Habitat use and habitat-specific behaviour of breeding female Eurasian kestrels (*Falco tinnunculus*) in a peak vole year in the boreal forest.

Habitatseleksjon og habitat-spesifikk adferd hos hekkende tårnfalkhunner (*Falco tinnunculus*) i et smågnagerår i barskog.

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Preface

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Abstract

I used radio telemetry to study the habitat use and habitat-specific behaviour of six female Eurasian kestrels (*Falco tinnunculus*). The field work was conducted in Trysil municipality, south eastern Norway, during the breeding season of 2011, a peak vole year. The study was conducted in a boreal forest area which also contained large areas with bog. A total of 374 plots were used in the analysis. I found that the female kestrels preferred using open habitats, edges and roads. A preference for bog without forest was found both through analysis of distances to habitats and habitats in buffer zones. The kestrels had an aversion regarding both distance to, and proportion of coniferous forests within buffers. Larger distances to water were preferred. Unproductive forest land and highest available ranked forest land were preferred in buffer zones, while lowest available ranked forest land, agricultural areas and settlements were avoided within buffer zones. Preferred habitat characteristics while perching was forested areas, the poorest and richest soil available, and forestry class II. The preference for bog is in accordance with previous findings in a low vole year. The aversion for agricultural areas is in contrast to most previous studies of the habitat use of the kestrel, but may be explained by the high vegetative cover in these areas during the field observations.

Sammendrag

Radio-telemetri ble brukt til å studere habitatseleksjon og habitat-spesifikk adferd hos seks tårnfalkhunner (*Falco tinnunculus*). Feltarbeidet ble utført i Trysil kommune, i sørøst Norge, i hekkesesongen 2011, et smågnagerår. Studien ble utført i et barskogområde som også omfattet store myrområder. Totalt 374 observasjoner ble brukt i analysene. Jeg fant at tårnfalkhunnene prefererte åpent habitat, kantsoner og veier. Både gjennom analyse av avstand til habitat og andel habitat i buffer fant jeg en preferanse for myr uten skog. Tårnfalkene unngikk barskog, både med tanke på avstand og andel i buffer. Impediment og jord med høyest tilgjengelige bonitet ble preferert i buffersoner. Lavest tilgjengelige bonitet, jordbruksområder og bebyggelse ble unngått i buffersonene. Når tårnfalkhunnene hadde sittpost foretrakk de å sitte i skogområder, i lavest og høyest klassifisert bonitet og hogstklasse II. Preferansen for myr er i samsvar med tidligere funn i et dårlig smågnagerår. At tårnfalkhunnene unngikk jordbruksområder stemmer ikke overens med de fleste funnene i tidligere studier av habitatseleksjon hos tårnfalk, men kan muligens forklares av den tette vegetasjonen i disse områdene under feltobservasjonene.

Contents

1. Introduction

A habitat is the place where an organism lives, and every habitat provides many different niches, so that several species can live in, and use, one habitat (Begon et al. 2006). Habitat use is the manner in which habitat is used by a species or an individual to meet its life requirements (Block & Brennan 1993). Habitat selection, or habitat preference, is innate and acquired behavioural responses to various aspects of a habitat, possibly giving a disproportional use of that particular habitat, influencing the survival and fitness of the individual making the selection (Block & Brennan 1993).

According to optimal foraging theory, a predator should forage in patches which maximize its feeding efficiency. In order to find the most optimal patches, the predator should sample different patches within its territory, and limit the foraging activity to patches which gives the highest feeding efficiency (Barnard 2004).

Studies of raptors have shown that the vegetative cover in the foraging habitats can have a negative correlation with the use of, or the proportion of, prey captured in these habitats (Southern & Lowe 1968; Bechard 1982). The northern goshawk (*Accipiter gentilis*) appears to not choose foraging habitat based on prey abundance, but rather prey availability, where prey availability is defined by favorable habitat where prey can be found above a minimum threshold (Beier & Drennan 1997). Prey abundance has been suggested to be less important than the vegetative cover when the swainson's hawks (*Buteo swainsoni*) choose their foraging sites (Bechard 1982). Baker and Brooks (1981) found a similar tendency for the red-tailed hawk (*Buteo jamaicensis*) and the rough-legged hawk (*Buteo lagopus*); these were found more often in areas where there was a large abundance of food, but they were found to be more abundant in habitats which had less vegetative ground cover. On the other hand, Widén (1994) found no correlation between the vegetative cover in clear cuts and number of observations of the two raptor species he studied, namely the common buzzard (*Buteo buteo*) and the Eurasian kestrel (*Falco tinnunculus*).

The Eurasian kestrel, hereafter called kestrel, is a relatively small raptor, with a body mass of c. 200 g (Cramp 1980). The female is somewhat larger than the male (Cramp 1980). It has a relatively long tail and long wings, with a wingspan of 71-80 cm (Cramp 1980; Village 1990). This feature makes the kestrel easy to recognize when it perches. Further, the kestrel is also easily recognized by its hunting behaviour where it frequently hovers above hunting grounds, and the red-brown colour of its back makes it conspicuous (Village 1990).

The kestrel is the most common diurnal raptor in much of the western Palearctic (Cramp 1980). However, the population fluctuates as a response to rodent populations and as an effect of harsh winters. In some areas the population has also decreased because of the extensive use of pesticides (Cramp 1980). Furthermore, the kestrel is mainly a migratory bird in the northern and eastern parts of its range. In other parts of Europe it is partially migratory or dispersive (Cramp 1980).

The kestrel has a rather distinct habitat preference; i.e. it prefers open habitats such as moorlands, bogs and clear cuts (Village 1990; Løken 2009). One reason is its hunting strategy, which requires open habitats where the kestrel can easily obtain a good overview of the area (Village 1990). However, kestrels can be found in a wide range of habitats (Cramp 1980). Village (1990) explained the habitat diversity of the kestrel as a function of its diverse diet, which in Northern Europe consists of rodents, birds, lizards, insects and earthworms amongst others. However, the diet of kestrels consists mainly of *Microtus* spp. voles (Village 1990).

A study of the Eurasian kestrel has found individual preferences for different prey, and there was findings suggesting that these preferences were not necessarily an effect of prey abundance, but possibly a result of individual hunting efforts and skills (Costantini et al. 2005). However, the study of Costantini et al. (2005) also indicated that the kestrel take the locally more plentiful prey species.

Most raptors that hunt ground-living prey use a “pause-travel” tactic when foraging (Sonerud 1992a and references therein). Studies of raptors have shown that there is a positive relationship between the use of clear cuts and available perches (Sonerud 1985; Widén 1994). Widén (1994) found that the use of clear cuts by the common buzzard and the kestrel was reduced if there were no perches available in the clear cuts. For the red-tailed hawk in Oregon, USA, prey availability may be more important to the reproductive success than the prey abundance *per se*; reproductive success was correlated with the number of available perches in the territories of the studied individuals (Janes 1984).

Hunting from perches requires relatively little energy, and is a hunting technique the kestrels use most frequently in the winter, when they only need to provide food sufficient to support their own survival (Village 1990). In the summer, the most frequent hunting technique is flight hunting, but the switch from perching to flight hunting is more prominent in the males than females (Village 1990).

Whereas several studies have been done on the kestrel's use of agricultural land and on the interactions between this use and the abundance of prey (e.g. Pettifor 1984; Village 1990; Aschwanden et al. 2005; Butet et al. 2010), few studies have investigated the foraging habitats of the kestrel on a more general basis. In a mountainous region in Spain during the autumn-winter period the kestrel had a preference for areas with larger proportions of open areas occupied by scrubland and pastureland (Tapia et al. 2008). In England kestrels had a preference to forage in cut grass areas, despite the fact that this habitat constituted rather small proportions of the observed foraging range (Garratt et al. 2011).

This study was designed to identify the use of habitats by the kestrel and its habitat-specific behavioural activity during the breeding season in Norway, using radio-telemetry. To my knowledge, I am the first to study the habitat use of female kestrels in a boreal forest with this method. I aimed to answer the following questions: 1) Does the kestrel prefer open or closed habitats? Does it prefer edges? 2) Which habitats are preferred, and which are avoided? 3) Which soil productivity classes are preferred, and which are avoided? 4) Are there any behavioural activity that are used more or less in any of the habitats, soil productivity classes, or forestry classes? 6) Are there any differences between pre- and post-fledge habitat use?

2. Methods

2.1 Study area

The field work was performed in Trysil municipality, Hedmark county, south eastern Norway, during the breeding season of 2011, from the middle of June until the end of July, where 2011 was a peak vole year (Geir A. Sonerud, unpubl. data). The study area (61°38´-61°56´ N; 12°23´-12°33´ E) is found in the northern- and mid- boreal zone (Moen 1998), and consists mainly of coniferous forest comprising five different age classes, from clear-cuts to mature forest (Figure 1). In addition there are many large bogs in the study area.

Six locations were used during the field work; Bryn, Flenvoll, Tørråsen, Husfliden, Storflendammen and Storfallet. The nests studied were not chosen entirely at random because logistical reasons made it necessary to have some limitations. Thus the nests chosen for observations were relatively close to forest roads as to make them easily accessible. Further, we attempted to not use nests located near rivers and other large obstacles to avoid problems with the kestrels flying over to the other side to hunt, where we would be unable to follow. Avoiding rivers turned out to be difficult, because there is a fairly large river running along large parts of the study area. Thus, at two of our six nest locations there was a river that was frequently crossed by the tagged birds. At the first (Storflendammen) there was a small bridge where the observers could cross. At the second (Tørråsen) the observers used a rubber boat, and a handmade rope bridge attached to the boat, to cross the river.

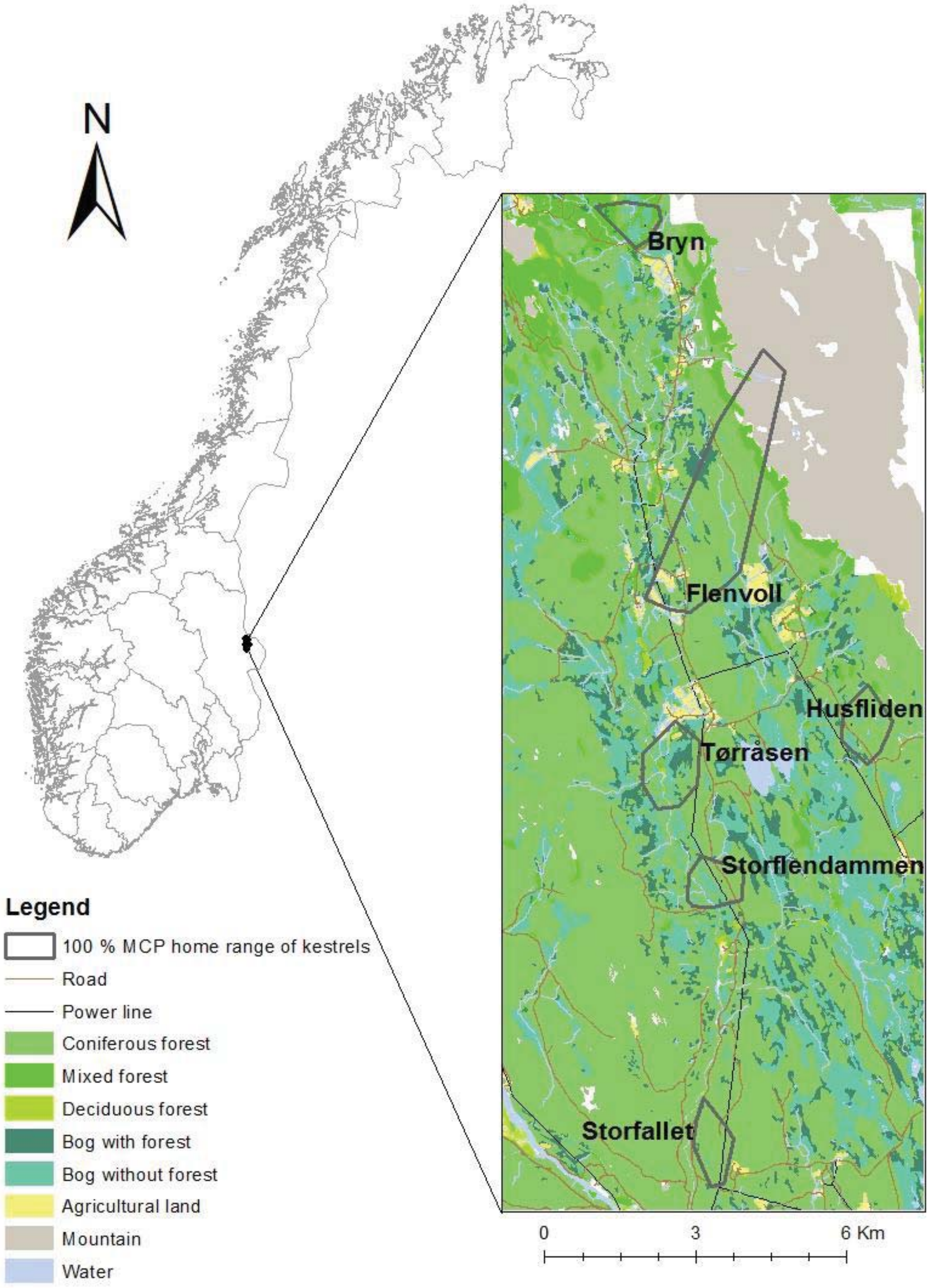

Figure 1. The study area, mainly consisting of coniferous forest, with 100% MCP home ranges outlined.

2.2 Trapping and tagging

The female kestrel starts helping the male with the food provisioning when the nestlings are approximately ten days old (Village 1990). Further, the peak in rate of prey mass delivered at the nests of kestrels occur when the nestlings are 17 days (Steen et al. 2012). Thus, to obtain representative data of the habitat use of the female kestrel, we tagged the female kestrels when the nestlings were around two weeks old, because the female would be hunting during the period of tracking, and the rate of food provisioning would be high.

We trapped six female kestrels and equipped them with a radio transmitter. Five of the females were captured in a tunnel trap mounted on the nest box. The kestrel nests were in nest boxes, and the trap was a rectangular, short tunnel with a swing-door trap. The trap was mounted on the outside of the entrance. When the female entered the nest box with prey for the nestlings, she passed the swing-door, which fell down behind her. The female was thereby enclosed in the nest box. The trap was kept under continuous surveillance from a hide which was placed approximately 15-30 m away from the nest. A trigger connected to the trap was placed in the hide, and was used to release the swing-door when the kestrel entered the nest box. The female was then removed from the nest box immediately after trapping.

At some of the nests we placed a bal-chatri trap at the same time as the swing-door trap was mounted on the nestbox. This trap was also kept under continuous surveillance from a hide or a car. The bal-chatri is a cage made of chicken wire (approximately 40cm x 30cm x 20cm) with a double wall, and a small rodent (dwarf hamster, *Phodopus campbelli* and *P. roborovskii*) inside, posing as prey. In total, six dwarf hamsters were used in the trapping attempts. On the outside the cage was equipped with many small hangman knot loops of thin nylon thread (fishing line) (Berger & Mueller 1959). One of the females was captured by use of a bal-chatri trap. When the kestrel landed on the cage to catch the rodent inside the cage, its talons was trapped in the loops. The kestrel was removed from the trap immediately after capture. Outside of the trapping attempts, the hamsters were treated as pets.

The radio transmitter was of the type TW-4 from the Biotrack company in England, and weighed approximately 3 g. The female kestrel weighs c. 200 g, so the radio transmitter is equivalent to approximately 1.5% of the body mass of the bird to which it was attached. The transmitter was mounted at the base of one of the mid tail feathers, with the antenna pointing backwards along the tail feathers. The transmitter was first glued on to the feather with super glue, and then sewn on (Figure 2). This is a standard attachment method for radio transmitters on kestrels in particular, and on diurnal raptors in general (Kenward 1978; Village 1990). The advantage is that the transmitter is shed when the tail feathers are moulted in late summer. The method was also successfully employed on three male kestrels in Trysil in 2008 (Løken 2009).

Figure 2. Radio-tagged female kestrel at the location Storfallet.

2.3 Radio-tracking

Each female was tracked irregularly during the weeks following tagging. The reason why the birds were not tracked continuously was that the spring was very early in 2011, and the food was abundant. Hence, the kestrels had started breeding early, and at the time when we started our attempts to trap them, a large portion of the kestrels in the area had come too far in their breeding for us to observe them. Thus, the kestrels had to be trapped within a short time period. To make sure we had data on all the females before they lost their tag, or in case of transmitter malfunction, we had to carry out the tracking at the different nests irregularly. The tracking corresponded with the video monitoring that was being executed following tagging (Støvern 2012). Each time a tagged kestrel was encountered, a number of data was noted on a registration form.

2.4 GIS

To analyze the habitat selection of the kestrel I used ArcGIS Desktop 10.0 (ESRI 2010) to examine information about the habitats in the study area. I added an area resource map (AR5) (Norwegian Forest and Landscape Institute 2011) for Trysil into ArcGIS to obtain the specific habitat information I needed. Because most of the information in the AR5 map is included in a single shape-file I had to create separate shape-files for the individual habitats. This was done using the "select by attributes function" where I selected the attributes for the individual habitats, as characterized in the cartography for AR5 maps (Bjørkelo et al. 2009). The habitats reclassified from the AR5 map were agricultural land (habitat type 21, 22, 23), bog with forest (habitat type 60; tree type 31, 32, 33), bog without forest (habitat type 60), coniferous forest (habitat type 30; tree type 31), mixed forest (habitat type 30; tree type 33) and deciduous forest (habitat type 30, 32). In addition I created a layer for mountain (habitat type 50) (Norwegian Forest and Landscape Institute 2012), using an AR50 map (Norwegian Forest and Landscape Institute 2011). Water polygon, water line, road polygon, road line and power line was pre-separated as individual layers in AR5 and was included in the analysis without further adjustments. Thus, I used a total of 12 different habitat categories for the further analysis.

To obtain information on the available habitat in the study area I generated 100 random plots in all of the home ranges, by using the sampling tool "generate random points" in the extension program "Hawth's Analysis Tools" (Hawthorne 2010) for the ArcGIS 9.3. version (ESRI 2009). The home ranges were estimated as 95% minimum convex polygons (MCP), and were provided by Sari Cunningham. I chose 95% MCP's to get a conservative analysis of the habitat use (cf. Strøm & Sonerud 2001; Smedshaug et al. 2002). In the further analysis, the random plots were regarded as response 0, whereas the observed plots were regarded as response 1.

All plots, both observed and random, were added to ArcGIS 10.0 where I extracted information on the distance from every plot to the habitats. This was done using the join function, where each point was given the attributes of the line that was closest to it, for each of the 12 individual habitat categories for which I had layers.

ArcGIS was also used to create buffer zones around all plots. This buffer had a radius of 25 m and thus, a total area of 1963 m^2. Within each buffer, the amount of various habitats was estimated using the tools "intersect" and "dissolve" in ArcGIS. It was not possible to use these tools on some of the habitat variables. Thus, the ones included in this analysis were agricultural land, bog with forest, bog without forest, coniferous forest, mixed forest, deciduous forest and mountain.

A separate analysis was also done with the buffer zones, where the amount of productivity classes within the buffer zones was estimated. The productivity classes are commonly used to indicate the productive ability of the soil. The productivity classes represented in the study area were unproductive forest land, low productivity, medium productivity, and agricultural areas and settlements.

2.5 Statistics

Statistical analyses were performed with the software R version 2.13.2 (R Development Core Team 2011).

Six different analyses were done to evaluate if the kestrel had any preferences or aversions for any of the habitat variables in the study area, and to analyze the kestrel's behaviour in the various habitats. The analyses considered 1) distance to open and closed habitat, 2) distance to habitat, 3) habitat in buffer, 4) productivity class in buffer, 5) behaviour in habitats, and 6) comparison of pre- and post-fledge habitat use.

Data

In the analysis only plots of the female were included. Plots of the female on the nest and range plots were not included. Range plots was defined as plots made of the kestrel without visual contact, or plots where the kestrel had been so far away from the observer at the time of the observation that it would be difficult to establish the habitat of the plot with certainty. At one of the locations (Tørråsen), observations from the first two days of tracking were excluded because I suspected an abnormal behaviour. During the tracking on these two days, the female only moved very short distances, and had very long periods of perching (up to 99 minutes). I suspected that her behaviour was affected by the hide that had been placed in the vicinity of the nest to observe prey deliveries. Therefore, the hide was removed for the rest of the tracking period at this specific location.

A total of 374 plots were sampled at the six locations pre-fledge (number of plots at each locality in parenthesis): Bryn (97), Flenvoll (36), Tørråsen (58), Husfliden (93), Storflendammen (57), and Storfallet (33). For the analysis of habitat use, one plot included in the analysis, from the locality Storflendammen, was an observation made prior to tagging the bird. However, because only one out of 374 plots was recorded prior to tagging, the effect of this plot on the analysis would be negligible.

Distance to open and closed habitat

The frequency of distance to open and closed habitat was examined. The number of observations was 488, and included observations of the female both pre- and post-fledge. Open habitats were defined where the distance between individual trees was longer than the height of the trees at the plot. Closed habitats were defined where the distance between individual trees was shorter than the height of the trees at the plot. During the field work we restricted the distance to open and closed habitat to 100 m. If the distance was larger we characterized it as 100+. In the histograms distances characterized as 100+ were pooled with the distance 100 m. If a plot was characterized as edge, or as open to dense, and the distance to open and closed habitat was missing, I corrected the distance to 5 m to both open and closed habitat.

Distance to habitat

To find the most appropriate model to analyze distance to habitats I first created a general linear mixed model (GLMM) using the “lmer” function in the package “lme4” (Bates et al. 2011) in R, where all the variables were included. The model included kestrel ID as random variable, to control for individual differences. Using this model I used backward selection based on the p-values of the individual variables. I removed the variable with the highest p-value in the model, ran the model again, and repeated this until all the variables in the model had a significant p-value ($p<0.05$). Using the same data I also created a correlation-matrix where all the variables were included. From this matrix I chose which variables to include in a separate Akaike information criterion-analysis (AIC) to find the most appropriate model to explain the variation in habitat use. The variables were chosen so that none of those included in the AIC-analysis were intercorrelated. I set the limit for intercorrelation at 0.5, and if the correlation was higher than this between two variables, they were regarded as intercorrelated.

In the analysis of distance to habitat the ratio n/K, where n is sample size and K is number of parameters, was relatively large (>40). Thus, I chose to look at ΔAIC (Burnham & Anderson 2002), and selected a model on the basis of this. If ΔAIC is ≤ 2 the level of empirical support of the model is substantial (Burnham & Anderson 2002). Based on the principle of parsimony

(Burnham & Anderson 2002) I chose to move further with the candidate model which had ΔAIC $\leq$2, and at the same time had the fewest variables included.

Using the formula for logistic regression,

$$E(y) = \frac{e^y}{1 + e^y}$$

$$where\ y = \beta_o + \beta_1 x_1 + \beta_2 x_2 + . \ldots + \beta_k x_k$$

β_0 is the intercept, and β_1, β_2 … β_k is the regression coefficients of x_1, x_2… x_k respectively (Montgomery et al. 2006), I estimated values that could be used to generate figures to illustrate the effect of the various habitats. From the best model I used the estimates for the variables and the intercept as inputs in the formula. Furthermore, the formula for logistic regression was also used to transform the estimate of nest ID to find the line for the expected probability of a random distribution in the analysis of distance to habitat, proportion of habitat in buffer zones, and proportion of productivity classes in buffer zones, i.e. to find the dotted line in Figure 4, Figure 5 and Figure 6.

Habitat and productivity class in buffer

A separate analysis was done to analyze if the proportion of the individual habitat types and productivity classes in a buffer-zone around plots had an effect on the kestrels presence. The areas of the various habitat types and productivity classes within the buffer zones are not independent, because the area within the buffer is constant at 1963 m^2. Thus, if the area of one variable decreases, the area of the other variables will increase. Therefore it was not possible to do backward selection and AIC-analysis on the proportion of habitat and productivity class. Thus, to analyze the effect of amount of habitat within the buffer zones I looked separately at those variables for which $p < 0.05$ in general linear mixed models. The estimates for intersect and the variable was used in the formula for logistic regression to estimate values for the proportion of the individual variables in the habitat. This was done without including the other variables into the formula because the result would be erroneous due to the fact that the values of the variables are not independent.

Behaviour

In a separate analysis of behaviour I tested if there was any trend for the kestrel to use a specific type of behaviour in a specific habitat, productivity class or forestry class. The data used in this analysis was solely based on data collected during the field work, to obtain a clearer impression of the habitat in the specific points where the kestrel had been plotted. As the behaviour was analyzed, it would be useful having the specific habitat in the plots to be able to pinpoint if there was any small habitat characteristics affecting the specific behavioural features. The behaviour was divided into four categories (number of plots in behaviour category indicated in parenthesis), namely perching (214), flying (82), hovering (32), and prey capture (14). The latter may include both attempts of prey capture and actual prey capture.

In the analysis of behaviour, general linear mixed models were used. All the habitat variables that were included in the three separate habitat analyses (see above) were included, to test if any of the variables were significantly different from any of the other ones. In order to get the transformed estimates, I used the formula for linear regression. For prey capture there are some habitat variables that are not represented. Thus, they are not included in the prey capture analysis. Nest ID was included as random effect, and the figures for the analysis of behaviour was made using SigmaPlot (SPSS 2008).

The habitat and soil productivity ability was classified using Fremstad (1997) and Larsson & Søgnen (2003). The habitats were classified as (number of plots in each habitat category indicated in parenthesis): coniferous forest (172) (dominated by spruce (*Picea abies*) and pine (*Pinus sylvestris*)), mixed forest (21) (dominated by spruce, pine, birch (*Betula pubescens*) and other deciduous trees), deciduous forest (2) (dominated by birch and other deciduous trees), bog with forest (53) (dominated by pine), bog without forest (76), mountain (5), water (5), road/power-line (5) and agricultural land (5). The habitat categories water, deciduous forest, mountain, road/power-line and agricultural land had too few plots to provide a meaningful test, and they were excluded from the further analysis of behaviour.

The productive ability of the soil was divided into four classes, based on what was available in the study area (number of plots in each productivity class indicated in parenthesis). Class one was designated where the ground vegetation was dominated by species indicating very poor soil (54) (e.g. lichen (*Cladonia spp.*), cowberry (*Vaccinium vitis-idaea*), and heather (*Calluna vulgaris*)). Class two was designated where the ground vegetation was dominated by species indicationg poor soil (37) (e.g. cowberry, crowberry (*Empetrum nigrum*), heather, and bog bilberry (*Vaccinium uliginosum*)). Class three was designated where the ground vegetation was dominated by species indicating medium soil (105) (e.g. blueberry (*Vaccinium myrtillus*), wavy hair-grass (*Deschampsia flexuosa*), and horsetail (*Equisetum spp.*)). Class four was designated where the ground vegetation was dominated by species indicating relatively rich soil (32) (e.g. herbs, raspberry (*Rubus idaeus*), and juniper (*Juniperus communis*)).

The forestry classes were divided using a Norwegian age system commonly used in forestry. The classes range from I (clear cut) to V (mature forest). The number of plots in each of the forestry classes was 16, 66, 31, 26 and 52, respectively.

For a complete overview of the number of observations used in the final analysis, of the behavioural categories, and the specific number of observations of these in the various habitats, productivity classes and forestry classes, see Appendix 1.

In the field, the habitat characteristics were roughly identified, and were processed further after the field work was completed. Some adjustments were then made: 1) If a plot was indicated as natural forest, that is, forestry had not been visibly performed in the plot (the forest would then have to have been > c. 100 years old), it was still registered as forestry class V to indicate that it was a mature forest. 2) Bog with forest was registered as forestry class "na". 3) Forestry classes indicated as III-IV was registered as III, and forestry classes indicated as IV-V was registered as V, to mark that a forest indicated as III-IV is younger than a forest indicated as IV-V. 4) Bog with forest was registered as productivity class 1. 5) Bog without forest was registered as productivity class "na".

At first I made a dataset with two columns for each of the three habitat variables. If a plot was in an edge, the open habitat would be plotted in the first column, and the closed habitat would be plotted in the second column. If, on the other hand, the plot was not an edge plot, the habitat plotted in the two columns would be equal. In the further analysis I could only have one value for each habitat variable for each plot. Thus, where there were two different values given for one plot, I decided which value to use in the analysis from a coin toss.

Post-fledge

For two of the locations, Storflendammen and Tørråsen, data were also collected post-fledge. Habitat availability is not constant post-fledge, because the birds may move over a larger area than when they are bound to the nest. Thus, it was not possible to do the same kind of analysis for the post-fledge data as for the pre-fledge data. To get an impression of the habitat use post-fledge I created a percentage frequency distribution of distance to habitat pre- and post-fledge separately in the two locations. Both random and observed plots were included in the post-fledge analysis. The percentage frequency distribution was done using the “Hist” function on the package “Rcmdr” (Fox et al. 2012) in R. For the results of the percentage frequency distribution, see Appendix 2.

I looked specifically at the four habitats that I had used in the pre-fledge analysis of distance to habitat, because these were the ones that appeared to explain the variation in distance to habitat best. There were 94 plots used for the post-fledge analysis, 42 plots at Tørråsen and 52 plots at Storflendammen.

To test if the effect of distance was different between the two stages pre- and post-fledge I looked at the interaction term between distance and stage and tested if the slopes of the regression line for the two stages were significantly different from each other. The interaction term was removed from the model when it was not significant, whereas I only looked if there was a difference between the two stages considering the intercept (i.e. whether the regression lines for pre- and post-fledge was higher or lower from each other). These tests were done using a general linear mixed model. Nest ID was included as random variables.

2.6 Ethical note

Permission to conduct trapping, handling, tagging and follow-up of all radio-tagged individuals has been given by the Directorate for Nature Management and the National Animal Research Authority of Norway, and all procedures was conducted in accordance with the ethical standards provided by these two entities.

3. Results

3.1 Distance to open and closed habitat

Most plots of the female kestrels were < 10 m from open habitat (Figure 3a). The number of plots < 10 m from closed habitat was similar to that > 90 m from closed habitat (Figure 3b). Because the segment > 90 m includes distances > 100 m this pattern suggests that the kestrel either has a tendency to avoid closed habitats, or a preference for open habitats and edges, because plots in edges would give distances of < 10 m to all habitats.

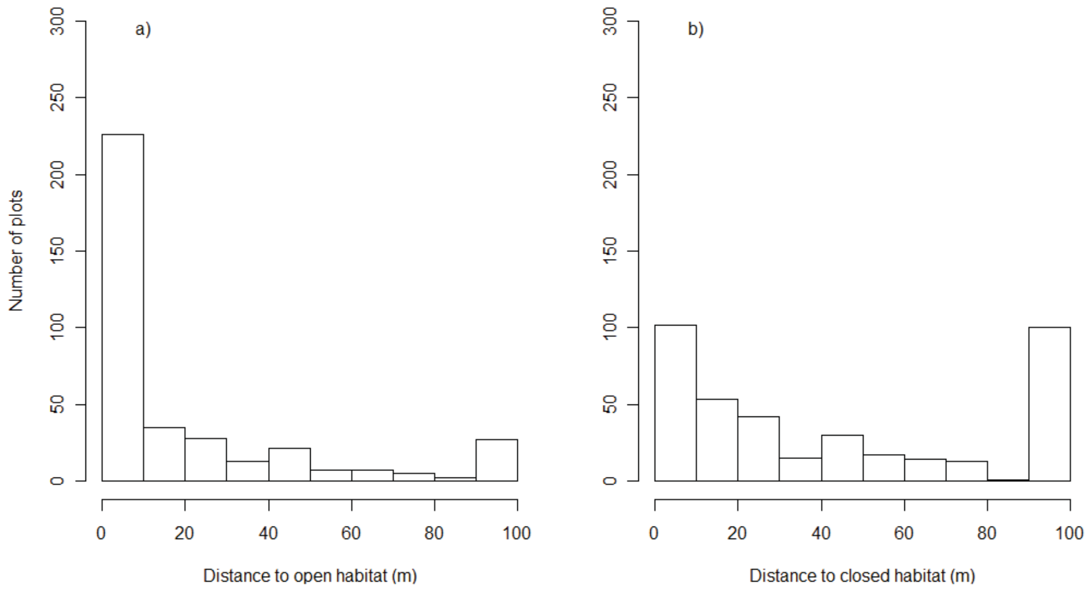

Figure 3. Frequency distribution of distance to open and closed habitat based on 488 plots of six radio-tagged kestrels. a) Distance to open habitat, and b) distance to closed habitat.

3.2 Distance to habitat

Four variables were included in the model for distance to habitat based on backward selection; bog with forest, coniferous forest, water indicated as polygon and road indicated as polygon. It was conflicting to choose whether to include road polygon or road line, because these two were intercorrelated (Table 1), but at the same time not correlated to any of the other variables that were included. Based on the results from the backward selection I chose to include road polygon, because this was most suitable in the previous model. The same applies for water polygon and water line. The variables included in the AIC-analysis (Table 2) were agricultural land, bog with forest, bog without forest, coniferous forest, mixed forest, road polygon and water polygon.

Table 1. Correlation matrix for the variables with distance to habitats.

	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)	(11)
(1) Agricultural land											
(2) Bog with forest	-0.048										
(3) Bog without forest	-0.355	-0.278									
(4) Coniferous forest	0.223	-0.058	-0.329								
(5) Deciduous forest	-0.784	-0.219	0.518	-0.243							
(6) Mixed forest	0.073	-0.127	-0.027	0.167	-0.073						
(7) Mountain	-0.493	-0.197	0.600	-0.248	0.734	0.146					
(8) Water polygon	0.380	0.171	-0.136	-0.060	-0.318	-0.146	-0.100				
(9) Road polygon	-0.256	-0.238	0.121	-0.243	0.327	-0.040	0.139	-0.028			
(10) Road line	0.174	0.261	-0.056	0.156	-0.239	0.048	-0.079	0.161	-0.806		
(11) Power line	-0.220	-0.434	0.507	-0.313	0.518	0.342	0.747	0.064	0.162	-0.074	
(12) Water line	-0.125	-0.334	-0.211	0.085	0.197	-0.068	-0.011	-0.521	0.130	-0.165	0.068

In accordance with the principle of parsimony, the best model included bog without forest, coniferous forest, water polygon and road polygon (Table 2, Model 1).

Table 2. The top 20 models with lowest ΔAIC from the AIC-analysis of distance to habitats.

Model	Variables	AIC	Δ AIC
1	Bog without forest+Coniferous forest+Water +Road	1242.754	0
2	Bog with forest+Bog without forest+Coniferous forest+Water +Road	1243.978	1.223
3	Agricl. land+Bog without forest+Coniferous forest+Water +Road	1244.452	1.698
4	Bog without forest+Coniferous forest+Mixed forest+Water +Road	1244.626	1.871
5	Agricl. land+Bog with forest+Bog without forest+Coniferous forest+Water +Road	1245.149	2.395
6	Bog with forest+Bog without forest+Coniferous forest+Mixed forest+Water +Road	1245.824	3.070
7	Agricl. land+Bog without forest+Coniferous forest+Mixed forest+Water +Road	1246.458	3.703
8	Bog without forest+Coniferous forest+Road	1247.085	4.330
9	Agricl. land+Bog with forest+Bog without forest+Coniferous forest+Mixed forest+Water +Road	1247.103	4.348
10	Agricl. land+Bog without forest+Coniferous forest+Road	1247.608	4.853
11	Agricl. land+Bog with forest+Bog without forest+Coniferous forest+Road	1247.690	4.936
12	Agricl. land+Bog without forest+Coniferous forest+Mixed forest+Road	1248.042	5.287
13	Agricl. land+Bog with forest+Bog without forest+Coniferous forest+Mixed forest+Road	1248.070	5.315
14	Agricl. land+Coniferous forest+Mixed forest+Road	1248.426	5.671
15	Agricl. land+Bog with forest+Coniferous forest+Road	1248.434	5.679

The probability of a plot being of the kestrel rather than random increased with distance from coniferous forest and with distance from water polygons, and decreased with distance from bog without forest and with distance from road polygons (Table 3, Figure 4). The parameter estimates in Table 3 has been used in these figures. The kestrels preferred to be < 140 m from bog without forest and < 293 m from road, and > 20 m from coniferous forest and > 265 m from water (Figure 4). For estimated figures for minimum and maximum values of this analysis, see appendix 3.The difference is that the constant values that have been used in the formula for linear regression has been the minimum, mean, and maximum values for the variables.

Table 3. Parameter estimates for variables in the model of distance to habitats.

	Estimate	SE	z	p
(Intercept)	-0.3132	0.1996	-1.57	0.117
Bog without forest	-0.0023	0.0005	-4.45	< 0.0001
Coniferous forest	0.0050	0.0012	4.03	< 0.0001
Water polygon	0.0011	0.0004	2.52	0.012
Road polygon	-0.0012	0.0004	-3.33	0.001

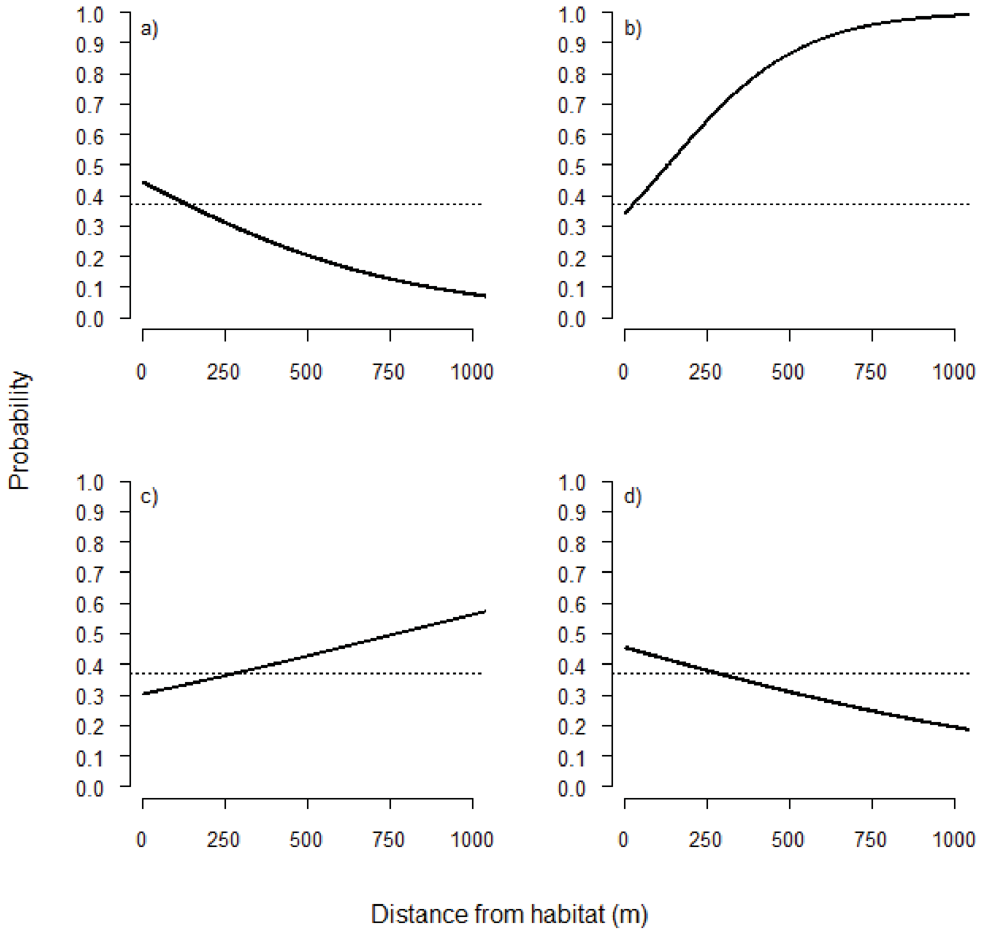

Figure 4. Probability of a plot being of a kestrel rather than random as a function of distance to the four habitats a) bog without forest, b) coniferous forest, c) water polygon and d) road polygon. Based on the parameter estimates in table 3, and mean values of the habitats used in the analysis. The dotted line indicates expected probability of a random distribution.

3.3 Habitat in buffer

Two habitats had a significant effect on the probability that a plot in a buffer was of a kestrel rather than random; bog without forest and coniferous forest (Table 4, Figure 5).The kestrel preferred to be in buffer zones with > 253 m^2 bog without forest, and < 105 m^2 coniferous forest. When the area of coniferous forest in the buffer exceeded 1000 m^2, i.e. approximately half of the area in the buffer, the probability of a plot being of a kestrel approached zero.

Table 4. Parameter estimates for the variables with significant values for amount of habitat within a buffer. a) Bog without forest and b) coniferous forest.

	Estimate	SE	z	p
a)				
(Intercept)	-0.6080	0.0953	-6.38	< 0.0001
Bog without forest	0.0002	0.0001	2.20	0.028
b)				
(Intercept)	-0.1707	0.1442	-1.18	0.236
Coniferous forest	-0.0036	0.0004	-9.80	< 0.0001

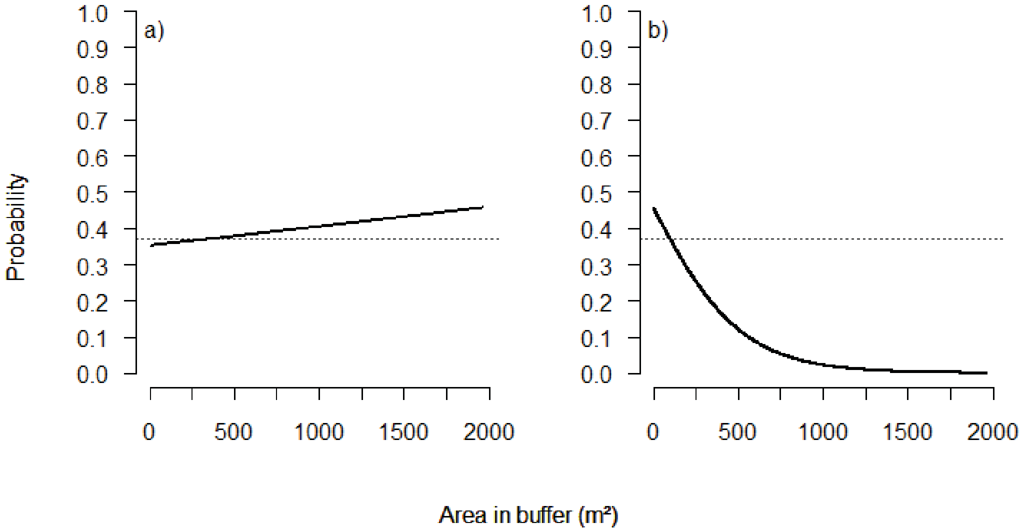

Figure 5. Probability of a plot being of a kestrel rather than random as a function of area of the habitat within a buffer zone of 1963 m^2, for the habitats a) bog without forest and b) coniferous forest. The dotted line indicates expected probability of a random distribution.

3.4 Productivity class in buffer

All four productivity classes that are represented in the study area had significant effects on the probability that a plot was of a kestrel rather than random (Table 5, Figure 6). The probability of a plot being of the kestrel rather than random increased with proportions of unproductive forest land, and medium productive forest land, and decreased with proportions of low productive forest land and agricultural areas and settlements. The kestrels preferred to be in buffer zones with > 503 m^2 unproductive forest land (including bog). This supports the results found in the analysis of habitat in buffers. The kestrels also preferred to be in buffer zones with < 561 m^2 low productive forest land, and > 863 m^2 medium productive forest land, i.e. the kestrels showed a preference for the highest available productivity class, which in the study area would be medium (Figure 6b and Figure 6c). The kestrel also preferred to be in buffer zones with < 32 m^2 agricultural areas and settlements.

Table 5. Parameter estimates for the significant values of amount of productivity classes within a buffer. a) Unproductive forest land, b) low productive forest land, c) medium productive forest land and d) agricultural areas and settlements.

	Estimate	SE	z	p
a)				
(Intercept)	-0.6974	0.1028	-6.78	< 0.0001
Unproductive forest land	0.0003	0.0001	3.31	0.001
b)				
(Intercept)	-0.2638	0.0950	-2.78	0.005
Low	-0.0005	0.0001	-5.22	< 0.0001
c)				
(Intercept)	-0.9130	0.2518	-3.63	0.0003
Medium	0.0004	0.0001	4.04	< 0.0001
d)				
(Intercept)	-0.5076	0.1623	-3.13	0.002
Agriculture and settlement	-0.0014	0.0006	-2.17	0.030

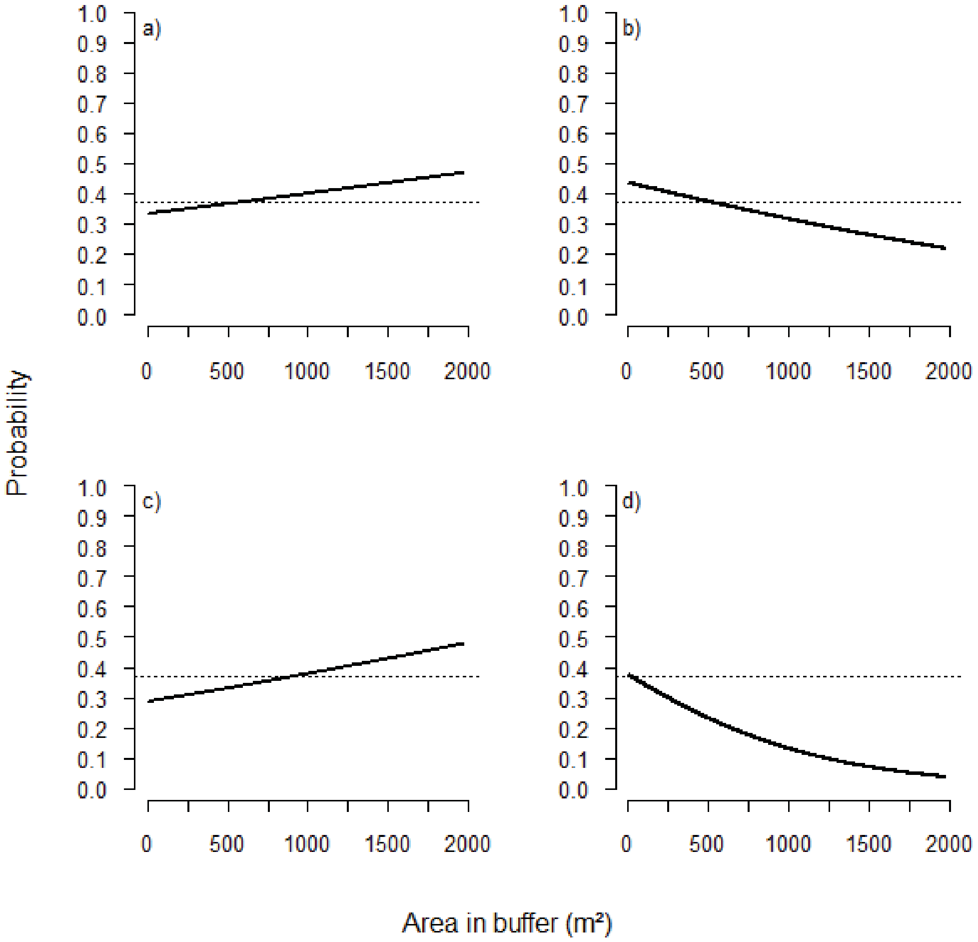

Figure 6. Probability of a plot being of a kestrel rather than random as a function of area of the productivity class within a buffer zone of 1963 m^2, for a) unproductive forest land, b) low productive forest land, c) medium productive forest land and d) agricultural areas and settlements. The dotted line indicates expected probability of a random distribution.

3.5 Behaviour

Behaviour in habitat

The analysis of the occurrence of perching versus the other behavioural categories in various habitats showed that the effect of bog without forest was significantly different from the effect of coniferous forest (0.33 vs. 0.69, $p < 0.0001$) (Figure 7a; Appendix 4, Table IVa, IVd) and bog with forest (0.33 vs. 0.77, $p < 0.0001$) (Figure 7a; Appendix 4, Table IVc, IVd). There was also a trend that the effect of bog without forest was different from the effect of mixed forest (0.33 vs. 0.55, $p = 0.10$) (Figure 7a; Appendix 4, Table IVb, IVd).

In the analysis of the occurrence of hovering versus the other behavioural categories in different habitats, the effect of the various habitats did not differ (Figure 7b; Appendix 4, Table V). The same was found in the analysis of flying versus the other behavioural categories (Figure 7c; Appendix 4, Table VI). For the behavioural category prey capture, or prey capture attempt, the effect of only three habitats were tested, namely coniferous forest, mixed forest and bog without forest. None of these effects differed significantly from each other (Figure 7d; Appendix 4, Table VII). However, because there were very few plots of prey capture in total (14), these latter results should be interpreted with caution.

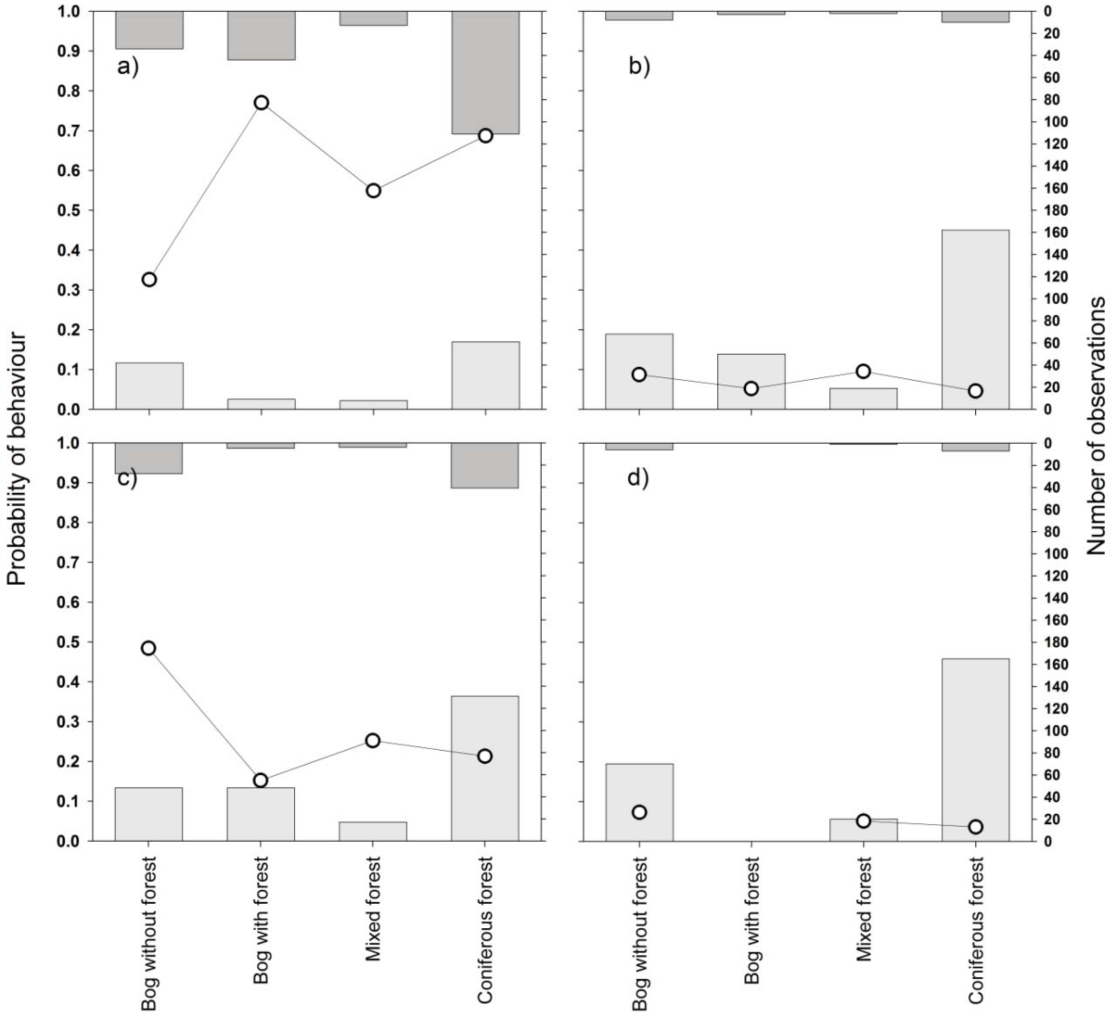

Figure 7. Probability of a behavioural category in the various habitats, given by the circles and the left y-axis. The upper bars indicate the number of observations in the focal behavioural category, given by the right y-axis. The lower bars indicate the number of observations in the other three behavioural categories pooled, given by the right y-axis. a) Perching, b) hovering, c) flying , and d) prey capture. There were no observations of prey capture in bog with forest.

Bog with forest had a significant positive effect on the probability of a plot of the kestrel being a perching plot compared to the other behavioural categories. There was also a trend for a positive effect of coniferous forest (Figure 7a; Appendix 4, Table IV). Furthermore, all four habitats had a significant negative effect on the probability of a plot of the kestrel being a hovering plot compared to the other behavioural categories (Figure 7b; Appendix 4, Table V). Both coniferous forest and bog with forest had a significant negative effect on the probability of a plot of the kestrel being a flying plot compared to the other behavioural categories (Figure 7c; Appendix 4, Table VI). For the behaviour category prey capture, all three habitat variables that were tested, had a significant negative effect on the probability of a plot of a kestrel being one of prey capture compared to the other behavioural categories (Figure 7d; Appendix 4, Table VII).

Behaviour in productivity classes

In the analysis of behaviour in productivity classes, the effects of the productivity classes did not differ significantly from each other; either for perching (Figure 8a; Appendix 4, Table VIII), hovering (Figure 8b; Appendix 4, Table IX) or prey capture (Figure 8d; Appendix 4, Table XI). In the analysis of flying, there was a trend that the effect of productivity class 2 was different from the effect of productivity class 1 (0.28 vs. 0.11, p= 0.098) (Figure 8c; Appendix 4, Table Xa, Xb).

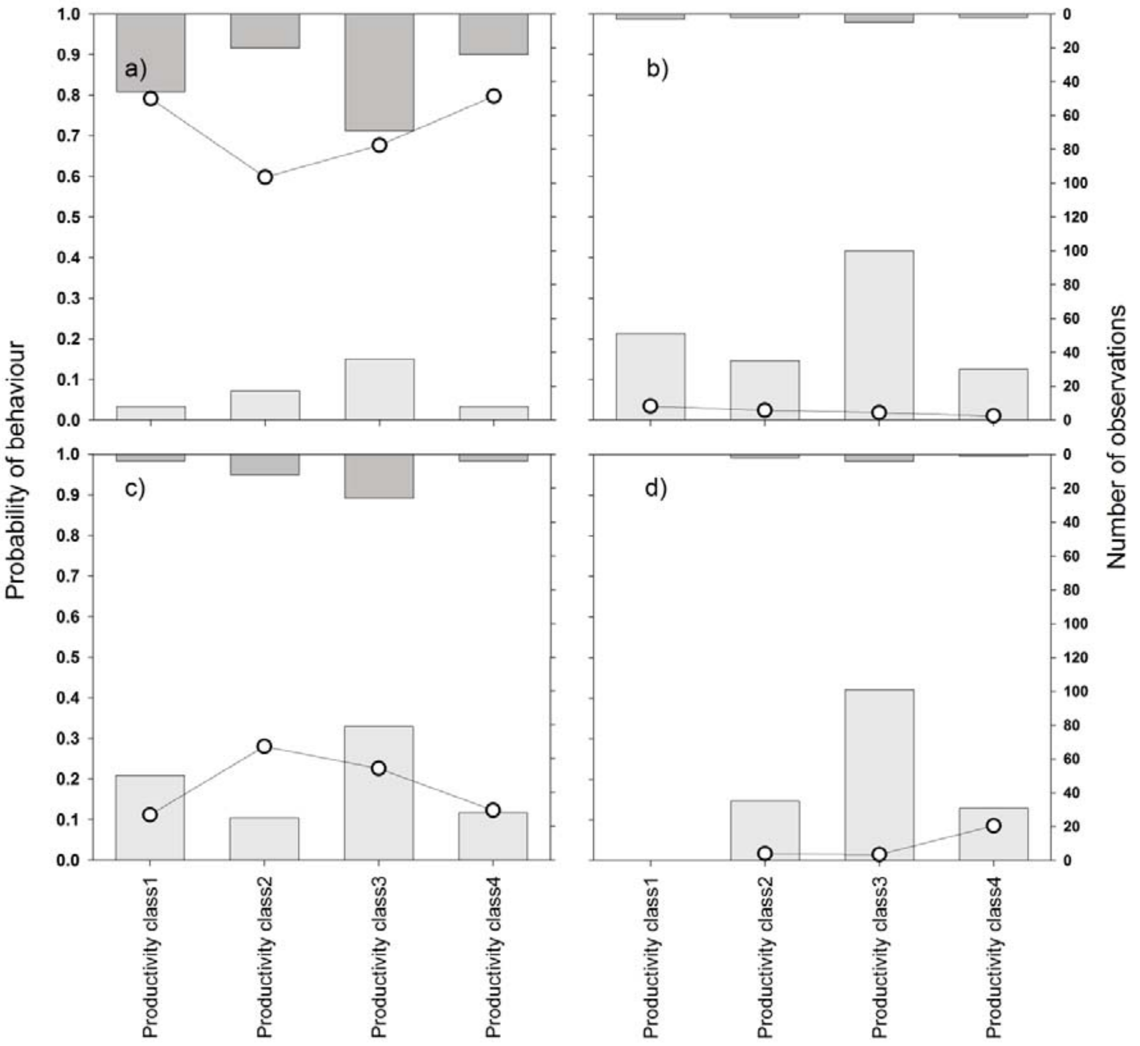

Figure 8. Probability of a behavioural category in the various productivity classes, given by the circles and the left y-axis. The upper bars indicate the number of observations in the focal behavioural categories, given by the right y-axis. The lower bars indicate the number of observations in the other three behavioural categories pooled, given by the right y-axis. a) Perching, b) hovering, c) flying and d) prey capture. There were no observations of prey capture in productivity class 1.

Productivity class 1 and 4 had a significant positive effect on the probability of a plot of the kestrel being a perching plot compared to the other behavioural categories (Figure 8a; Appendix 4, Table VIII). In the analysis of hovering compared to the other behavioural categories, there was a significant negative effect of all four classes (Figure 8b; Appendix 4, Table IX). In the analysis of flying compared to the other behavioural categories there was a significant negative effect of classes 1, 3 and 4. There was also a trend for a negative effect of class 2 (Figure 8c; Appendix 4, table X). Furthermore, there was a significant negative effect of class 2 and 3 on the probability of a plot of the kestrel being one of prey capture compared to the other behavioural categories (Figure 8d; Appendix 4, Table XI).

Behaviour in forestry classes

In the analysis of perching versus the other behavioural categories in the various forestry classes, there was a trend for the effect of forestry class V being different from the effect of forestry class II (0.56 vs. 0.77, p = 0.053) (Figure 9a; Appendix 4, table XIIb, XIIe). Furthermore, in the analysis of hovering and flying, there was a trend of the effect of forestry class V being different from the effect of forestry class IV (0.03 vs. 0.14, p = 0.080, Figure 9b; Appendix 4, table XIII, and 0.28 vs. 0.09, p = 0.056, Figure 9c; Appendix 4, Table XIV, respectively). In the analysis of prey capture there was a trend of the effect of forestry class V being different from the effect of forestry class II (0.08 vs. 0.01, p = 0.094) (Figure 9d; Appendix 4, Table XVa, XVd).

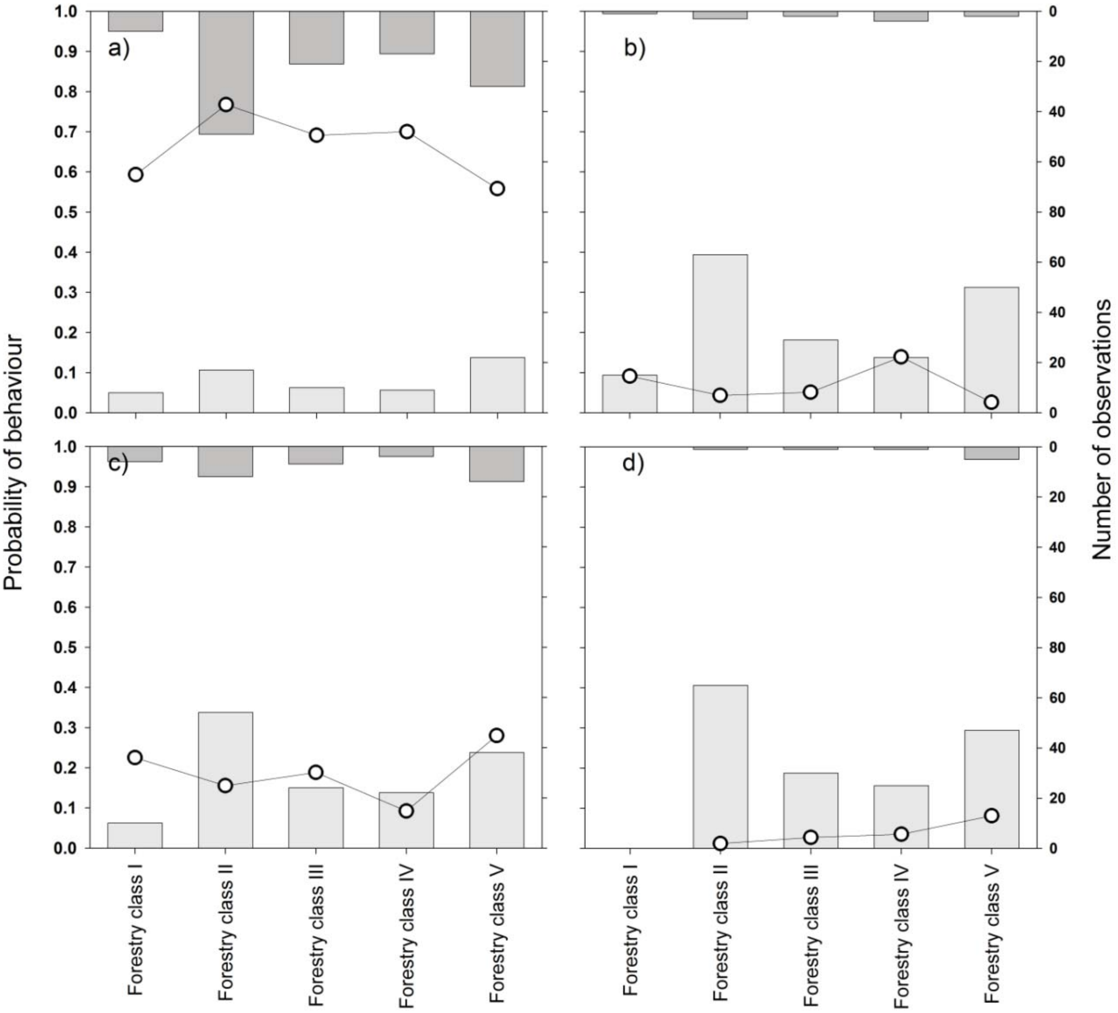

Figure 9. Probability of a behavioural category in the various habitats, given by the circles and the left y-axis. The upper bars indicate the number of observations in the focal behavioural category, given by the right y-axis. The lower bars indicate the number of observations in the other three behavioural categories pooled, given by the right y-axis. a) Perching, b) hovering, c) flying and d) prey capture. There were no observations of prey capture in forestry class I.

There was a significant positive effect of forestry class II on the probability of a plot of the kestrel being one where the kestrel was perching compared to the other behavioural categories (Figure 9a; Appendix 4, Table XII). In the analysis of hovering compared to the other behavioural categories, all five forestry classes had a significant negative effect (Figure 9b; Appendix 4, Table XIII). Forestry class II, III and IV had a significant negative effect on the probability of a plot of the kestrel being one of flying compared to the other behavioural categories, and there was a trend for the same effect of forestry class V (Figure 9c; Appendix 4, Table XIV). The analysis of prey capture showed that all forestry classes represented had a significant negative effect on the probability of a plot of the kestrel being one of prey capture compared to the other behavioural categories (Figure 9d; Appendix 4, Table XV).

3.6 Post-fledge

In the comparison of pre- and post-fledge habitat use, the effect of distance was not significantly different between the stages (cf. the interaction term, Table 6), in any of the four habitats tested, namely bog without forest, coniferous forest, road polygons and water polygons. The distance between the slopes of pre- and post-fledge did not differ significantly in any of the habitats. For histograms showing the comparison of the two stages, see Appendix 2.

Table 6. Parameter estimates for the comparance of distance to habitats pre- and post-fledge, where post-fledge was set as intercept. a) Bog without forest, b) coniferous forest, c) water polygon and d) road polygon.

	Estimate	SE	z	p
a)				
(Intercept)	-0.6985	0.1504	-4.65	< 0.0001
Bog without forest	-0.0018	0.0027	-0.66	0.509
Stage (pre-fledge)	0.2417	0.2100	1.15	0.250
Bog without forest*Stage	0.0004	0.0030	0.13	0.897
b)				
(Intercept)	-0.7687	0.1457	-5.28	< 0.0001
Coniferous forest	0.0006	0.0035	0.18	0.854
Stage (pre-fledge)	0.1316	0.1954	0.67	0.501
Coniferous forest*Stage	0.0039	0.0046	0.85	0.398
c)				
(Intercept)	-1.0226	0.2271	-4.50	< 0.0001
Water polygon	0.0013	0.0008	1.69	0.092
Stage (pre-fledge)	0.2665	0.3239	0.82	0.411
Water polygon*Stage	-0.0006	0.0010	-0.64	0.521
d)				
(Intercept)	-0.6154	0.2118	-2.91	0.004
Road polygon	-0.0004	0.0005	-0.81	0.420
Stage (pre-fledge)	0.2458	0.2864	0.86	0.391
Road polygon*Stage	-0.0001	0.0006	-0.22	0.824

4. Discussion

Kestrels do not choose their foraging habitats by random, and they travel to areas where the yield of prey is enhanced (Garratt et al. 2011). Consequently, the habitats and habitat characteristics I have found a preference for in my study should reflect some foraging habitat preferences of the kestrel.

4.1 Preferences for open habitats and edges

In the analysis of distance to open and closed habitat I found that the kestrels either had a tendency to avoid closed habitats, or had a preference for open habitats and edges. This may indicate that when the kestrels were in closed habitats, they were rarely far away from edges towards open habitat, whereas when they were in open habitat, the distance to closed habitat was irrelevant to them. A preference of edges between open habitats and forest was also found for pygmy owl (*Glaucidium passerinum*) (Strøm & Sonerud 2001) and hooded crows (*Corvus corone cornix*) (Smedshaug et al. 2002). A possible explanation for the affinity for edges could be the fact that edges between open and closed habitats provide perches from which the kestrel can hunt, for example in the edges between clear cuts and closed forest or open bogs and coniferous forests. Several studies have found higher densities of passerines in forest edges (e.g. Helle & Helle 1982; Hansson 1983; Jokimaki & Huhta 1996; Solonen 1996). Thus, the use of edges could possibly be explained by higher densities of prey in forest edges.

Several raptorial birds prey on kestrels (Newton 1979; Petty et al. 2003). This could also be a possible explanation for the preference for edges because this would provide more shelter for the kestrel while perching than if it was perching in a completely open habitat. Smedshaug et al. (2002) suggested that predators such as the goshawk would be easier detected by hooded crows when perching in edges between open and closed habitat.

4.2 Habitat preferences

The habitats preferred by the kestrel were relatively open, with low vegetative ground cover. Although I did not investigate the effect of vegetative cover, I found that there was a higher probability of finding the kestrels at shorter distances from bog without forest, and with an increasing proportion of bog without forest within buffer zones. Bogs are dominated by relatively short vegetation, such as *Sphagnum* spp. (Moen 1998), so the vegetative ground cover would thus have been low.

In a year with high vole abundance, Valkama et al. (1995) found that agricultural fields were the habitat most frequently used by kestrels. This is in contrast to my findings, where no effect of agricultural land on habitat use was found in a year with high vole abundance. My findings may be explained by the fact that the vegetation in the agricultural areas was rather tall during my observation period in June-July, so it would have been difficult for the kestrel to detect and capture prey under these circumstances. However, Valkama et al. (1995) did not appear to find an effect of vegetation cover on the use of agricultural land, because there was no change in utilization of this habitat during the course of the breeding seasons.

The preference I found for bog without forest is in accordance with the findings of Valkama et al. (1995) in a low vole year, when their kestrels foraged mostly over forests and marshland. In my study area there was relatively small proportions of agricultural land. Thus, the kestrels may have been forced to use habitats that under optimal circumstances would have been secondary choices. Furthermore, I found that the probability of a plot being of a kestrel increased with distance from coniferous forest, and decreased with increasing proportion of coniferous forest in buffer zones. This may suggest that coniferous forest is of even lower preference than bog without forest, because it was avoided in a high vole abundance year (my study), but used in a low vole abundance study (Valkama et al. 1995).

The study area of Valkama et al. (1995) largely consisted of agricultural land comprised of barley, oat, potato, hay fields and some fallow land. A possible explanation for the difference between their and my results could be the fact that the agricultural land in my study area only consisted of hay fields. Hay fields probably have a denser cover than many other agricultural fields, because the grass grows very dense. Cereals and vegetables are commonly sown with machines, with open space between neighbor plants so that these plants grow in a structured manner. It would probably be easier to spot small prey in these areas than in a densely vegetated hay field. Thus, such cultivated areas might provide better foraging habitats for kestrels than the hay fields found in my study area. Note that Valkama et al. (1995) made their field observations with binoculars and telescopes. The fact that they did not use radio telemetry could bias their results, because it would be more difficult to locate the kestrels when they were in closed habitats, such as forests, than when they were in open habitats, such as agricultural land.

I found that the probability of a plot being of a kestrel decreased with distance to road. In France motorway verges and roadside verges have been found to be good foraging habitats for the kestrel (Meunier et al. 2000). The verges were preferred by the kestrels in January and in spring, even though cultivated areas had higher populations of small mammals (common vole, *Microtus arvalis* and greater white toothed shrew, *Crocidura russula*) during this period. This was possibly because these habitats provides a reliable food source during winter, or because of high occurrence of available perches along the verges (Meunier et al. 2000). However, ditches close to roads are also good habitats for *Microtus* voles (Meunier et al. 1999; de Redon et al. 2010) Nevertheless, there may be a bias towards roads in my data set because the six locations we used were placed close to roads to ease the logistics. On the other hand, this potential problem should have been taken care of because my analysis was done on the basis of use and availability. However, the fact that Valkama and Korpimäki (1999) found that occupied nest boxes in their study area were further away from roads than unoccupied nest boxes, suggests that the kestrels in some way avoids roads. The roads in their study were mainly used by farmers, and had very little car traffic. Thus, it is difficult to find a good explanation for these conflicting findings.

I found that the kestrel had an avoidance pattern to water; the probability of finding a kestrel increased with distance to water. Also the red-footed falcon (*Falco vespertinus*) avoided water surfaces (Palatitz et al. 2011). Although some of the invertebrate prey of the red-footed falcon are connected to wetlands, these prey items may mainly be taken while the red-footed falcon is aerial hunting, which may explain the water avoidance pattern. Furthermore, the second most important vertebrate prey of the red-footed falcon are also connected to water. This suggests that habitats connected to water may have an indirect effect on the foraging habitat selection of the red-footed falcon (Palatitz et al. 2011).

My findings were similar to the findings for the red-footed falcon. However, because the main prey of the kestrels were voles (Støvern 2012), this pattern of avoiding water would be more expected in my study. This is supported by the fact that my observations were made in a peak vole year. On rare occasions other prey of the kestrel may include frogs (Steen 2010). Thus, if my observations had been made in a low rodent year it would have been expected that the avoidance pattern the kestrel had to water would have been weaker, or it could have disappeared altogether.

The analysis I made of habitat use in buffer zones reveals habitat preferences on a small scale, i.e. it shows the habitat preferences of a kestrel at the specific points where it had been observed. Because the areas of the different habitats in the buffers were not independent, I was unable to do an analysis with a model showing the effect of habitats in a common context. Thus, my analysis of habitat use in buffer zones does not tell anything about the effects the habitats have together. For this reason, the results of the analysis of habitat use in buffer zones should be treated with more caution than the results of the analysis of distance to the different habitats, which is an analysis showing the habitats that best explains the variation in habitat use in a common context.

4.3 Preference of unproductive and highly productive soil

I found that there was an increasing probability of finding a kestrel with increasing proportion of unproductive forest land and medium productive forest land in buffer zones around plots of the kestrel, while the opposite was the case for low productive forest land and for areas with agricultural land and settlements. The fact that root voles (*Microtus oeconomus*) prefer browsing on blueberries from sites in high productive forest rather than low productive forests (Pedersen et al. 2011) support my findings because it would be reasonable that the kestrels would be found in the preferred habitat of their prey. The increasing probability of finding a kestrel with increasing proportions of unproductive forest land could be explained by the high vole population during my study. The most optimal habitats for the voles would have been saturated, and this may have forced parts of the vole population to use less optimal habitats, such as bogs. Because the bogs are very open habitats it would have been more easy for the kestrel to locate and capture prey in this habitat than in other habitats with more cover. The wood lemming (*Myopus schisticolor*) was frequently observed on bogs during the field season (personal observation). Furthermore, an equal number of wood lemming and *Microtus* voles were caught in snap traps on bogs with and without forest in my study (Geir A. Sonerud, unpubl. data). Thus, a preference for unproductive forest land by the kestrel may be explained by the high vole density in my study.

The kestrel is relatively little affected by human activity (Village 1990), and it can readily breed in anthropogenic areas such as farms, villages and cities (e.g. Village 1990; Charter et al. 2007). However, findings on the kestrels response to human disturbance have been somewhat contrasting, and studies has shown that the breeding success of the kestrel may be reduced in highly disturbed areas (van der Zande & Verstrael 1985; Charter et al. 2007), and severe disturbance may in some cases make the kestrel abandon their breeding attempts (van der Zande & Verstrael 1985; Village 1990) . Avoidance of the productivity class with agricultural areas and settlement in my study may have been due to the fact that the kestrels did not have any preferences for these areas, but may also be caused by avoidance of areas with high human activity.

4.4 Hunting behaviour

Perching was the main hunting behaviour observed, and requires less energy than flight. Because my study was done in a peak vole year, it would seem unnecessary to use extra amounts of energy on flight hunting. Furthermore, I studied the female kestrels, and these have a larger tendency than males to use perching as a hunting technique in summer (Village 1990). Flight hunting yielded higher prey capture rates than perch hunting, both in males and females (Masman et al. 1988). In my study, all observations of perching were pooled into one category. However, it is difficult to distinguish between hunting and resting perched kestrels. According to Masman et al. (1988) most perching in summer is probably resting, while most perching in winter probably is hunting. Thus, a relatively large proportion of perching observations in my study were in fact resting, and the analysis I made of behaviour would be a more general analysis, rather than strictly an analysis of foraging behaviour. If this was the case, it may be explained by the high vole density. If voles were readily available, it would have been fairly easy to locate and capture a sufficient number of voles to cover the energy demand of both the adult kestrels and their nestlings. Thus, the remaining time would have been used perching, i.e. doing nothing productive in order to conserve energy reserves, a pattern also found in Masman et al. (1988).

4.5 Behavioural activity in habitats

In the analysis of behavioural activity in various habitats there was a higher probability of observing the kestrel perching in forested areas, i.e. bog with forest and coniferous forest, than in bog without forest. There was a higher probability of observing the kestrel showing other behaviours than hovering and prey capture in all habitats tested, and the same was found for flying in bog with forest and coniferous forest.

My results indicates that the kestrel preferred perching in areas where there were rich supplies of trees to perch in, rather than in open bogs where the kestrel would have to perch on the ground or in the scattered trees that are available there, which is in accordance with the findings of Meunier et al. (2000).

Previous findings have shown that diurnal birds of prey prefer high vantage points for perching (Sonerud 1980; Rice 1983; Sonerud 1997). This could possibly explain my results where I found that there was preference for edges, and the higher probability of observing the kestrel perching in forested areas. Despite the fact that hovering is the foraging behavior which gives the highest yield for the kestrel (Masman et al. 1988), the kestrel should choose perching locations from where it would be relatively easy to spot prey. In this way, the kestrel could strike lucky and spot prey while resting, because if the prey has a high enough profitability, every chance of prey capture should be utilized (Barnard 2004).

The results in the analysis of hovering, flying and prey capture were probably affected by the high number of observed perching relative to the other types of behaviour. Thus, because I did not have random plots included in the analysis, these behaviours would have been underrepresented relative to perching, and consequently, the results would have been skewed in favor of perching. Furthermore, there were only 14 observations of prey capture in total, and this could have led to a misrepresentation of the habitats used for prey capture.

4.6 Behavioural activity in productivity classes

I found that there was a higher probability of observing the kestrel perching rather than showing other types of behaviour in productivity class 1and 4. In all four productivity classes there was a lower probability of, or a lower tendency to, finding the kestrel hovering, flying, or capturing prey, than using any of the other behaviours. There was also an indication that the kestrel was observed flying more often in productivity class 2 rather than 1.

Taken together with my results of behaviour in habitats the increased probability of observing perch in productivity class 1 can be explained by the fact that bog with forest was included in this productivity class. The primary hunting method of the American kestrel (*Falco sparverius*) in the vicinity of the nest was perch hunting, which can be explained by the high number of available perches in the nest area (Liebana et al. 2009). Productivity class 4 is the class in my study area consisting of the plant species indicating the richest soil available. A possible explanation for the increased probability of observing perching in this productivity class could be that most of the observations made in this productivity class were in a clear cut where the nest at Husfliden was situated.

Observed flight is not necessarily foraging, but may rather often be transport observations, i.e. observations where the kestrel is travelling from one place to another, for example carrying prey to the nest(e.g. Masman et al. 1988; Sonerud 1992b). Although observations where the kestrels were carrying prey were removed from the data set before the analysis was made, some transport observations may not have been removed merely through this selection. Thus, the finding that the kestrel was observed more often flying in productivity class 2 than in productivity class 1, could simply indicate that the kestrel was more often observed flying above habitats such as coniferous forest and mixed forest, than over bog with forest, which is included in productivity class 1. This is not surprising, because large parts of the study areas consist of forest. Thus, in order to get to the nests, the kestrels would have to travel through such habitats. A preference for bog with and without forest, on the other hand, would indicate a more selective choice, as these habitats constitutes a smaller proportion of the study area than forests.

4.7 Behavioural activity in forestry classes

I found an indication of a higher probability of observing the kestrel perching in forestry class II, rather than V, and there was a tendency to a larger probability of observing perching rather than any of the other behaviours in forestry class III and IV. There was a tendency that the kestrel preferred hovering above areas of forestry class IV rather than V, and it appeared to prefer flying above forestry class V rather than IV. There was a higher probability of, or a tendency for, observing the kestrel using other behaviour than hovering, flying or prey capture in all forestry classes. Moreover, there was an indication of a higher probability of observing the kestrel capturing prey in forestry class V rather than IV.

Diurnal raptors that use their sight to locate prey have difficulties in utilizing old, dense, coniferous forests (Sonerud 1985). However, through clear cutting forested areas, voles in the field layer are rendered available to these raptors (Sonerud 1985). Clear cut areas which have a high number of reproducing voles also have a relatively dense vegetation in the field layer, which renders these areas unavailable for small raptors, such as the kestrel (Sonerud 1980). Forestry class II is generally a relatively open habitat with some scattered larger trees. These trees could have been used for perch-hunting because prey would have been relatively easy to detect in the open habitat. Furthermore, in accordance with Sonerud (1980), no pattern was found in forestry class I, which would have a dense field layer with large amounts of coarse woody debris, rendering this forestry class difficult to utilize for the kestrel.

Three of the six nests we studied were situated in areas with forestry class II, namely the nests at Husfliden, Storflendammen and Storfallet, something which could have contributed to this preference of forestry class II. Forestry class V included bog with forest in my study area, which has a less closed canopy and field layer than coniferous forest of forestry class IV. Thus, the effect here could be somewhat similar to the effect of clear cutting, apart from the denser canopy cover in bog with forest than in clear cuts. Hence, the kestrel could have a higher probability of spotting and capturing prey in forestry class V, or bog with forest.

I can offer no explanation for the preference I found for hovering in forestry class IV, and flying in forestry class V. If anything, the opposite would be expected because hovering would be hunting, while flying often would be transport. Therefore, hovering would be expected in the more open forestry class.

4.8 Pre- and post-fledge comparison

I found no differences in habitat use between pre- and post-fledge. To the best of my knowledge no other studies have compared the habitat use pre- and post-fledge of raptors with radio-telemetry. Nevertheless, my results indicate that the habitat use of the female kestrels did not change after the nestlings had fledged. A possible explanation for this could be that the variations in habitats between pre- and post-fledge home ranges were small. However, note that I only had post-fledged data for two female kestrels. Thus, I want to be cautious making any conclusions, and I suggest that future studies compare the habitat use of kestrels pre- and post-fledge with a larger sample size.

4.9 Possible data bias and future studies

Several factors may have contributed to various biases in my analysis. The utilization of closed habitats may have been underrepresented, the number of observations of perching kestrels may have been overrepresented, and the specific habitats in the immediate vicinity of the nests may have been overrepresented because one observer was placed close to the nest during tracking at five of the six nests studied.

Closed habitats may have been underrepresented in the observations because it would be more difficult to locate even radio tagged kestrels in these habitats, as has also been noted in previous studies (Masman et al. 1988; Garratt et al. 2011).

It would probably have been easier to spot the kestrels while they were perching, and this may have led to an overrepresentation of observed perching relative to the other types of behaviour. This may indicate that a relatively large proportion of perching observations in my study were in fact resting, and the analysis I made of behaviour would be a more general analysis, rather than strictly an analysis of foraging behaviour. However, the hawk owl (*Surnia ulula*) have been observed interrupting preening periods and suddenly attack prey, i.e. the prey was detected during preening (Sonerud 1992a). The hawk owl is a diurnal raptor and locates its prey visually (Nordberg 1987). Thus, the findings on the hawk owl may also apply for the kestrel, and observations of perching should not be disregarded, independent of the apparent intentions of the bird.

I suggest that future studies look into the utilization of the various forest age classes to see if the kestrel has any preferences for different age classes within the coniferous forest. From what is known about the kestrels use of clear cuts (Sonerud 1980; Sonerud 1985; Løken 2009), and the general aversion I found for coniferous forests in general, I predict that future studies will show that the kestrel avoids the older forestry classes, and prefers hunting in forestry class I and II. However, recently made clear cuts, i.e. younger than 2 years may not be utilized to the extent somewhat older clear cuts will be, because of the large amounts of coarse woody debris commonly found in these areas.

Because vegetative ground cover apparently is an important factor affecting the kestrels habitat utilization I suggest that future studies of the kestrel register vegetative ground cover and analyze the effect this has on the habitat use and behaviour.

Autocorrelation is a phenomenon where a position of an animal at the time $t + \Delta t$ is not independent of a position at the time t, i.e. two registered habitats will not be independent if they are autocorrelated (Rooney et al. 1998). This may have affected my data analysis. Rooney et al.(1998) suggested that a good measure for the time of independence would be the time it takes for an animal to travel across its entire range with the highest speed it can. The kestrel has an average speed of approximately 10 m/s (Geir A. Sonerud, unpubl. data). The largest distance between two points within a 100% MCP in my study area was 5440 m. Thus, it would have taken a kestrel 9 minutes to travel between these points at an average speed. With maximum speed the time would have been considerably shorter. I did not adjust my data for autocorrelation. However, the home range with distances up to 5440 m was a very large home range, and the time it would have taken a kestrel to cross other home ranges would have been even shorter. Nevertheless, I suggest that future studies should control for autocorrelation.

Poor weather conditions have been shown to have a negative effect on the proportion of flight hunting in kestrels; during periods of high winds and rain, flight hunting could be almost entirely suppressed (Masman et al. 1988). The effect of weather conditions should have been considered in my study as well, and would be interesting to investigate further in future studies.

4.10 Conclusion

I found that the female kestrels in my study area preferred foraging in habitats where prey may easily be detected. My results do not fit with those from the majority of previous studies, where the kestrel preferred agricultural areas. In contrast, I found, in a study conducted in a boreal forest area, a preference for bog without forest, roads, open habitats, edges, unproductive forest land and for medium productive forest land. I also found that the kestrel avoided coniferous forest, water, low productive forest land and agricultural areas and settlements. I suggest that future studies look into the habitat use and behaviour of the kestrel at a more detailed level, testing vegetative ground cover and forestry classes. Preferably, future studies will be conducted over several breeding seasons in order to get a more representative image of the habitat selection of the kestrel.

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Appendix 1

Table I. Number of observations of the behavioural categories, and the specific number of observations of these in the habitats included in the final analysis of behaviour.

Habitat	Perching	Not perching
Coniferous forest	111	61
Mixed forest	13	8
Bog with forest	44	9
Bog without forest	34	42

Habitat	Flying	Not flying
Coniferous forest	41	131
Mixed forest	4	17
Bog with forest	5	48
Bog without forest	28	48

Habitat	Hovering	Not hover
Coniferous forest	10	162
Mixed forest	2	19
Bog with forest	3	50
Bog without forest	8	68

Habitat	Capture	Not capture
Coniferous forest	7	165
Mixed forest	1	20
Bog without forest	6	70

Table II. Number of observations of the behavioural categories, and the specific number of observations of these in the productivity classes included in the final analysis of behaviour.

Productivity class	Perching	Not perching
Productivity class1	46	8
Productivity class2	20	17
Productivity class3	69	36
Productivity class4	24	8

Productivity class	Flying	Not flying
Productivity class1	4	50
Productivity class2	12	25
Productivity class3	26	79
Productivity class4	4	28

Productivity class	Hovering	Not hovering
Productivity class1	3	51
Productivity class2	2	35
Productivity class3	5	100
Productivity class4	2	30

Productivity class	Capture	Not capture
Productivity class2	2	35
Productivity class3	4	101
Productivity class4	1	31

Table III. Number of observations of the behavioural categories, and the specific number of observations of these in the forestry classes included in the final analysis of behaviour.

Forestry class	Perching	Not perching
Forestry class I	8	8
Forestry class II	49	17
Forestry class III	21	10
Forestry class IV	17	9
Forestry class V	30	22

Forestry class	Flying	Not flying
Forestry class I	6	10
Forestry class II	12	54
Forestry class III	7	24
Forestry class IV	4	22
Forestry class V	14	38

Forestry class	Hovering	Not hovering
Forestry class I	1	15
Forestry class II	3	63
Forestry class III	2	29
Forestry class IV	4	22
Forestry class V	2	50

Forestry class	Capture	Not capture
Forestry class II	1	65
Forestry class III	1	30
Forestry class IV	1	25
Forestry class V	5	47

Appendix 2

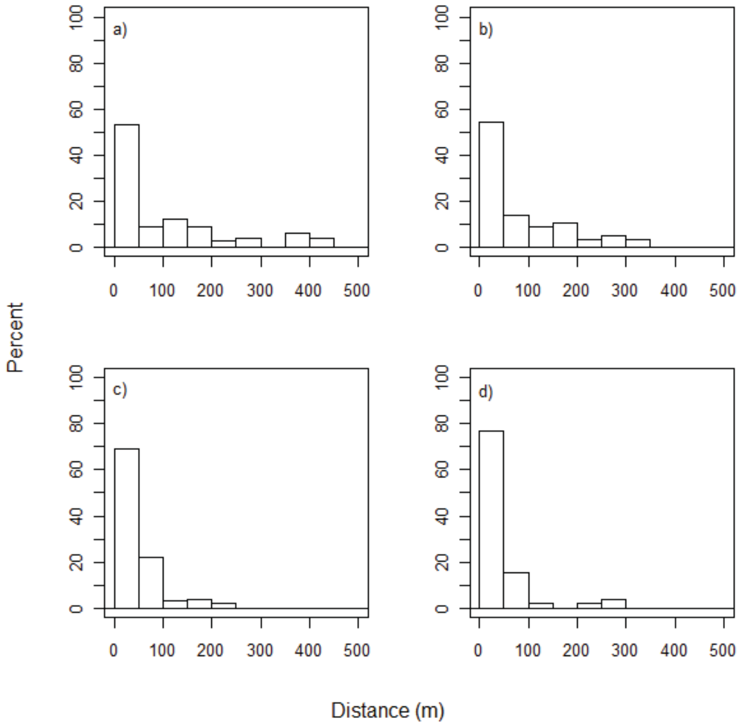

Figure I. Comparison of distance to bog without forest, pre- and post-fledge, at the location Storflendammen. a) Random plots pre-fledge, b) actual plots pre-fledge, c) random plots post-fledge and d) actual plots post-fledge.

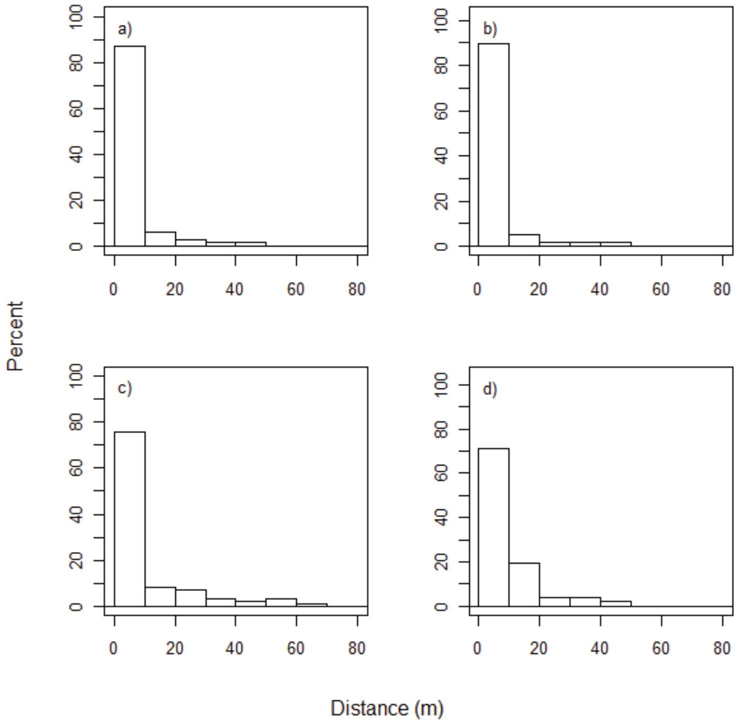

Figure II. Comparison of distance to coniferous forest, pre- and post-fledge, at the location Storflendammen. a) Random plots pre-fledge, b) actual plots pre-fledge, c) random plots post-fledge and d) actual plots post-fledge.

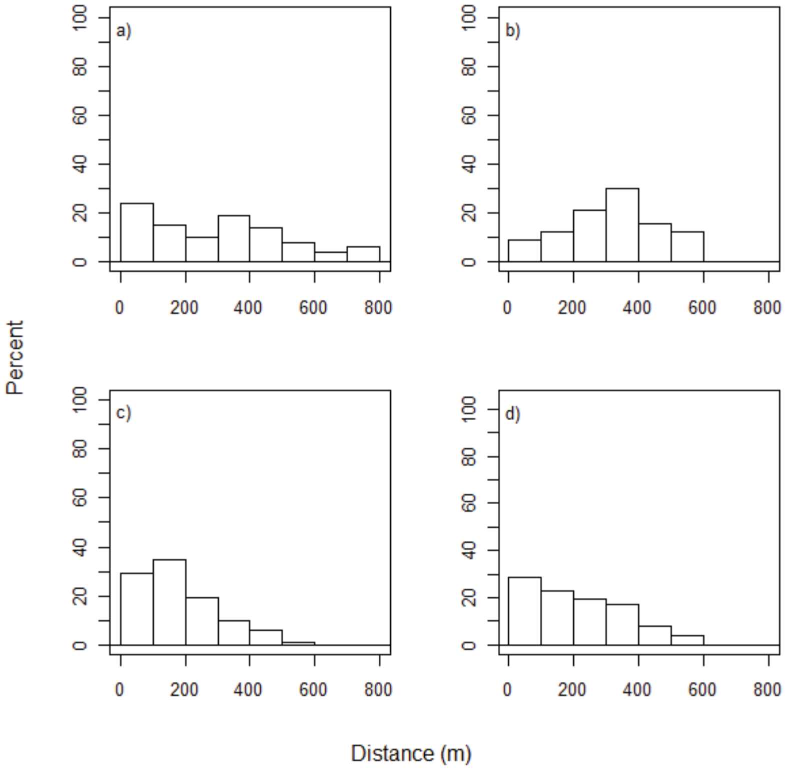

Figure III. Comparison of distance to water polygon, pre- and post-fledge, at the location Storflendammen. a) Random plots pre-fledge, b) actual plots pre-fledge, c) random plots post-fledge and d) actual plots post-fledge.

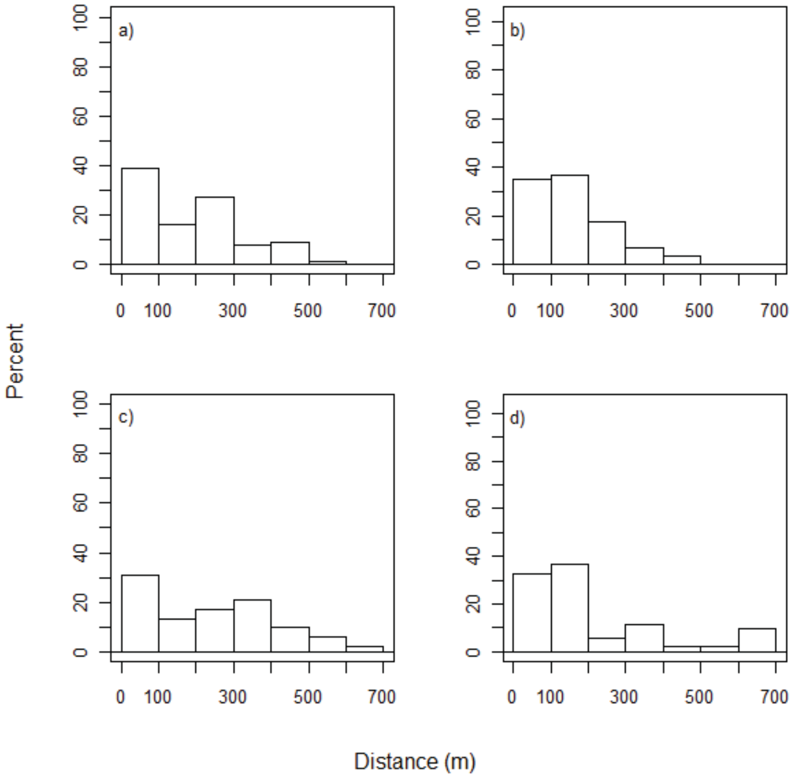

Figure IV. Comparison of distance to road polygon, pre- and post-fledge, at the location Storflendammen. a) Random plots pre-fledge, b) actual plots pre-fledge, c) random plots post-fledge and d) actual plots post-fledge.

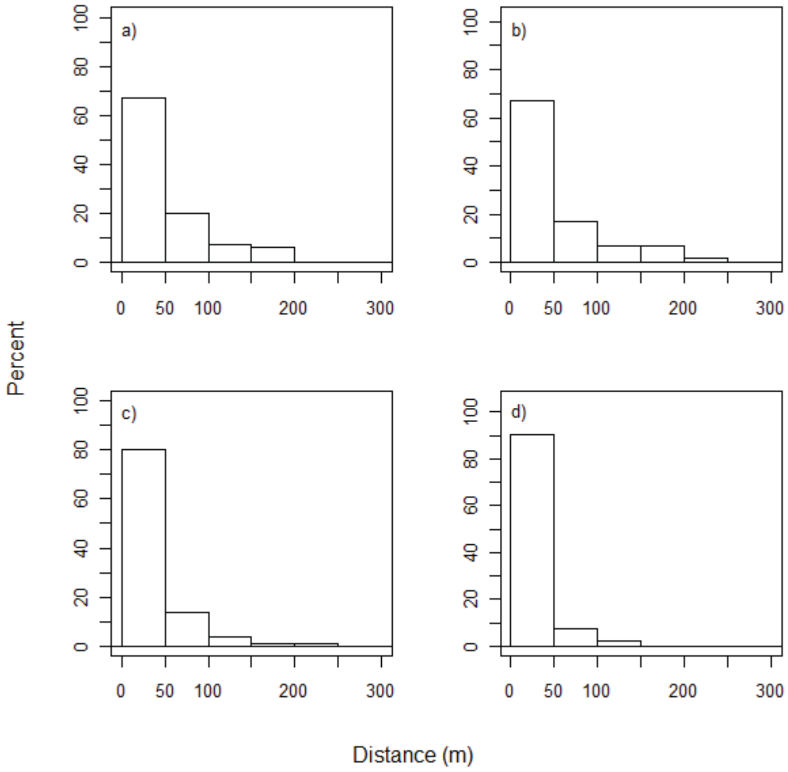

Figure V. Comparison of distance to bog without forest, pre- and post-fledge, at the location Tørråsen. a) Random plots pre-fledge, b) actual plots pre-fledge, c) random plots post-fledge and d) actual plots post-fledge.

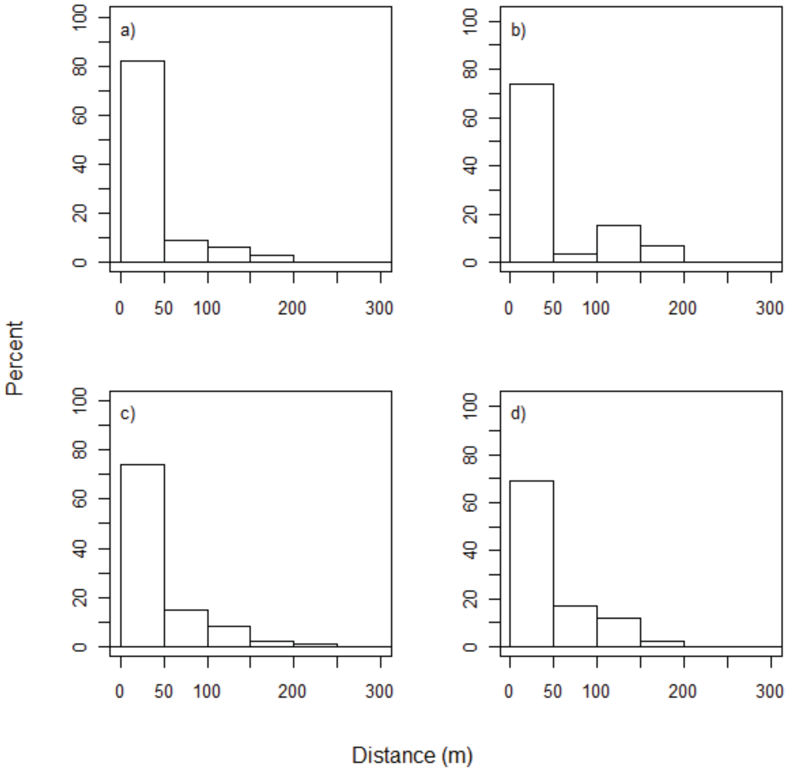

Figure VI. Comparison of distance to coniferous forest, pre- and post-fledge, at the location Tørråsen. a) Random plots pre-fledge, b) actual plots pre-fledge, c) random plots post-fledge and d) actual plots post-fledge.

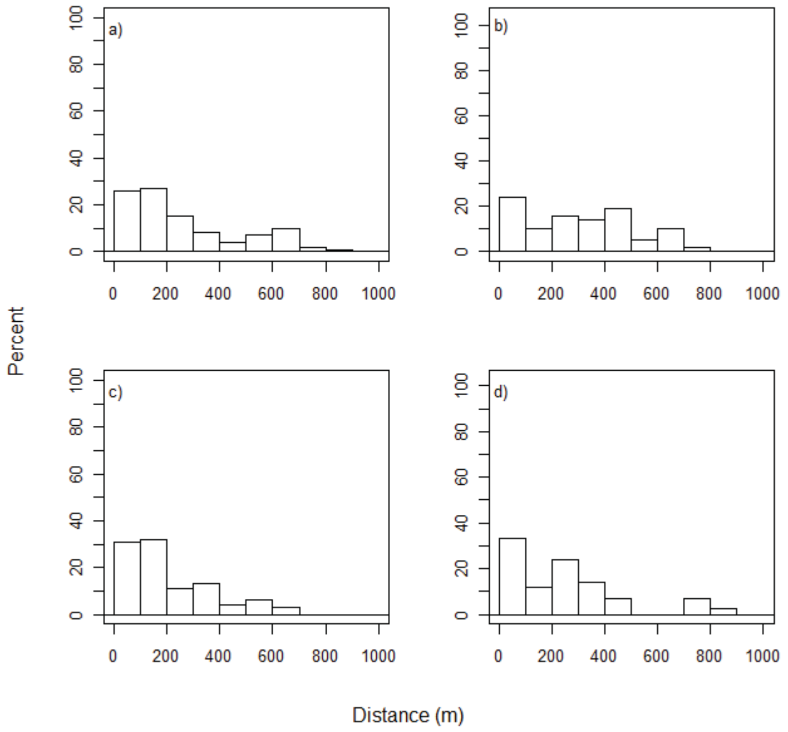

Figure VII. Comparison of distance to water polygon, pre- and post-fledge, at the location Tørråsen. a) Random plots pre-fledge, b) actual plots pre-fledge, c) random plots post-fledge and d) actual plots post-fledge.

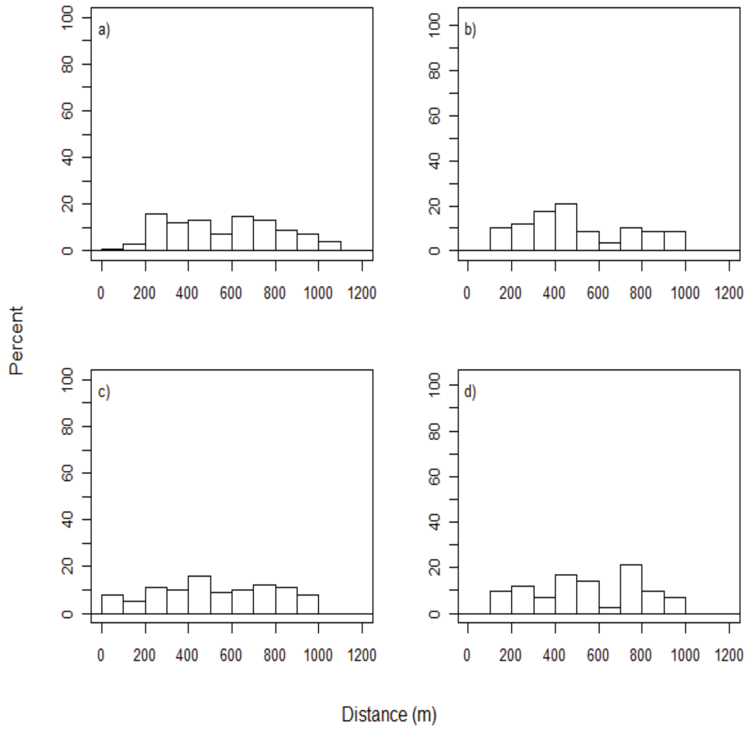

Figure VIII. Comparison of distance to road polygon, pre- and post-fledge, at the location Tørråsen. a) Random plots pre-fledge, b) actual plots pre-fledge, c) random plots post-fledge and d) actual plots post-fledge.

Appendix 3

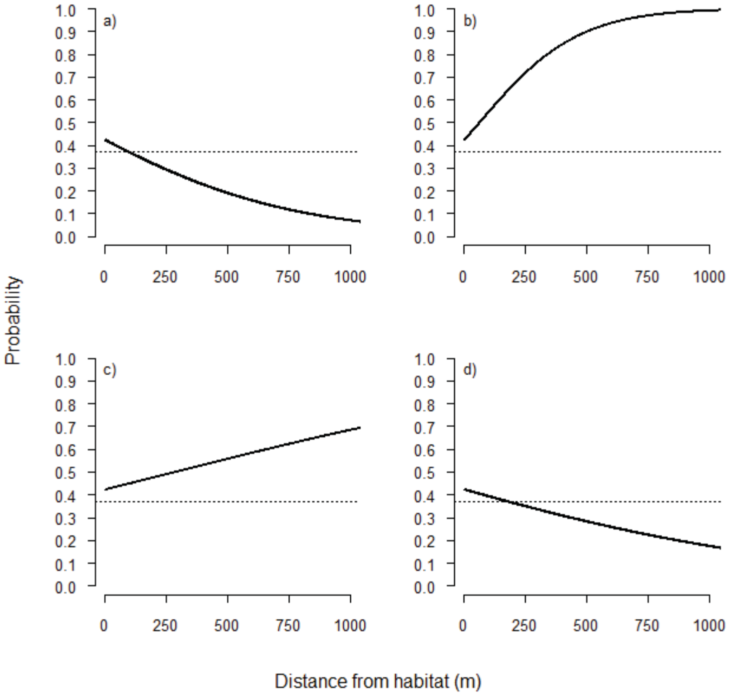

Figure IX. Probability of a plot being of a kestrel rather than random as a function of distance to the four habitats a) Bog without forest, b) coniferous forest, c) water polygon and d) road polygon. Based on the parameter estimates in table 3 and minimum values of the habitats used in the analysis. The dotted line indicates expected probability of a random distribution.

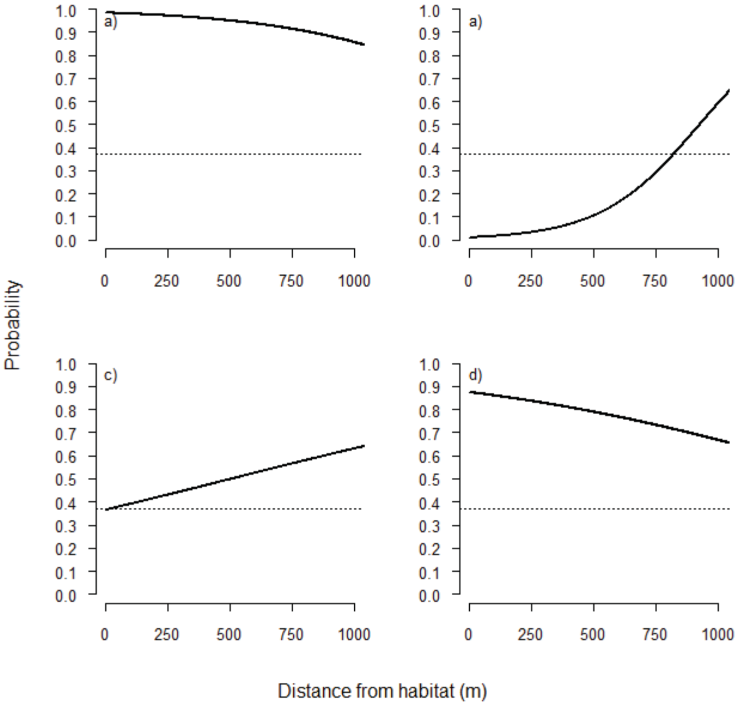

Figure X. Probability of a plot being of a kestrel rather than random as a function of distance to the four habitats a) Bog without forest, b) coniferous forest, c) water polygon and d) road polygon. Based on the parameter estimates in table 3, and maximum values of the habitats used in the analysis. The dotted line indicates expected probability of a random distribution.

Appendix 4

Table IV. Parameter estimates for perching versus other behaviour in habitats. a) Coniferous forest as intercept, b) mixed forest as intercept, c) bog with forest as intercept and d) bog without forest as intercept.

	Estimate	SE	z	p	Transformed estimate
a)					
Intercept	0.78	0.41	1.94	0.053	0.69
Mixed forest	-0.59	0.53	-1.12	0.263	
Bog with forest	0.42	0.47	0.91	0.364	
Bog without forest	-1.51	0.34	-4.39	<0.0001	
b)					
Intercept	0.19	0.61	0.32	0.750	0.55
Coniferous forest	0.59	0.53	1.12	0.263	
Bog with forest	1.01	0.64	1.57	0.115	
Bog without forest	-0.92	0.56	-1.65	0.100	
c)					
Intercept	1.21	0.55	2.19	0.028	0.77
Mixed forest	-1.01	0.64	-1.57	0.116	
Coniferous forest	-0.42	0.47	-0.91	0.364	
Bog without forest	-1.93	0.47	-4.12	<0.0001	
d)					
Intercept	-0.73	0.45	-1.61	0.108	0.33
Bog with forest	1.93	0.47	4.12	<0.0001	
Mixed forest	0.92	0.56	1.65	0.100	
Coniferous forest	1.51	0.34	4.39	<0.0001	

Table V. Parameter estimates for hovering versus other behaviour in habitats. a) Coniferous forest as intercept, b) mixed forest as intercept, c) bog with forest as intercept and d) bog without forest as intercept.

	Estimate	SE	z	p	Transformed estimate
a)					
Intercept	-3.03	0.44	-6.81	<0.0001	0.05
Bog without forest	0.67	0.54	1.24	0.215	
Bog with forest	0.12	0.73	0.16	0.871	
Mixed forest	0.77	0.85	0.91	0.362	
b)					
Intercept	-2.26	0.82	-2.76	0.006	0.09
Coniferous forest	-0.77	0.85	-0.91	0.362	
Bog without forest	-0.10	0.87	-0.11	0.909	
Bog with forest	-0.65	0.99	-0.66	0.510	
c)					
Intercept	-2.91	0.69	-4.24	<0.0001	0.05
Mixed forest	0.65	0.99	0.66	0.510	
Coniferous forest	-0.12	0.73	-0.16	0.871	
Bog without forest	0.55	0.72	0.77	0.441	
d)					
Intercept	-2.36	0.49	-4.78	<0.0001	0.09
Bog with forest	-0.55	0.72	-0.77	0.441	
Mixed forest	0.10	0.87	0.11	0.909	
Coniferous forest	-0.67	0.54	-1.24	0.251	

TableVI. Parameter estimates for flyingversus other behaviour in habitats. a) Coniferous forest as intercept, b) mixed forest as intercept, c) bog with forest as intercept and d) bog without forest as intercept.

	Estimate	SE	z	p	Transformed estimate
a)					
Intercept	-1.31	0.38	-3.43	0.001	0.21
Bog without forest	1.24	0.36	3.48	0.001	
Bog with forest	-0.41	0.55	-0.76	0.448	
Mixed forest	0.22	0.62	0.35	0.723	
b)					
Intercept	-1.09	0.66	-1.64	0.100	0.25
Coniferous forest	-0.22	0.62	-0.35	0.723	
Bog without forest	1.02	0.64	1.60	0.109	
Bog with forest	-0.63	0.76	-0.83	0.405	
c)					
Intercept	-1.72	0.59	-2.92	0.003	0.15
Mixed forest	0.63	0.76	0.83	0.406	
Coniferous forest	0.41	0.55	0.76	0.448	
Bog without forest	1.66	0.54	3.08	0.002	
d)					
Intercept	-0.07	0.42	-0.16	0.876	0.48
Bog with forest	-1.66	0.54	-3.08	0.002	
Mixed forest	-1.02	0.64	-1.60	0.109	
Coniferous forest	-1.24	0.36	-3.48	0.001	

Table VII. Parameter estimates for prey capture, or prey capture attempts versus other behaviour in habitats. There were no observations of prey capture in bog with forest. a) Coniferous forest as intercept, b) mixed forest as intercept and c) bog without forest as intercept.

	Estimate	SE	z	p	Transformed estimate
a)					
Intercept	-3.30	0.51	-6.50	<0.0001	0.04
Mixed forest	0.37	1.15	0.32	0.751	
Bog without forest	0.76	0.65	1.16	0.246	
b)					
Intercept	-2.93	1.11	-2.65	0.008	0.05
Coniferous forest	-0.37	1.15	-0.32	0.751	
Bog without forest	0.39	1.16	0.34	0.736	
c)					
Intercept	-2.54	0.56	-4.51	<0.0001	0.07
Mixed forest	-0.39	1.16	-0.34	0.736	
Coniferous forest	-0.76	0.65	-1.16	0.246	

Table VIII. Parameter estimates for perching versus other behaviours in productivity classes. a) Productivity class 1 as intercept, b) productivity class 2 as intercept, c) productivity class 3 as intercept and d) productivity class 4 as intercept.

	Estimate	SE	z	p	Transformed estimate
a)					
Intercept	1.33	0.62	2.15	0.032	0.79
Class 2	-0.94	0.59	-1.59	0.111	
Class 3	-0.60	0.51	-1.16	0.247	
Class 4	0.04	0.71	0.05	0.959	
b)					
Intercept	0.40	0.57	0.69	0.489	0.60
Class 1	0.94	0.59	1.59	0.111	
Class 3	0.34	0.44	0.76	0.445	
Class 4	0.97	0.65	1.49	0.136	
c)					
Intercept	0.74	0.49	1.50	0.133	0.68
Class 2	-0.34	0.44	-0.76	0.445	
Class 1	0.60	0.51	1.16	0.247	
Class 4	0.63	0.55	1.14	0.254	
d)					
Intercept	1.37	0.69	1.99	0.046	0.80
Class 3	-0.63	0.55	-1.14	0.254	
Class 2	-0.97	0.65	-1.49	0.136	
Class 1	-0.04	0.71	-0.05	0.959	

Table IX. Parameter estimates for hovering versus other behaviours in productivity classes. a) Productivity class 1 as intercept, b) productivity class 2 as intercept, c) productivity class 3 as intercept and d) productivity class 4 as intercept.

	Estimate	SE	z	p	Transformed estimate
a)					
Intercept	-3.35	1.00	-3.37	0.001	0.03
Class 4	-1.26	1.13	-1.11	0.268	
Class 3	-0.66	0.87	-0.76	0.450	
Class 2	-0.36	1.03	-0.35	0.725	
b)					
Intercept	-3.72	1.08	-3.43	0.001	0.02
Class 1	0.36	1.03	0.35	0.725	
Class 4	-0.89	1.15	-0.78	0.438	
Class 3	-0.29	0.93	-0.32	0.751	
c)					
Intercept	-4.01	0.92	-4.36	<0.0001	0.02
Class 2	0.29	0.93	0.32	0.751	
Class 1	0.66	0.87	0.76	0.450	
Class 4	-0.60	0.92	-0.65	0.514	
d)					
Intercept	-4.61	1.17	-3.93	<0.0001	0.01
Class 3	0.60	0.92	0.65	0.514	
Class 2	0.89	1.15	0.78	0.438	
Class 1	1.26	1.13	1.11	0.268	

Table X. Parameter estimates for flying versus other behaviours in productivity classes. a) Productivity class 1 as intercept, b) productivity class 2 as intercept, c) productivity class 3 as intercept and d) productivity class 4 as intercept.

	Estimate	SE	z	p	Transformed estimate
a)					
Intercept	-2.08	0.69	-3.02	0.003	0.11
Class 4	0.11	0.87	0.13	0.898	
Class 3	0.84	0.62	1.36	0.175	
Class 2	1.13	0.69	1.65	0.098	
b)					
Intercept	-0.94	0.57	-1.67	0.095	0.28
Class 1	-1.13	0.69	-1.65	0.098	
Class 4	-1.02	0.75	-1.37	0.171	
Class 3	-0.29	0.46	-0.63	0.532	
c)					
Intercept	-1.23	0.48	-2.58	0.010	0.23
Class 2	0.29	0.46	0.63	0.532	
Class 1	-0.84	0.62	-1.36	0.175	
Class 4	-0.73	0.66	-1.11	0.267	
d)					
Intercept	-1.97	0.76	-2.60	0.009	0.12
Class 3	0.73	0.66	1.11	0.267	
Class 2	1.02	0.75	1.37	0.171	
Class 1	-0.11	0.87	-0.13	0.898	

Table XI. Parameter estimates for prey capture, or prey capture attempts, versus other behaviours in productivity classes. There were no observations of prey capture in productivity class 1. a) Productivity class 2 as intercept, b) productivity class 3 as intercept and c) productivity class 4 as intercept.

	Estimate	SE	z	p	Transformed estimate
a)					
Intercept	-4.07	1.15	-3.54	0.000	0.02
Class 3	-0.14	0.96	-0.15	0.881	
Class 4	1.70	1.68	1.01	0.313	
b)					
Intercept	-4.21	1.00	-4.22	<0.0001	0.01
Class 2	0.14	0.96	0.15	0.881	
Class 4	1.84	1.59	1.16	0.248	
c)					
Intercept	-2.37	1.59	-1.49	0.135	0.09
Class 3	-1.84	1.59	-1.16	0.248	
Class 2	-1.70	1.68	-1.01	0.313	

Table XII. Parameter estimates for perching versus other behaviours in productivity classes. a) Forestry class I as intercept, b) forestry class II as intercept, c) forestry class III as intercept, d) forestry class IV as intercept and e) forestry class V as intercept.

	Estimate	SE	z	p	Transformed estimate
a)					
Intercept	0.38	0.68	0.55	0.580	0.59
Forestry class II	0.82	0.70	1.16	0.245	
Forestry class III	0.43	0.72	0.59	0.553	
Forestry class IV	0.47	0.72	0.66	0.512	
Forestry class V	-0.14	0.69	-0.21	0.837	
b)					
Intercept	1.19	0.49	2.46	0.014	0.77
Forestry class I	-0.82	0.70	-1.16	0.245	
Forestry class III	-0.39	0.52	-0.75	0.454	
Forestry class IV	-0.35	0.55	-0.63	0.532	
Forestry class V	-0.96	0.50	-1.94	0.053	
c)					
Intercept	0.80	0.53	1.51	0.132	0.69
Forestry class II	0.39	0.52	0.75	0.454	
Forestry class I	-0.43	0.72	-0.59	0.553	
Forestry class IV	0.04	0.59	0.07	0.942	
Forestry class V	-0.57	0.54	-1.05	0.294	
d)					
Intercept	0.85	0.56	1.51	0.132	0.70
Forestry class III	-0.04	0.59	-0.07	0.942	
Forestry class II	0.35	0.55	0.63	0.532	
Forestry class I	-0.47	0.72	-0.66	0.512	
Forestry class V	-0.61	0.58	-1.07	0.286	
e)					
Intercept	0.23	0.47	0.50	0.620	0.56
Forestry class IV	0.61	0.58	1.07	0.286	
Forestry class III	0.57	0.54	1.05	0.294	
Forestry class II	0.96	0.50	1.94	0.053	
Forestry class I	0.14	0.69	0.21	0.837	

Table XIII. Parameter estimates for hovering versus other behaviours in productivity classes. a) Forestry class I as intercept, b) forestry class II as intercept, c) forestry class III as intercept, d) forestry class IV as intercept and e) forestry class V as intercept.

	Estimate	SE	z	p	Transformed estimate
a)					
Intercept	-2.30	1.17	-1.97	0.049	0.09
Forestry class V	-1.34	1.41	-0.95	0.344	
Forestry class IV	0.48	1.27	0.38	0.704	
Forestry class III	-0.61	1.37	-0.45	0.656	
Forestry class II	-0.79	1.32	-0.60	0.549	
b)					
Intercept	-3.10	0.75	-4.13	<0.0001	0.04
Forestry class I	0.79	1.32	0.60	0.549	
Forestry class V	-0.55	1.08	-0.51	0.613	
Forestry class IV	1.27	0.84	1.51	0.131	
Forestry class III	0.18	0.99	0.18	0.855	
c)					
Intercept	-2.91	0.85	-3.43	0.001	0.05
Forestry class II	-0.18	0.99	-0.18	0.855	
Forestry class I	0.61	1.37	0.45	0.656	
Forestry class V	-0.73	1.14	-0.64	0.523	
Forestry class IV	1.09	0.94	1.16	0.247	
d)					
Intercept	-1.82	0.69	-2.64	0.008	0.14
Forestry class III	-1.09	0.94	-1.16	0.247	
Forestry class II	-1.27	0.84	-1.51	0.131	
Forestry class I	-0.48	1.27	-0.38	0.704	
Forestry class V	-1.82	1.04	-1.75	0.080	
e)					
Intercept	-3.64	0.88	-4.14	<0.0001	0.03
Forestry class IV	1.82	1.04	1.75	0.080	
Forestry class III	0.73	1.14	0.64	0.523	
Forestry class II	0.55	1.08	0.51	0.613	
Forestry class I	1.34	1.41	0.95	0.344	

Table XIV. Parameter estimates for flying versus other behaviours in productivity classes. a) Forestry class I as intercept, b) forestry class II as intercept, c) forestry class III as intercept, d) forestry class IV as intercept and e) forestry class V as intercept.

	Estimate	SE	z	p	Transformed estimate
a)					
Intercept	-1.24	0.75	-1.64	0.101	0.22
Forestry class V	0.29	0.73	0.40	0.690	
Forestry class IV	-1.05	0.81	-1.30	0.195	
Forestry class III	-0.22	0.77	-0.29	0.770	
Forestry class II	-0.46	0.75	-0.61	0.540	
b)					
Intercept	-1.70	0.58	-2.94	0.003	0.16
Forestry class I	0.46	0.75	0.61	0.540	
Forestry class V	0.75	0.54	1.40	0.162	
Forestry class IV	-0.59	0.69	-0.86	0.389	
Forestry class III	0.23	0.58	0.40	0.687	
c)					
Intercept	-1.46	0.63	-2.30	0.021	0.19
Forestry class II	-0.23	0.58	-0.40	0.687	
Forestry class I	0.22	0.77	0.29	0.770	
Forestry class V	0.52	0.61	0.85	0.394	
Forestry class IV	-0.83	0.73	-1.13	0.260	
d)					
Intercept	-2.29	0.73	-3.14	0.002	0.09
Forestry class III	0.83	0.73	1.13	0.260	
Forestry class II	0.59	0.69	0.86	0.389	
Forestry class I	1.05	0.81	1.30	0.195	
Forestry class V	1.34	0.70	1.91	0.056	
e)					
Intercept	-0.95	0.56	-1.70	0.089	0.28
Forestry class IV	-1.35	0.70	-1.91	0.056	
Forestry class III	-0.52	0.61	-0.85	0.394	
Forestry class II	-0.75	0.54	-1.40	0.162	
Forestry class I	-0.29	0.73	-0.40	0.690	

Table XV. Parameter estimates for prey capture, or prey capture attempts versus other behaviours in productivity classes. There were no observations of prey capture in forestry class I. a) Forestry class II as intercept, b) forestry class III as intercept, c) forestry class IV as intercept and d) forestry class V as intercept.

	Estimate	SE	z	p	Transformed estimate
a)					
Intercept	-4.43	1.13	-3.92	<0.0001	0.012
Forestry class IV	1.11	1.53	0.72	0.470	
Forestry class III	0.86	1.51	0.57	0.572	
Forestry class V	2.00	1.19	1.67	0.094	
b)					
Intercept	-3.57	1.12	-3.19	0.001	0.027
Forestry class II	-0.86	1.51	-0.57	0.572	
Forestry class IV	0.25	1.52	0.16	0.870	
Forestry class V	1.14	1.20	0.96	0.340	
c)					
Intercept	-3.32	1.13	-2.93	0.003	0.035
Forestry class III	-0.25	1.52	-0.16	0.870	
Forestry class II	-1.11	1.53	-0.72	0.470	
Forestry class V	0.89	1.21	0.74	0.461	
d)					
Intercept	-2.43	0.60	-4.03	<0.0001	0.081
Forestry class IV	-0.89	1.21	-0.74	0.461	
Forestry class III	-1.14	1.20	-0.96	0.340	
Forestry class II	-2.00	1.19	-1.67	0.094	