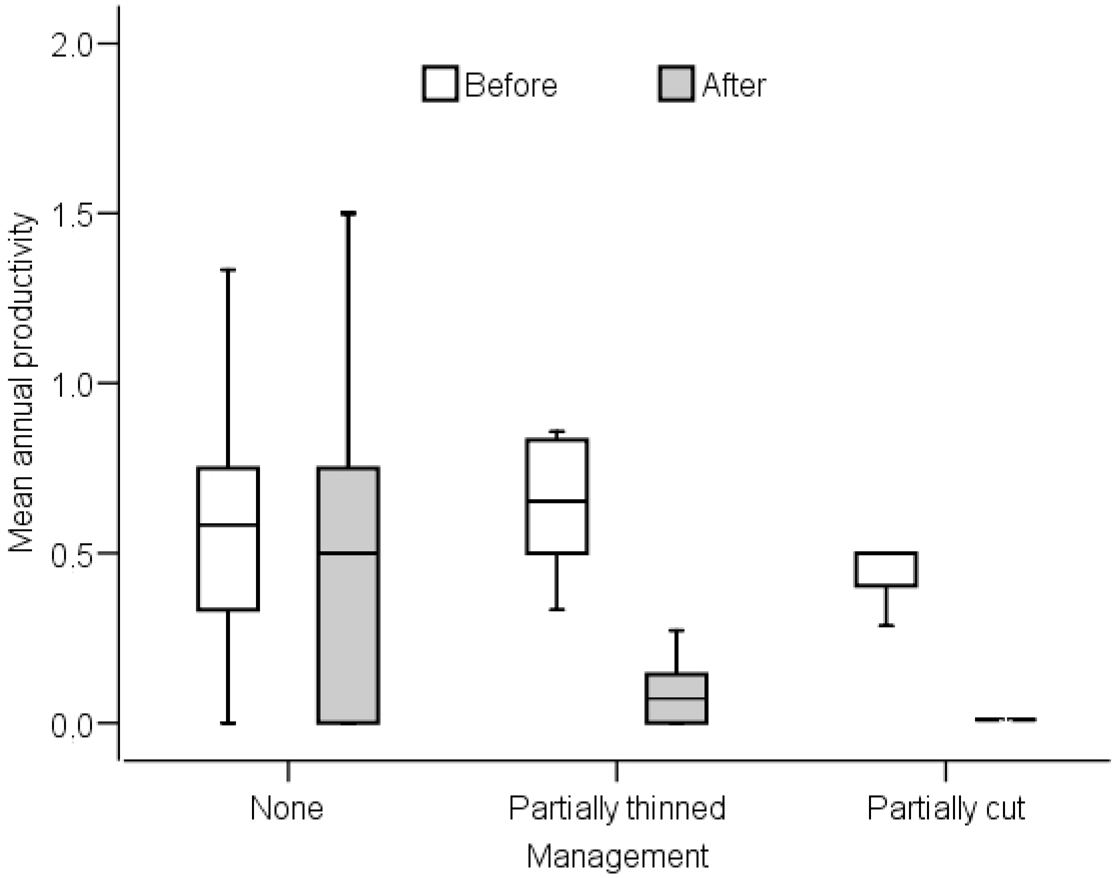
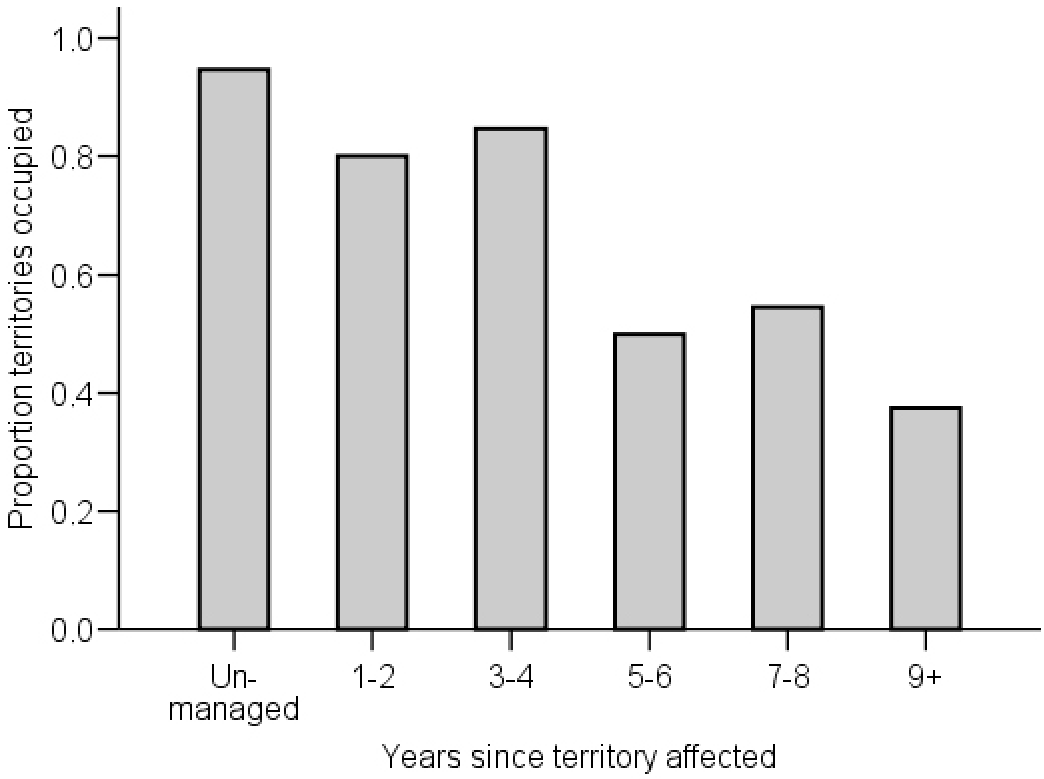

Before
After
2.0
1.5
1.0
0.5
0.0
Mean annual productivity
None
Partially thinned
Partially cut
Management

Figure 3.



1.0
0.8
0.6
0.4
0.2
0.0
Proportion territories occupied
Un-
managed
1-2
3-4
5-6
7-8
9+
Years since territory affected