NEST BOX SELECTION IN THE EURASIAN KESTREL (FALCO TINNUNCULUS) IN THE TRYSIL REGION IN NORWAY

HEKKEKASSEPREFERANSE HOS TÅRNFALK (FALCO TINNUNCULUS) I TRYSIL I NORGE

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Abstract

Nest box selection in the Eurasian kestrel (*Falco tinnunculus*) in Southern Norway was estimated from fieldwork in Trysil Municipality in 2007 and by use of additional field data from 2005 and 2006. Used versus not used nest boxes was used as response variables and tested against multiple explanatory variables. In 2007, time of hatching was recorded and used as response variable as well, because early arrivals were hypothesized to select the best nest boxes or the best habitats. Microhabitat analyses within a 0.1 ha quadrate around the nest boxes and macrohabitat analyses outside this quadrate gave "general preference" over time, "year effect preference" and "early arrival preference". Kestrels generally selected nest boxes in open, flat habitats such as bogs and clear-cuts, and where there were not too many competing pairs nearby. Kestrels selected nest boxes in close proximity to developed areas in 2005 when voles were scarce, probably because of higher density of alternative prey, such as birds, lizards and insects. Neither nest box size nor construction was important for nest box selection, but kestrels seemed to prefer boxes where the entrance hole was not too large. Some degree of cover around the nest box tree, measured as number of trees around the nest box, also seemed to matter. In addition, south facing nest boxes were selected earlier than others. I recommend using time of hatching in addition to nest box use as response variable in further studies on nest box selection by kestrels.

Sammendrag

Hekkekassepreferanser hos tårnfalk (*Falco tinnunculus*) i Sør-Norge ble undersøkt gjennom eget feltarbeid i Trysil kommune i 2007, og ved bruk av data innsamlet av lokale ornitologer i 2005 og 2006. Brukte versus ikke brukte hekkekasser ble brukt som responsvariabel og testet mot flere forskjellige forklaringsvariabler. Klekketidspunkt ble også brukt som responsvariabel i 2007, ettersom de beste hekkekassene og/eller de beste habitatene antas å bli okkupert først. Mikrohabitatanalyser, foretatt innenfor et kvadrat på ett dekar (0,1 hektar) rundt hekkekassene, og makrohabitatanalyser, foretatt innenfor en sirkel på 1,5 km^2, ble brukt for å gi "generell preferanse" over tid, samt for å se om det var en "år-effekt" og "tidlig ankomst preferanse". Tårnfalkene selekterte generelt hekkekasser i åpent flatt habitat, som for eksempel myrer og hogstflater, hvor det ikke var mange konkurrerende par i nærheten. Tårnfalkene valgte hekkekasser i nærheten av bebygde områder i 2005, da det var få smågnagere, trolig fordi de da søkte etter alternative byttedyr som fugler, firfirsler og insekter. Hverken kassenes størrelse eller utforming så ut til å ha vesentlig betydning for tårnfalkenes valg, men det så ut til at de foretrakk at kassene ikke hadde for store innganghull. Videre så grad av skjul ut til å ha en viss betydning, i form av antall trær på utsiden av hekkekassen. I tillegg ble sørvendte hekkekasser tatt i bruk tidligere enn kasser med andre himmelretninger. Jeg anbefaler å bruke klekketidspunkt i tillegg til brukte versus ikke brukte hekkekasser som responsvariabel i videre forskning på hekkekassepreferanse hos tårnfalk.

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Introduction

The function of a bird's nest is to protect the vulnerable eggs and young from predators and adverse weather conditions (Elkins 2004). In mature unmanaged forests, natural tree holes are plentiful, and many bird species are therefore adapted to utilize these cavities as nest sites, which give particularly good protection against predators. However, in the case of younger managed woods, which are the dominating forest type in much of Western Europe today, such cavities are almost invariable (Newton 2003). The breeding density of many non-excavating cavity-nesting birds is therefore limited by shortage of nest-sites (Newton 2003). Hence, cavity nesting bird species will often use artificial nest sites, and humans can thus influence their breeding density by putting up nest boxes. Nest box provision has almost always increased the local breeding density of one or more species of hole-nesting birds (Newton 2003).

Another factor limiting the abundance and distribution of a bird species is food supply, which depends on food quantity, quality and availability. Therefore bird densities are usually limited either by nest sites or food, whichever is in shortest supply (Newton 2003). Food quantity is of special importance for birds of prey, which usually raise more nestlings when prey are abundant, e.g. in good vole years (Newton 1979). When a prey species is surplus, birds of prey may even cache food in the nest if the male bring more prey than the female and nestling can eat. Food quality may also vary to some extent, due to variations in fat content or the presence of ecto- and endoparasites in prey, but this variation will be much less than for herbivorous birds, which are affected by the impact of season and weather on plant quality. Eating living prey also means that the food is usually fresh and thus of better quality than for instance stored seeds or old carcases. Food availability, however, is of greatest importance for birds of prey. Large numbers of prey are to little help if most of them are difficult to detect or capture.

The Eurasian kestrel (*Falco tinnunculus*), hereafter called the kestrel, is one of the most studied raptors of the World (Village 1990). There could be several reasons for this, but that it is familiar with humans, is one advantage when studying this species. The Kestrel is a relatively small raptor species with a mean body weight in the breeding season of 195 and 250 g for male and female, respectively (Village 1990). The Kestrel is connected to open landscapes (Charter et al. 2007), it is widely spread geographically, and it operates often numerous compared to other raptors. Kestrels are adapted to a great variety of open or moderately wooded terrains, normally with herbaceous vegetation or low shrubs, such as grasslands, steppes, moorlands, cultivations, wetlands with sparse vegetation and even sub-deserts, from coasts to pastures above the tree line in mountains, occasionally reaching 4500 meters above sea level (Cramp 1980). It is also found in villages, towns and even cities, on outskirts and lightly built-up areas (Cramp 1980). In Norway, the kestrel is most common above the tree line, but it also occurs regularly along the coast and in open forests and agricultural landscapes (Olsen 2007). The majority of the kestrels breeding in Norway migrate southwards in winter.

In Norway, the kestrel populations fluctuate to some extent with the abundance of microtine rodents, which are the most common prey (Hagen 1952). In recent decades, artificial nest-boxes for kestrels have frequently been put up in several countries. Kestrels, as other falcons, do not build their own nests. Adaptations to breed in different sites, such as stick nests build by other species, cliff ledges, buildings, and cavities and holes in trees appear to be the kestrel's way of solving this problem. Kestrels even regularly nest at the ground on some Scottish islands were there are no mammalian predators (Newton 1979). However, lack of cliffs, buildings, holes in trees or other suitable places for nesting seems to limit the distribution of the kestrel (Village 1990). In Spain, a large increase in the number of breeding pairs was observed after installation of nest boxes (Fargallo et al. 2001). In my study area in Trysil in southern Norway, close to 400 nest boxes have been set up. This has multiplied the population resulting in 301 box-nesting pairs in the summer of 2007.

The design and size of nest boxes has been assumed to be an important factor for the kestrel's selection of nest sites. Boxes of an intermediate size (base: 34 * 35 cm) were selected before small boxes (base: 25 * 27,5 cm) by kestrels in Finland (Valkama and Korpimäki 1999). The intermediate nest box size used in Finland corresponds approximately to the average nest box size used in Trysil. Orientation also seems to affect the selection, as sheltered boxes were occupied more frequently than exposed boxes (Valkama and Korpimäki 1999). Orientation and size of boxes were associated with nest box selection, whereas laying date, cyclic food abundance and the habitat characteristics around the nest were important for the breeding success (Valkama and Korpimäki 1999). Laying date may, however, also reflect important factors in nest box selection if early arrivals occupy the best nest sites, as for birds in general (Newton 1979).

In Finland, kestrels' nest box occupancy rate was positively correlated with distances to forest, road and buildings (Valkama and Korpimäki 1999), the latter indicating that disturbances from humans is a factor that affect nest site selection. Height above the ground also seem to influence the choice of nests, since kestrels have generally avoided lower heights (Shrubb 1993). Weather conditions may also influence nest site selection, and this factor may be especially important for open-habitat nesting raptors, such as the kestrel, compared to dense-habitat nesting raptors such as the goshawk (*Accipiter gentilis*) and the sparrowhawk (*Accipiter nisus*).

My aim was to study kestrels' selection of nest boxes with regard to box size, design, orientation, height, arrival, time of hatching and micro- and macrohabitat characteristics around the nest. I looked at the importance of different habitat variables on nest site selection by comparing habitat variables from plots around nest boxes selected by kestrels with those that were not selected, i.e. used versus not used nest boxes. Annual variations in vole abundance on a larger scale were used to check whether there were different box preferences due to the availability of food. I predicted that selection for boxes could vary between good and poor vole years, and that the impact of habitat is more pronounced during vole-poor years, as reported for the common buzzard (*Buteo buteo*) (Löhmus 2003). If so, selection for boxes near habitats with alternative prey such as lizards, birds, shrews and insects could be expected in low vole years.

Questions to be answered:

1. What is the most preferred height when it comes to nest box selection?
2. What is the most preferred nest box size?
3. What are the main habitat characteristics for nest box selection?
4. What is the most preferred orientation of nest box?
5. Are there different preferences for nest boxes at low versus high vole density?
6. Is there different selection for nest box size at low versus high vole density?
7. Is there different selection for nest box habitat at low versus high vole density?
8. What is the ideal space or openness around the nest box?
9. Adaptations to breed in different sites; is nest box size and construction important?

Methods

Study area

The study was conducted in the boreal and hemi-boreal zones in Trysil Municipality in Hedmark County, in south-eastern Norway (61°07'–61°42'N, 11°35'–12°51'E), at altitudes of 300–900 m above sea level. The area is dominated by coniferous forests intensively managed by modern forestry techniques. The proportion of bogs is relatively high, whereas the proportion of agricultural land is low. Scots pine (*Pinus silvestris*), Norway spruce (*Picea abies*) and mountain birch (*Betula pubescens*) are the most common tree species.

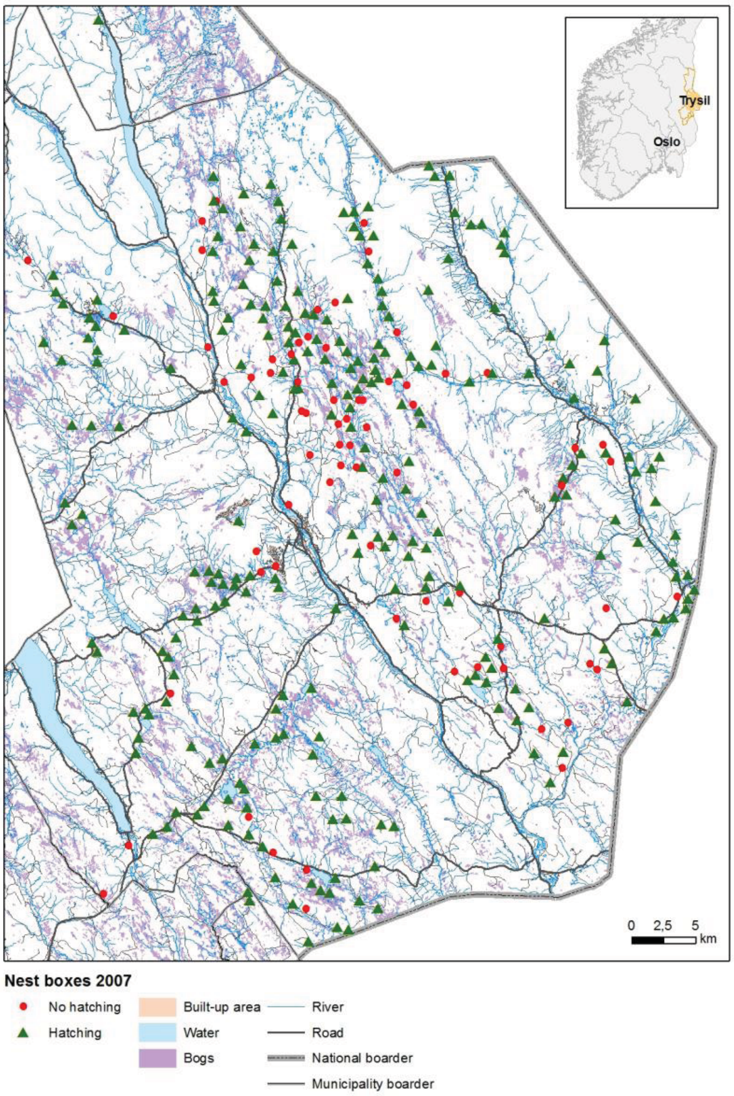


Figure 1. The study area in Trysil Municipality showing the location of the kestrel nest boxes checked in this study in 2007.

Material

In 2007, a total of 392 nest boxes, most of them put up in pine trees, were available, but for different reasons I had access to only 325 of these boxes. This summer was an all time high for the kestrel with 258 breeding pairs in the nest boxes I investigated, which means that 79 percent of the nest boxes were occupied. Nest boxes were mostly located in bogs and clear-cuts, surrounded by coniferous forest. There were also small patches of agricultural and developed areas in the surroundings of some of the nest boxes.

In June and July 2007 I registered which nest boxes were used for nesting or nesting attempt. "Nesting" was when the kestrels were present with eggs or nestlings, and "attempt of nesting" was when abandoned eggs were found. Attempts of nesting were considered as "nesting" in the nest box selection analysis. I also had information on the number of breeding pairs and marked nestlings in 2005 and 2006. The yearly turnover of breeding kestrels was high in the area (Foyn and Blestad pers. com.), corresponding with earlier findings (Valkama and Korpimäki 1999). The year 2005 was considered to be a poor year for kestrels, whereas 2006 was the second best year ever after 2007. Vole populations in the study area were considered to be small in 2005, increasing in 2006 and peaking in 2007 (Wiig, A. Ø. pers. com.).

The sizes and design of the nest boxes varied a lot, but many nest boxes were standards with approximately base: width 34 cm * length 30 cm, height 28 cm and entrance: width 34 cm and 15 cm height. All measurements are internal, reflecting the nesting space available for the kestrel inside the nest boxes. The size of the nest box base varied from 414 cm^2 to 1452 cm^2, with a mean size of 978 cm^2 in 2007. To get access to the nest boxes I used a six meters long ladder. Field assistants also helped me most of the time. I controlled approximately ten boxes a day, and checked them all during 38 days in June–July. In addition, local ornithologist registered the number of fledglings, which were marked with aluminium or steel rings.

The analyses were divided into two habitat characteristic categories, which were microhabitat on a small scale around the nest box, and macrohabitat on a larger scale.

Microhabitat analyses

Microhabitat analyses were conducted within plots covering a 0.1 ha quadrate around the nest box, with edges of 31.6 m (31.6 m * 31.6 m = 998.6 m²). This was the nearby characteristics, such as nest box measurements, nest tree specifications and other trees around the nest box. Height measurements were conducted with a measuring tape from the bottom of the nest box to the ground. For the nest box tree, species and total height were registered. Number of branches below the nest box and the distance from the bottom of the box to the nearest branch were also measured. A compass was used to register the orientation of the nest box entrance, graduated within 360°. The graduation was measured with a graduated arc, which stretches from northeast (1–90°), southeast (91–180°), southwest (181–270°) and northwest (271–360°), and also south (91–270°) and north (271–90°). I suppose that nest-boxes with a southern orientation receive more solar radiation during cloudless summer days. The main direction of the terrain with regard to slope was registered with a compass and categorized as north-east (1–90°), south-east (91–180°), south-west (181–270°) or north-west (271–360°).

The nest box condition was classified as 1) poor, 2) functional or 3) good. Nest boxes classified as poor had one or several defects such as hole in bottom, ceiling and/or walls. Nest boxes classified as functional had no serious defects, while boxes in good conditions were as good as new. Nest box inside measurements, i.e. length, breadth, height, bottom area and volume, as well as entrance hole measurements, i.e. breadth, height and area, were also registered. The forest type was classified into one of five categories according to the succession stage, where 1) was recently cut and 5) was mature forest. Vegetation was categorized in different vegetation types, organized under three main vegetation types in the analyses. These were 1) forest, 2) bogs and 3) cutting areas. The percentage of vegetation cover was the proportion of area covered by trees and bushes in the quadrate around the nest box when looking from above. All trees >7 cm in breast height (1.3 m above ground) were counted and identified to species.

Further, to examine the possible impact of weather conditions on annual breeding success, which may be indicative for the kestrels' choice of nest sites in the study area, I used mean temperatures and mean rainfall (mm) in the spring months March–May. Mean temperatures and mean rainfall is hereafter called temperature and rainfall. I assumed that weather condition has a direct effect by influencing the choice of nest-box, i.e. that nest-boxes which are more exposed to tough weather will be less used. The meteorological data from Trysil were obtained from Rena-Haugedalen Meteorological Station (61°20'N, 11°40'E, 240 m above sea level).

Macrohabitat analyses

The openness around each nest box was measured both from the nest box and outside the quadrate plots of 0.1 ha surrounding the nest box. A Nikon Laser Rangefinder (Laser 1200 s 7 * 25) was used. This was initially meant to be a measure for how visible the nest box is for predators, but it also gives an estimate of the occurrence of open habitats, i.e. favorable hunting grounds, around the nest box. Laser measurements were conducted in a straight line in front, back, right and left of the nest boxes. It measured the distance to the nearest forest area from the same height as the nest boxes. Exact measurements for distances longer than 500 m were difficult to obtain, because it was hard to keep the laser steady, especially in strong wind. Measurements >500 m were classified as 750 m and >1000 m were classified as 1250 m. Even though laser measurements were taken from the 0.1 ha quadrate, I categorized it in the macrohabitat analysis. Angle of gradient was measured with a Suunto PM-5 Combined height- and clinometers. This measurement was taken from the ground under the nest box and out of the quadrate based on my view of the main directions of the slope. This angle of gradient is more based on the main slope in the surrounding terrain than in the quadrate alone, and is therefore also categorized to the macrohabitat analyses.

The rest of the macrohabitat analyses were conducted with ArcMap Version 9.2 hereafter called GIS analyses. All nest boxes were plotted into a handhold GPS and transferred to the GIS program. A circle of 0.7 km radius was assumed to be an appropriate estimate of the kestrel`s constructed home range (0.7 km * 0.7 km * 3.14 = 1.54 km^2). Village (1990) reported the mean home range of kestrels to be less than 1 km^2 in good vole years, but over 10 km^2 in low vole years. Because both 2006 and 2007 were relatively good vole years in my study area, I assumed that 1.5 km^2 would be a good basis for home range analyses for this period. In 2005, however, home ranges may have been larger due to low vole abundance, but the approach used may still reflect what kind of habitat the kestrels prefer. It was also important to use the same area between years to keep analyses as plainly as possible.

The proportion of different habitat types within the constructed home range (1.54 km^2) was estimated by use of a digital soil type map (DMK) constructed by the Norwegian Forest and Landscape Institute. I used FTEMA, which included areas of water, developed areas and roads, and ATIL, which are area conditions defining natural terrain types. I gathered some codes together to simplify the material, resulting in the variables water (code 3000), developed areas (code 5200), roads (code 7200), bogs (code 11), bogs with forest (codes12, 13 and 14), agricultural areas (codes 21, 22 and 23), forests (codes 24, 25 and 26) and other areas (codes 27, 28, 29 and 31). In addition, the distances from the nest boxes to the nearest water above 0.3 hectares, bog, road and developed area were measured. The digital maps used were from the period 2002–2007. This means that some maps could be five years older than others. However, I do not think this is a serious source of error, because developed areas, roads, bogs, bogs with forest, agricultural areas and other areas are all proportionally stable environments. Forest is probably the variable that could change most between years, because of clear-cutting of old forest stands.

The total of nest boxes within 3 km radius was summed up to look for density dependence, giving a 3 km * 3 km * 3.14 = 28.26 km^2 circle around the nest boxes.

In addition to checking for use versus no use, I estimated the time of hatching based on estimated nestling ages, because I predicted that early arriving kestrels would lay eggs earlier, so that early time of hatching would indicate early arrival. The time of hatching data was presented as days after first of May. I used time of hatching as an additional response variable, to test whether early arriving kestrels selected the best habitats and the best nest boxes. The early arrivals have numerous of empty nest boxes to choose from and their selection may be important for the understanding of the nest box selection. In 2007, I checked all the boxes myself, and therefore I could also register nesting attempts. This was when kestrel had started to breed, but did not fulfil. Nesting attempts were only included in 2007 and this could be a source of error when it comes to nest box selections, because most likely there were some nesting attempts also in 2005 and 2006, not included in the analyses.

The main predators on kestrel nests in the study area are the pine marten (*Martes martes*) and corvids. In addition, other raptors can predate kestrels or exclude them from nest sites through competition. For instance, a hawk owl (*Surnia ulula*) pair nested in one of the nest boxes early in the season 2007, and no kestrels nested here later on this year. This nest box was excluded from the analyses. Three cases of nest boxes with unhatched goosander (*Mergus merganser*) eggs and lots of feather were also excluded from the analyses. A common buzzard was observed close to one empty nest box, but this nest box was still included in the analyses. One dead adult kestrel female was found under a nest box, although the fledglings had already abandoned the nest. In two nest boxes there were sign of egg predation and in two abandoned eggs were found. When looking at use versus no use a total of 260 nest boxes were included in the analyses in 2005, 2006 and 2007. It was important to use the same boxes for comparison between years, and unfortunately some of the younger nest boxes therefore had to be refused also including three nesting attempts out of five in 2007. A total of 229 nest boxes were included in the time of hatching- analyses in 2007, because there was no record of time of hatching of all the nest boxes used.

Nest box age and previous nesting success

Nest box age was categorized as new when they were one year or younger, or old when they were two years or older. Because I used the same boxes in comparisons between years, nest boxes one year and younger were excluded in 2006 and two years and younger were excluded in 2007. Nesting in the previous year was when there had been nesting in the same nest box in the previous year. The variables "nest box age" and "nesting in the previous year" did not influence micro- or macrohabitat directly, and were therefore not categorized as either of them.

Statistical analyses

Statistical analyses were performed using the statistical software JMP 4.0 (SAS, 2002). Means are given with ± SE of different variables for nest boxes not used and used. Values of $P < 0.05$ were accepted as significant. Univariate and Multivariate Logistic regression models with Likelihood Ratio Test and Nominal Logistic fit for Hatching used as response variable in 2005, 2006, 2007 and all year pooled together (2005-2007) was conducted. Univariate and Multivariate Logistic regression models with Likelihood Ratio Test and Nominal Logistic fit for Time of Hatching used as response variable in 2007 was also conducted. AIC values were calculated by hand from JMP values. Oneway Analysis of Time of Hatching as response variable in 2007, are given with ± SE and 95% confidence limits for different variables. Bivariate fit of Time of Hatching as response variable in 2007 are given with Linear Fit of different variables.

Results

Reproduction in relation to weather conditions and food abundance

The nesting season of 2007 was very good and kestrels seemed to use the majority of the boxes, resulting in 79% nest boxes used (Table 1). Average hatching time in 2005 was 50 days after first of May, in 2006 54 days after first of May, and in 2007 only 44 days after first of May. The mean brood size was 3.76 in 2005, 4.04 in 2006 and 5.13 in 2007 (Table 1). In 2007, there was one brood with eight nestlings, the highest number ever recorded in this area. Five broods with seven nestlings were also ringed this year. There was a huge difference in the total number of ringed offspring between years, with more than five times as many in 2007 compared to 2005 (Table 1). The snow cover disappeared late in 2006, which together with a low mean temperature and much rainfall in April–May may explain the late hatching date this year (Table 1). Still, this year had the shortest period from snow cover disappearance to the date of hatching, only 58 days (Table 1).

Table 1. Annual variation 2005–2007 in vole abundance (Wiig, A. Ø. pers. com. 2008), date of snow cover disappearance, rainfall and mean temperature in spring, hatching time, brood size and nestling numbers. Weather data are from a meteorological station in Rena-Haugedalen.

	2005	2006	2007
Vole population	Small	Increasing	Peak
Date of snow cover disappearance	05.04	27.04	14.04
Rainfall (mm) April–May	108	153	58
Mean temperature (°C) April–May	5.7	5.5	6.8
Proportion (%) nest boxes occupied	31	41	79
	(n = 260)	(n = 289)	(n = 325)
Mean hatching time, days after first of May	50	54	44
	(n = 25)	(n = 51)	(n = 119)
Days from snow disappearance to hatching	76	58	61
Mean brood size	3.76	4.04	5.13
	(n = 62)	(n = 108)	(n = 243)
Total number of nestlings ringed	233	436	1246

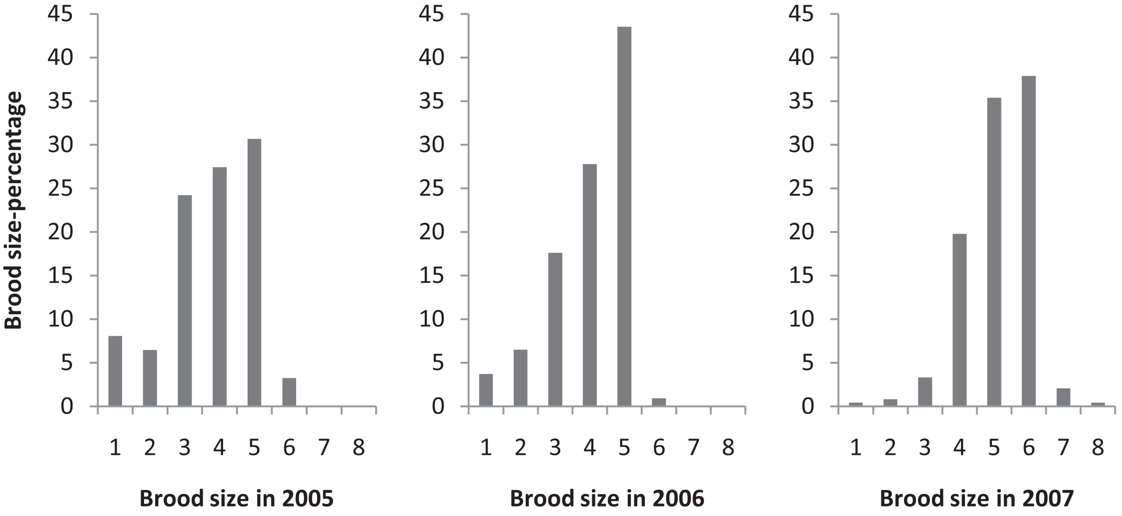


Figure 2. Proportion (%) of broods of different sizes in each study year. N = 62, 108 and 243 in 2005, 2006 and 2007, respectively.

Analyses based on used and not used nest boxes

In 2005, only two variables differed significantly between nest boxes used and not used (Table 2). Used nest boxes had a larger percentage of developed areas (Fig 3c) and more inhabited houses in the surrounding area (Fig. 3d) than those not used. In addition, there was a tendency for nest boxes with age ≥ 2 years to be used more than younger boxes, and for nest boxes situated in older cutting classes to be used more used than those situated in younger cutting classes (Table 2).

In 2006, seven independent variables differed significantly between the nest boxes used and those not used (Table 2). Kestrels appeared to select nest boxes used in the previous year and with few alternative nest boxes within 3 km. Boxes with smaller entrance hole breadth were selected before those with wider entrance, and nest boxes with smaller entrance hole area were selected before those with larger. For boxes used, there was a longer average distance in metres to the nearest forest (Fig. 3a). Boxes in flat terrain were selected before boxes in steep terrain and boxes situated in bogs and clear cuts were selected before those in forests (Table 2). There was a tendency that nest boxes surrounded by few deciduous trees were selected before those surrounded by several deciduous trees (Table 2).

In 2007, there were four significant results with regard to nest box selection (Table 2). Nest boxes used had significantly fewer nest boxes within the 3 km radius than those not used (Table 2, Fig. 4), indicating density dependence. Openness, represented by longer distances to the nearest forest (Fig 3a) and high bog percentage (Fig. 3b), seemed to be preferred. Kestrels also preferred boxes with few nearby buildings (Table 2). There was an almost significant preference for boxes with longer internal length and smaller entrance hole breadth, and for boxes situated in flat terrain and with several branches under the nest box (Table 2). There also was a tendency for nest boxes used in the previous year to be used more than those not used in the previous year (Table 2).

Table 2. Results from likelihood-ratio tests in univariate logistic regression models with kestrel nest boxes used or not used as response variable. For each year, all results with P < 0.1 are given.

Year	Variable	χ^2	df	P
2005	Percentage developed area	7.99	1	0.005
	Houses per nest box	4.28	1	0.039
	Nest box age 2005	3.37	1	0.066
	Cutting class	6.44	3	0.092
2006	Nesting 2005	22.55	1	<0.001
	Area entrance hole	6.78	1	0.009
	Angle of gradient	6.08	1	0.014
	Nest boxes within 3 km	5.60	1	0.017
	Entrance hole breadth	5.02	1	0.025
	Vegetation type	7.19	2	0.027
	Average laser	4.49	1	0.034
	Deciduous trees	2.76	1	0.097
2007	Nest boxes within 3 km	9.03	1	0.003
	Average laser	5.54	1	0.019
	Buildings per nest box	4.55	1	0.033
	Bog percentage	4.15	1	0.042
	Nest box breadth	3.52	1	0.061
	Nest box length	3.47	1	0.062
	Angle of gradient	3.37	1	0.066
	Number of branches	3.15	1	0.076
	Nesting 2006	3.13	1	0.077

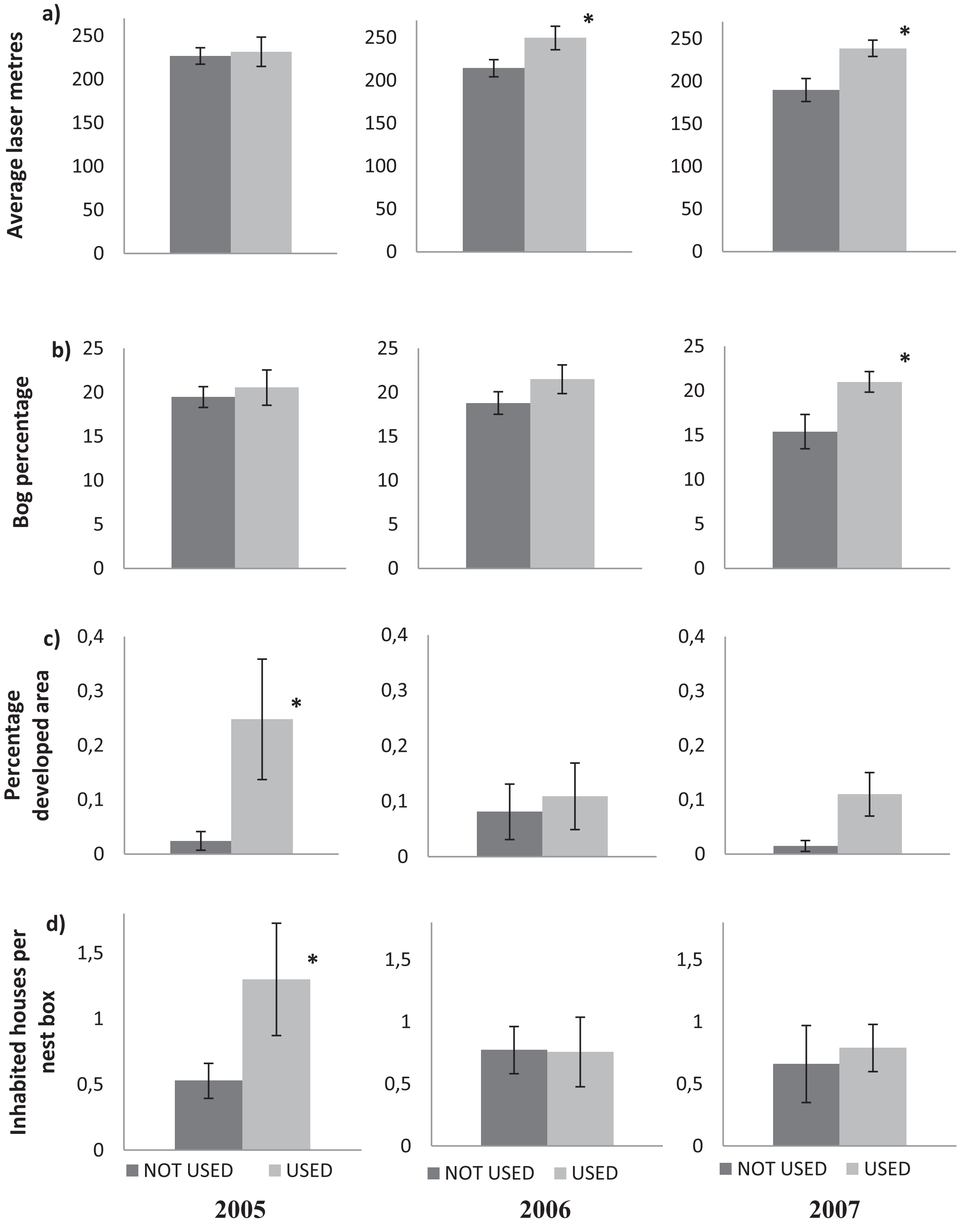
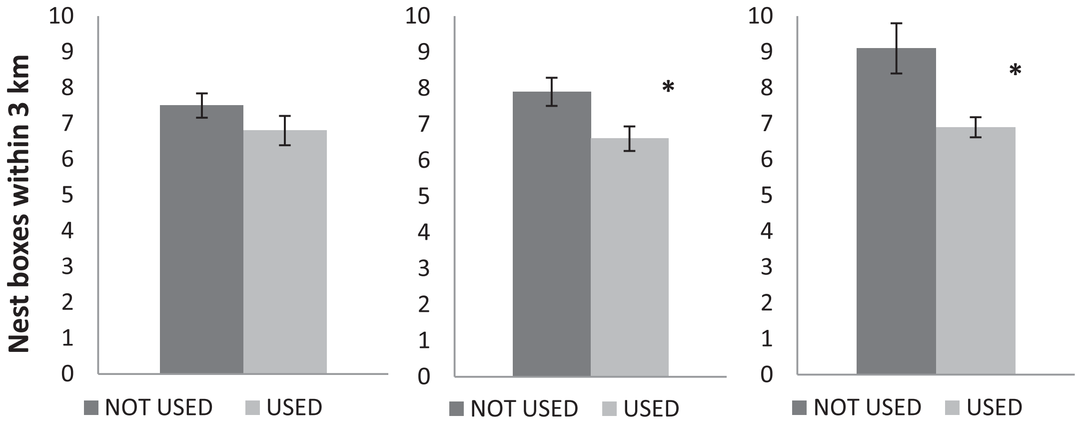


Figure 3. Mean values (± SE) of different variables for nest boxes not used and used. a) Average laser in metres to nearest forest. b) Proportion (%) of bog within the constructed home range (1.54 km²). c) Proportion (%) of developed area within the constructed home range (1.54 km²). d) Number of inhabited houses per nest box within the constructed home range (1.54 km²). N = 260 all years * = P < 0.05.

In 2006 and 2007, nest boxes used had significantly fewer nest boxes within a 3 km radius from the nest box, than nest boxes not used (Fig. 4). There was a similar tendency in 2005, but this year the result was not significant.



2005 **2006** **2007**

Figure 4. Mean number (± SE) of alternative nest boxes within 3 km radius (28.26 km²) for nest boxes not used and used. Nest boxes used had significantly fewer alternative nest boxes within 3 km radius than those not used in both 2006 and 2007. Not used, n = 179 and used n = 81 in 2005. Not used, n = 145 and used n = 115 in 2006. Not used, n = 47 and used n = 213 in 2007. * = $P < 0.05$.

No specific traits of nest box size were significant in any years, neither with regard to volume nor base area. The average nest box base size in Trysil was 978 cm² and varied from 414 cm² to 1452 cm². In 2007, nest box internal length was almost significantly longer for nest boxes used than for those not used. Entrance hole breath differed significantly in 2006, where narrow entrance holes were selected before wider entrances. In addition, kestrels selected smaller area entrance holes before larger. There were only eleven small nest boxes ≤ 700 cm². For these, there were an occupancy percentage of 0, 45 and 73 in 2005, 2006 and 2007, respectively. For 2006 and 2007, this was almost similar to the overall occupancy percentage (Table 1).

For 2005, the best multivariate model, based on AIC value and number of variables, included only the percentage of developed areas (Table 3, model C). Nest boxes situated in areas with high percentage developed areas were preferred (Fig. 3c). 2005 differed from the other years with regard to nest box selection. Whether the nest box was used in the previous year may have been important also in 2005, but I had no data for nest box use in 2004.

Table 3. Results from likelihood-ratio tests in multivariate logistic regression models with kestrel nest boxes used or not used in 2005 as response variable.

Model	Variable	χ^2	df	P	ΔAIC
A	Percentage developed area	7.39	1	0.007	
	Nest box age 2005	2.77	1	0.096	0.00
B	Percentage developed area	8.16	1	0.004	
	Succession stage	6.60	3	0.086	0.17
C	Percentage developed area	7.99	1	0.005	0.77
D	Percentage developed area	2.73	1	0.098	
	Houses per nest box	1.45	1	0.228	1.28
E	Houses per nest box	4.28	1	0.039	4.49

The best multivariate model in 2006 with regard to AIC value and number of variables contained the variables nesting 2005 and area entrance hole (Table 4, model C).

The best multivariate model in 2007 with regard to AIC value and number of variables contained the variables nest boxes within 3 km, buildings per nest box, bog percentage and nest box breadth (Table 5, model B).

Table 4. Results from likelihood-ratio tests in multivariate logistic regression models with kestrel nest boxes used or not used in 2006 as response variable.

Model	Variable	χ^2	df	P	ΔAIC
A	Nesting 2005	20.83	1	<0.001	
	Area entrance hole	5.96	1	0.015	
	Angle of gradient	3.33	1	0.029	0.00
B	Nesting 2005	21.35	1	<0.001	
	Area entrance hole	6.38	1	0.012	
	Nest boxes within 3 km	3.30	1	0.069	0.03
C	Nesting 2005	22.41	1	<0.001	
	Area entrance hole	6.85	1	0.009	1.34
D	Nesting 2005	22.55	1	<0.001	7.02
E	Area entrance hole	6.78	1	0.009	24.90
F	Angle of gradient	6.08	1	0.014	26.78
G	Nest boxes within 3 km	5.60	1	0.018	27.25

Table 5. Results from likelihood-ratio tests in multivariate logistic regression models with kestrel nest boxes used or not used in 2007 as response variable.

Model	Variable	χ^2	df	P	ΔAIC
A	Nest boxes within 3 km	17.47	1	<0.001	
	Average laser	1.88	1	0.172	
	Buildings per nest box	8.71	1	0.003	
	Bog percentage	7.67	1	0.006	
	Nest box breadth	5.82	1	0.016	
	Nest box length	2.40	1	0.121	0.00
B	Nest boxes within 3 km	19.34	1	<0.001	
	Buildings per nest box	7.29	1	0.007	
	Bog percentage	17.46	1	<0.001	
	Nest box breadth	5.58	1	0.018	0.27
C	Nest boxes within 3 km	17.70	1	<0.001	
	Average laser	1.87	1	0.171	
	Buildings per nest box	7.87	1	0.005	
	Bog percentage	9.38	1	0.002	
	Nest box breadth	6.09	1	0.014	0.40
D	Nest boxes within 3 km	19.09	1	<0.001	
	Buildings per nest box	7.31	1	0.007	
	Bog percentage	14.66	1	<0.001	3.85
E	Nest boxes within 3 km	17.48	1	<0.001	
	Average laser	1.36	1	0.244	
	Buildings per nest box	7.75	1	0.005	
	Bog percentage	7.82	1	0.005	4.49
F	Nest boxes within 3 km	10.93	1	<0.001	
	Average laser	8.20	1	0.004	
	Buildings per nest box	6.58	1	0.010	10.31
G	Nest boxes within 3 km	10.03	1	0.002	
	Average laser	6.54	1	0.011	14.90
H	Nest boxes within 3 km	9.03	1	0.003	19.44
I	Average laser	5.54	1	0.019	22.93
J	Buildings per nest box	4.55	1	0.033	23.92
K	Bog percentage	4.15	1	0.042	28.32

Table 6 shows significant results from univariate analyses when the years were pooled. There was an effect of year, which can be explained by differences in food supply (Table 1). Old nest boxes and nest boxes with few occupied boxes within 3 km were most often used (Table 6, Fig. 5a). Also angle of gradient was highly significant, where nest boxes in areas with smaller angle were selected (Table 6, Fig. 5b). Nest boxes used had significantly higher average laser in meters, than those not used (Table 6, Fig. 5c). Boxes in areas with a high percentage of developed areas were selected before those with less developed areas (Table 6). Bog percentage, which also represents openness around the nest box, was almost significantly higher for the nest boxes used than for those not used (Table 6, Fig. 5f).

Table 6. Results from likelihood-ratio tests in univariate logistic regression models with kestrel nest boxes used or not used in 2005–2007 as response variable. All results with $P < 0.1$ are given.

Variable	χ^2	df	P
Year	152.71	2	<0.001
Nest box age	18.64	1	<0.001
Nest boxes within 3 km	11.71	1	<0.001
Angle of gradient	9.47	1	0.002
Average laser	5.66	1	0.017
Percentage developed area	4.58	1	0.032
Cutting class	7.96	3	0.047
Bog percentage	3.83	1	0.053

The best multivariate model with regard to AIC value and number of variables when all three years were pooled contained the variables: year, nest box age, nest box within 3 km, angle of gradient, percentage developed area, percentage developed area * year, average laser and cutting class (Table 7, model A). The interaction effect between percentage developed area and year reflects that nest boxes close to developed areas were selected only in 2005 (Table 2, Table 7, Fig. 3c), when vole population levels were low.

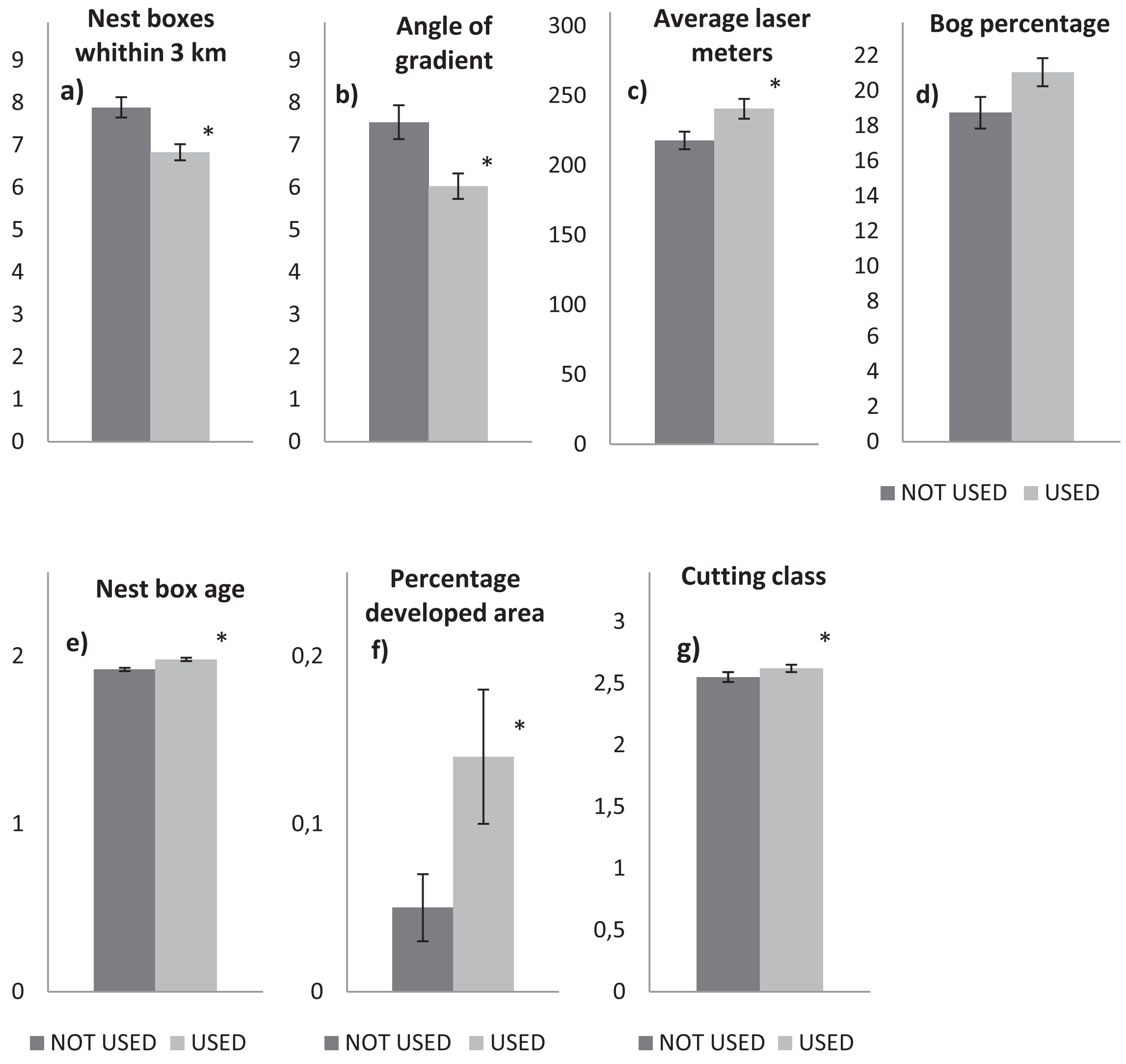


Figure 5. Different variables from all three years pooled together with mean values (± SE) of not used and used nest boxes for a) number of nest boxes within 3 km radius (28.26 km²) from the nest box; b) angle of gradient in the main direction from the nest box in degrees between 0–90°; c) average laser measurements in meters from the same height as the nest boxes position in the nesting tree and in four direction from the nest box, i.e. average meters from front, back and both sides to nearest woodland; d) bog percentage representing the portion of bogs within the constructed home range of 700 m radius from the nest box (1.54 km^2); e) nest box age where values close to 1 mean larger proportion of young nest boxes (one year and newer), while values close to 2 mean larger proportion of older nest boxes (two years and older); f) percentage developed area where higher percentage was selected before lower; g) cutting class where higher cutting classes were selected before lower. N = 780. * = $P < 0.05$.

Table 7. Results from likelihood-ratio tests in multivariate logistic regression models with kestrel nest boxes used or not used in 2005–2007 as response variable.

Model	Variable	χ^2	df	P	ΔAIC
A	Year	139.59	2	<0.001	
	Nest box age	2.62	1	0.106	
	Nest boxes within 3 km	19.14	1	<0.001	
	Angle of gradient	19.56	1	<0.001	
	Percentage developed area	7.85	1	0.051	
	Percentage developed area * Year	6.08	2	0.048	
	Average laser	6.42	1	0.011	
	Cutting class	16.82	3	<0.001	0.00
B	Year	135.68	2	<0.001	
	Nest box age	3.22	1	0.073	
	Nest boxes within 3 km	18.54	1	<0.001	
	Angle of gradient	12.96	1	<0.001	
	Percentage developed area	6.87	1	0.009	
	Percentage developed area * Year	4.40	2	0.111	
	Average laser	4.17	1	0.041	10.83
C	Year	134.97	2	<0.001	
	Nest box age	3.36	1	0.067	
	Nest boxes within 3 km	18.39	1	<0.001	
	Angle of gradient	18.05	1	<0.001	
	Percentage developed area	6.35	1	0.012	
	Percentage developed area * Year	4.21	2	0.012	13.00
D	Year	142.85	2	<0.001	
	Nest box age	4.00	1	0.045	
	Nest boxes within 3 km	20.41	1	<0.001	
	Angle of gradient	17.79	1	<0.001	18.37
E	Year	139.92	2	<0.001	
	Nest box age	3.83	1	0.050	
	Nest boxes within 3 km	14.72	1	<0.001	34.16
F	Year	137.80	2	<0.001	
	Nest box age	3.38	1	0.066	46.88
G	Year	152.71	2	<0.001	49.90

Calculated home range

The results shown in Fig. 5a suggest that there is a density dependent factor affecting nest box selection. When there were more than seven nest boxes within 3 km radius of the nest box kestrels appeared to prefer other nest boxes with fewer nest boxes in their surroundings.
Converted to km² this will be: Area = 3 km * 3 km * 3.14 = 28.26 km².
This divided on seven surrounding nest boxes and the one in the centre which is eight gives:
28.26 km² / 8 nest boxes within the 3 km radius = 3.53 km² per nest box.
Empty nest boxes have not been taking into consideration in this calculation. To include area per used nest box we must divide with nesting percentage and multiply with 100. This could be a good indicator of average home range based on a circular home range with the nest box in centre.

Kestrels home range formula: $\frac{3.53}{Nesting\ \ percentage\ \ *100}$

Kestrels calculated home range in 2005: 3.53 km² / 31 * 100 = 11.39 km².
Kestrels calculated home range in 2006: 3.53 km² / 41 * 100 = 8.61 km².
Kestrels calculated home range in 2007: 3.53 km² / 79 * 100 = 4.47 km².

Analyses based on time of hatching in 2007

When using time of hatching as response variable, I found eight significant results, of which seven were not significant in the analyses of nest box use. These variables were compass point, height above sea level, number of pine trees around the nest box, nesting 2006, distance to water, entrance hole height and number of conifer trees around the nest box. In addition, angle of gradient was also significant (Table 8, Fig. 6, Fig. 7, Fig. 8).

The best multivariate model with time of hatching as response variable included compass point N or S, numbers of pine around nest box, nesting in 2006, and entrance hole height (Table 9).

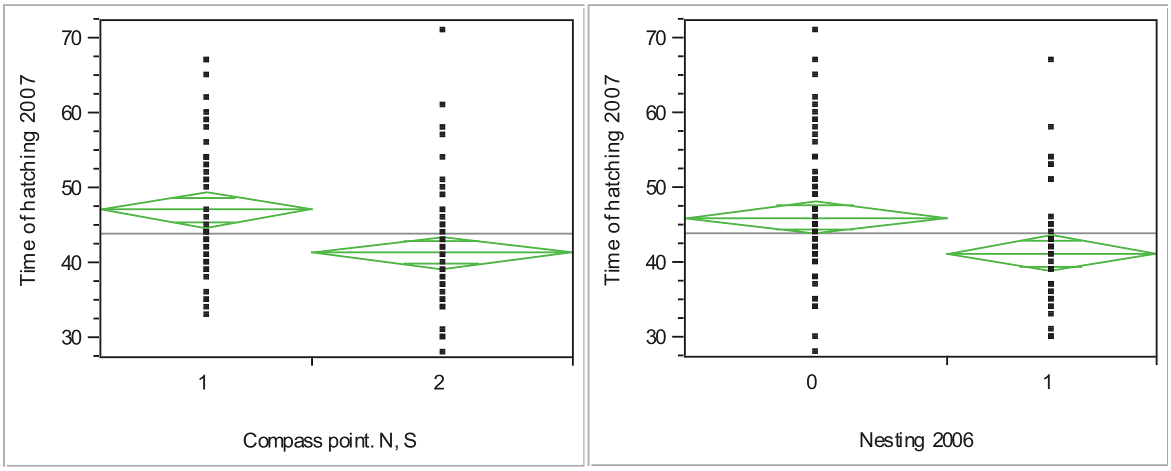
Table 8. Results from univariate linear regression models with time of hatching 2007 as response variable. All results with $P < 0.1$ are given.

Variable	df	F	P	R^2
Compass point N, S	1	12.42	<0.001	0.104
GPS height above sea level	1	10.59	0.002	0.090
Pine around nest box	1	9.74	0.002	0.083
Nesting 2006	1	8.38	0.005	0.073
Angle of gradient	1	7.16	0.009	0.063
Distance water	1	5.96	0.016	0.053
Entrance hole height	1	5.39	0.022	0.048
Conifer around nest box	1	5.30	0.023	0.047
Bog / forest percentage	1	3.40	0.068	0.031
Deciduous around nest box	1	3.40	0.068	0.031
Distance bog	1	3.12	0.080	0.028
Bog percentage	1	2.82	0.096	0.026

Table 9. Best multivariate models with time of hatching 2007 as response variable.

Variable	df	F	P	R^2	ΔAIC
Compass point N, S	1	14.57	<0.001		
GPS height above sea level	1	11.03	0.001	0.19	9.37
Compass point N, S	1	14.57	<0.001		
Pine around nest box	1	11.86	<0.001	0.19	8.60
Compass point N, S	1	13.34	<0.001		
Pine around nest box	1	12.61	<0.001		
Nesting 2006	1	8.02	0.006	0.25	2.58
Compass point N, S	1	14.74	<0.001		
Pine around nest box	1	9.73	0.002		
Nesting 2006	1	7.80	0.006		
Entrance hole height	1	4.47	0.037	0.28	0.00

Nest boxes oriented south were preferred, as they were in general occupied five days earlier than those orientated north (Fig. 6a). The time of hatching was almost five days earlier in nest boxes that had been used in the previous year (Fig. 6b).



a) **b)**

Figure 6. Oneway analysis comparing time of hatching 2007 between a) boxes faced north (1) and south (2), $P < 0.001$, and b) boxes where there was nesting in the previous year (1) and those where there was not (0), $P = 0.005$. Time of hatching numbers are days after the first of May. The figure gives mean values (± SE) and 95% confidence limit. N = 229.

Nest boxes with more pine and coniferous trees within the 0.1 hectares quadrate around the nest box were selected before nest boxes with fewer pines or conifers (Fig. 7a, b). There was a tendency for kestrels to start hatching earlier in areas with a high percentage of bogs (Fig. 7c) and forests/bogs (Fig. 7d), the latter being a mix of forests with openings of bogs. The same appeared for boxes surrounded by several deciduous trees (Fig. 7e), and boxes close to bogs (Fig. 7f).

Hatching time was earlier in close proximity to water above 0.3 hectares (Fig. 8a). Boxes with smaller entrance hole height were occupied before those with higher entrance holes (Fig. 8b). Hatching started earliest at low altitudes (Fig. 8c), and where the angle of gradient was low (Fig. 8d), indicating that Kestrels selected flat terrain before hilly.

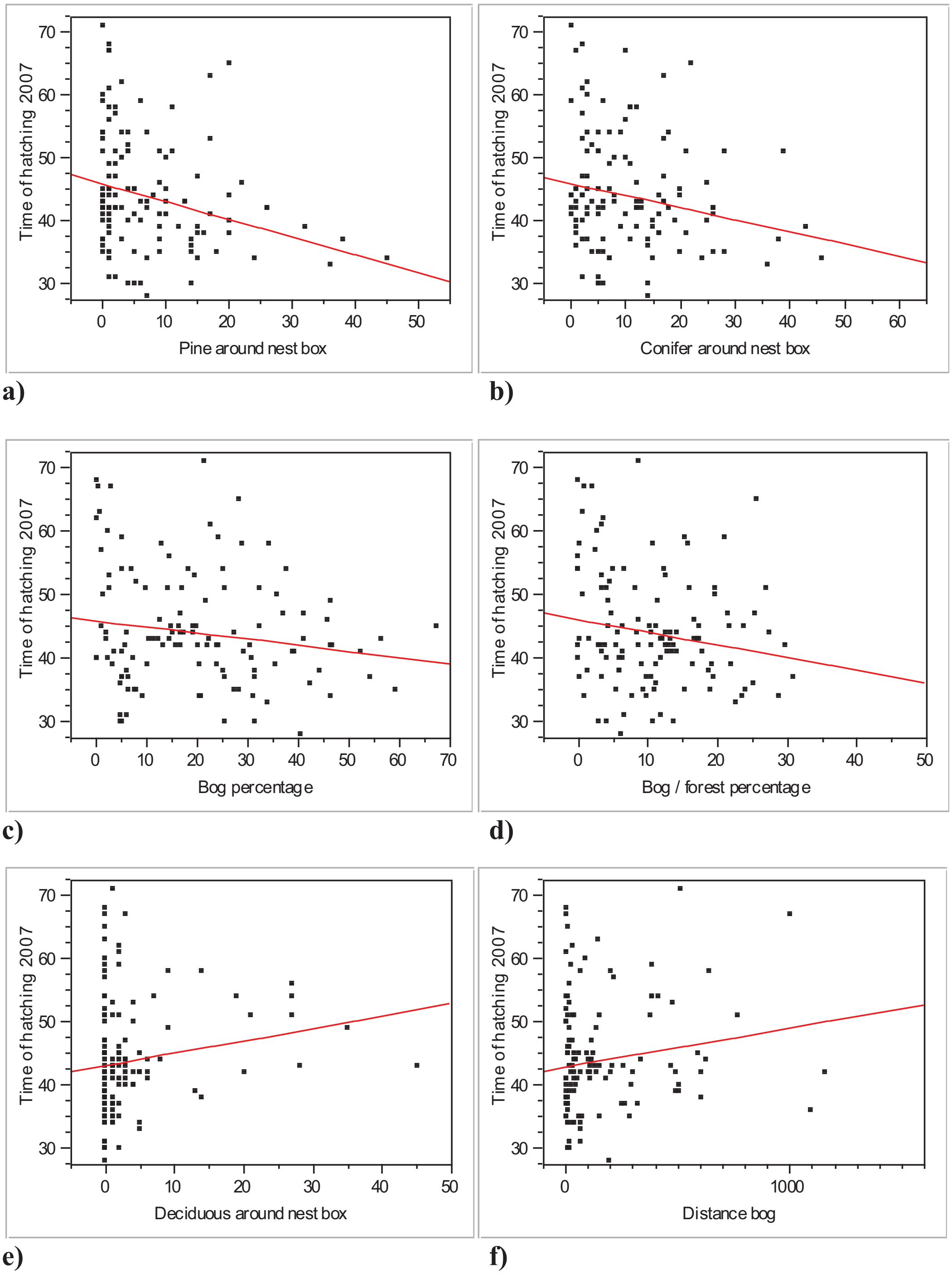
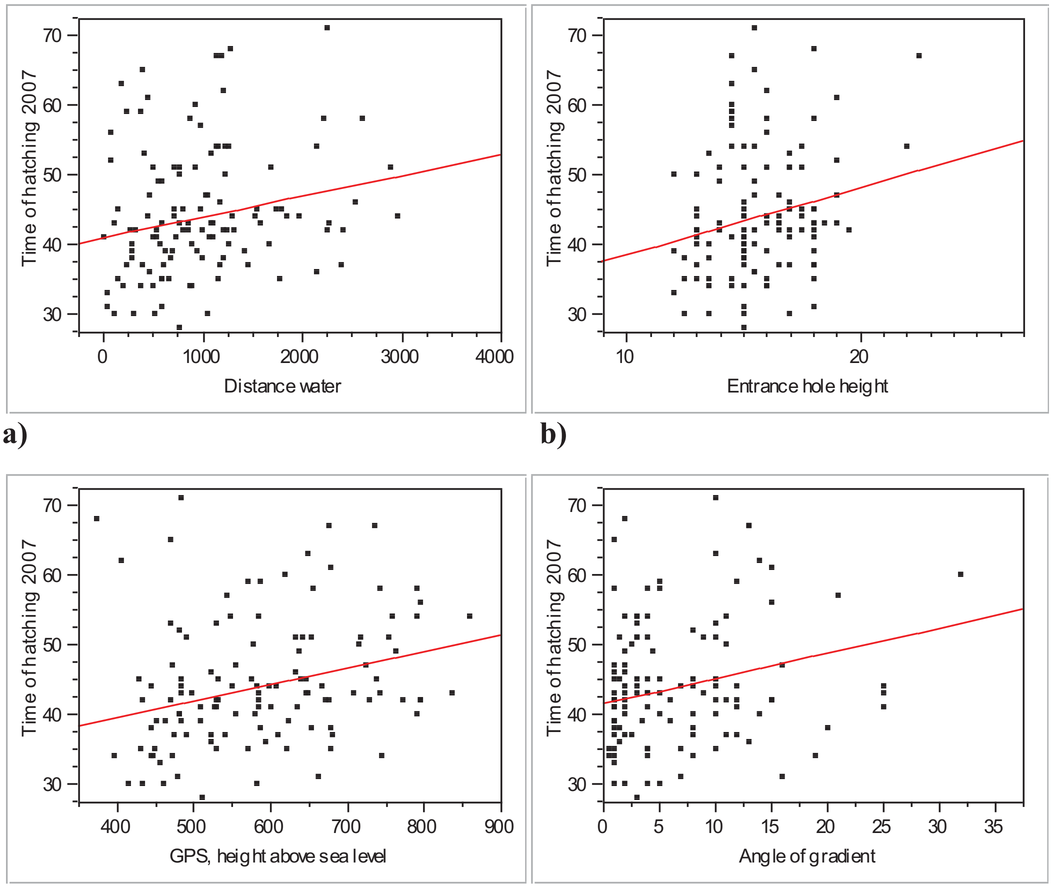


Figure 7. Time of hatching 2007 in relation to different explanatory variables, linear fit. Times of hatching numbers are in days after the first of May; a) The number of pine around the nest box (P = 0.002); b) The number of conifer around the nest box (P = 0.023); c) Proportion (%) of bog around the nest box (P = 0.096); d) Proportion (%) of bog / forest around the nest box, which is a mix of forest and bog (P = 0.068); e) The number of deciduous trees around the nest box (P = 0.068); f) Distance in metres from the nest box to the nearest bog (P = 0.080). N = 229.



a) **b)**

c) **d)**

Figure 8. Time of hatching 2007 in relation to different explanatory variables, linear fit. Time of hatching numbers are days after the first of May; a) Distance in metres from nest box to nearest water above 0.3 hectares (P = 0.016); b) Entrance hole height in centimetres (P = 0.022); c) Height above sea level in meters (P = 0.002); d) Angle of gradient (P = 0.009). N = 229.

Discussion

Density dependence

An important aspect in the study of kestrel nest site selection is that density dependence may prevent a nest box from being used, even if it is situated in an otherwise favourable environment. In my study, more than seven other nest boxes within a 3 km radius from a nest box seemed to affect nest box selection negatively. Before offering nest boxes to kestrels in the Trysil region, approximately 20–30 kestrel pairs were known to breed in the area (Blestad and Foyn. 2007). After the introduction of nest boxes from 1996 onwards, the kestrel breeding population gradually increased. Hence, scarcity of nesting places, and not food, has probably limited the distribution of kestrel in this region in the past.

Kestrels can nest in close proximity to each other, and compensate for proximity by hunting in different directions (Village 1990). Overlapping hunting areas between pairs are also reported (Village 1982, 1983), indicating that they do not defend all their range. Nevertheless, it seems to be a limit for how many kestrels that can nest within a given area. Some areas in central Trysil region had lower proportion of occupied nest boxes than others, and these areas also had a high density of nest boxes. Village (1990) found that vacant nest sites were present within the territories of some established pairs, but that territorial behaviour could prevent access by other individuals. In my study, density dependence occurred significantly in 2006 and 2007, and when all three years were pooled together. In 2005, when voles were less available, only 80 out of 260 nest boxes were used, probably because of larger territories. Hence, nest box density was less important for nest box selection when voles were scarce.

European kestrel populations are declining in the Paleartic because of the intensification of agriculture (Village 1990). In many modern high-intensity farmland areas in Britain, where artificial nest boxes have been provided, low availability of voles and insects seem to limit kestrel abundance (Shrubb 1993). In Spain, kestrel populations have been stable since the 1970s. In the Serena region, occupancy of nest boxes was highest in pasturelands (47.5%), while other habitats had much lower occupancy, ranging approximately 2–25%. This was probably due to lower habitat quality (Aviles et al. 2001). In my study, occupancy varied from 31 to 79%. Nevertheless, the population may continue to increase. This is because nesting places still seem to limit the kestrel population in parts of the Trysil region in years with high vole abundance.

Selection of old nest boxes

Another possible confounding factor in the study of nest box selection is that old nest boxes may be occupied before new ones, either because kestrels return to nest boxes they have successfully used in a previous year, or because they seek boxes they know exist. When all three years were pulled together, kestrels significantly selected older nest boxes before younger. I do not have data on previous nest box use for 2005, but kestrels showed a significant preference for nest boxes used in the previous year in 2006, and there was a similar tendency in 2007. This year, the mean time of hatching was almost five days earlier in nest boxes that had been used in 2006, indicating that nest boxes used in the previous year were actually preferred also in 2007. However, in Trysil, there has been a high yearly turnover of breeding kestrels (Foyn and Blestad pers. com.), as also found in Finland (Valkama and Korpimäki 1999). Hence, a preference for nest boxes used in the previous year may be explained rather by conspecific attraction or conspecific habitat copying, i.e. kestrels select nest boxes with signs of previous nesting success. Pajero et al. (2004) found evidence for this in Spain, where nest boxes successfully used in the previous year had almost double chance of being reoccupied in the subsequent year.

In my study, good nest box condition was not essential in any year. In fact, the tendency was that nest boxes in good condition were selected last, after poor and functional nest boxes, not significant. This was probably because nest boxes in good condition in general were younger than poor and functional nest boxes. It seems likely that kestrels discover new nest boxes easily, but that they prefer boxes with old prey remains and droppings, because this is an indication of previous breeding success. In Spain, both rollers (*Coracias garrulus*) and kestrels preferred nest boxes occupied by kestrels in the previous year before non-used boxes (Aviles et al. 2001, Pajero et al. 2004).

Nest box selection and weather

In my study, kestrels hatched earlier at lower altitudes, as could be expected due to earlier snow cover disappearance. Habitat quality is important for the ability to breed early (Verhulst and Nilsson 2008), and voles are more available for kestrels when the ground is snow-free. Although I did not find any effects of altitude in the analyses of used versus not used boxes, there could theoretically be other advantages at lower altitudes, related to habitats or prey abundances.

Kestrels seemed to be able to compensate for a late snow melting when vole populations were increasing. Despite a nine-day earlier snow melting in 2005, the average hatching day was six days earlier in 2007 than in 2005. The snow cover disappeared earliest in 2005; still the kestrels used 76 days forth to average hatching date. According to Wiebe et al. (2000), delaying incubation is possible when food is scarce. The early hatching, high proportion of occupied nest boxes and high nestling production in 2007 was probably first of all due to the peak in vole numbers. However, favourable weather conditions probably contributed to make this an extra good year for kestrels. In 2007, mean temperature was the highest and the amount of precipitation the lowest during the three-year period. Hence, hatching time seems to depend on several factors, where snow cover, rainfall, temperature and vole abundance are important.

Macrohabitat analyses – the impact of habitat and prey abundances

The reason why artificial nest boxes are used at all is that they provide better nesting conditions than ordinary nest sites. The placing and construction of nest boxes should be expected to affect the kestrels' selection if some nest boxes give advantages with regard to fitness. Optimal nest boxes should apply good nesting sites and low predation pressure, but also good hunting habitats in the surroundings. In Trysil, kestrels' nest box selection over time was mainly related to macrohabitat variables, indicating that the surrounding habitat is the basis for where kestrels choose to breed.

I estimated kestrels' home ranges to be 4–12 km² in my study period. This is quite similar to the 3–13 km² home ranges found by use of radio-telemetry in Scottish grasslands and English farmlands (Village 1990). In contrast, Casagrande et al. (2008) found the mean home range to be only 0.74 km² in Northern Italy. In my macrohabitat analyses, however, I used a 1.54 km² circle, because I regarded this to better capture the most important habitat characteristics inside the kestrels' real home ranges. Kestrel nest sites are often situated near the edge of their home range (Village 1990), so that the chance of capturing the real home range is highest close to the nest box. Carrillo and Gonzalez-Davila (2005) found a latitudinal increase in kestrel clutch size from south to north in the western Paleartic, probably because of a better food supply at northern latitudes. I therefore find it likely that in years with increasing and peaking vole populations, average home ranges are somewhat smaller in the Trysil area compared to Scotland and England.

The year effect identified in my study was most likely caused by fluctuations in vole density. The two major contributing factors for year-effects in studies on raptors are fluctuations in prey base and rainfall (Löhmus 2003). Differences between good and poor vole years have resulted in year-effects in studies of at least 18 species of raptors and owls (Löhmus 2003). The composition of kestrels' diet usually varies between years (Village 1990, Löhmus 2003, Steen 2004). In 2003, the food provided to kestrel nestlings in my study area was 31% voles, 24% reptiles, 20% birds and 24% shrews (Steen 2004; N = 203). Birds made up the largest biomass delivered, followed by voles, shrews and reptiles. In 2005, Løw (2006) found the following distribution of prey delivered to the nestlings: 12% voles, 10% reptiles, 61% birds and 17% shrews (N = 147). Homme (2008) conducted a similar study in 2007 and found the following distribution: 82% voles, 3% reptiles, 4% birds and 11% shrews (N = 3689). Insects and other prey were excluded in these comparisons. Vole populations were increasing in 2003, small in 2005 and peaking in 2007 (Wiig, A. Ø. pers. com.). Hence, voles were most important to kestrels in vole peak years, but compensation by other prey such as birds and lizards were important in poor vole years.

Kestrels in my study area also show a numerical response to vole numbers. Also in a farmland area in western Finland, the number of breeding kestrels fluctuated with spring densities of *Microtus* voles, and the number of fledglings was positively correlated with vole density (Korpimäki and Norrdahl 1991). In southern Sweden, raptor assemblages mainly exhibited functional responses (Erlinge et al. 1983). This agrees with the view that numerical responses dominate at higher latitudes, where prey abundances fluctuate more between years (Korpimäki and Norrdahl 1991). Numeric responses in raptors are typical in nomadic specialists, while functional responses often is due to resident generalists (Andersson and Erlinge 1977). Because of the numerical response by kestrels to vole numbers in my study area, I predicted that the impact of habitat would be more pronounced in poor vole years, such as 2005. In good vole years, such as 2007, kestrels may to a larger extent use the nest boxes available, making it difficult to reveal essential habitat and nest box preferences. However, the number of significant results with regard to habitat differences between nest boxes used and not used was not higher in 2005 than in 2006 and 2007. The best multiple model for the three years contained one, zero and two habitat variables, respectively.

In 2006 and 2007, both being relatively good vole years, average laser, representing bogs and clear cuts, was significantly higher for used nest boxes than for those not used. Percentage bog showed the same pattern, in 2007 used nest boxes had significantly higher percentage than those not used, and there was a similar tendency in 2006. Kestrels preferred flat terrain before slope in 2006, and when all three years were pulled together. In 2007, there was a tendency for early arriving kestrels to choose nest boxes in flat terrain before boxes in slopes. A likely explanation is that areas with a low angle of gradient hosted more bogs and open areas than hilly terrain, as indicated by the strong correlation between these variables (Appendix 1). When interpreting the results from all three years, kestrels seemed to prefer areas with more than 21 percent bog, and with more than 240 meters in average laser to the nearest forest. This means above 21 percent bog within the macrohabitat, which is $1.54 \text{ km}^2 * 0.21 = 0.32 \text{ km}^2$ bog. The laser measurements are average of the front, back, left and right side of the nest box, i.e. $0.24 \text{ km} + 0.24 \text{ km} * 0.24 \text{ km} + 0.24 \text{ km} = 0.23 \text{ km}^2$ of open habitat around the nest box.

There were little differences in average laser and bog percentage between used and not used nest boxes in 2005, when the vole abundance was low, possibly because kestrels to a larger extent searched for alternative prey in other habitats this year. Hence, the results indicate that openness in the macrohabitat around the nest box is important when the main prey voles are numerous. Bogs and clear cuts are important habitats for voles, and favourable hunting habitats for a raptor that hunt by sight (Aschwanden et. al. 2005). Kestrels are known to be able to recognize vole trails by scanning the UV reflectance of their scent marks (Zampiga et al. 2006, Olsen 2007), and by doing so they easily detect good vole habitats. Areas with nest boxes selected by kestrels could therefore be thought to have a higher availability of favourable hunting habitats in the surroundings than areas with boxes not selected. But a favourable habitat for voles does not always mean a favourable habitat for kestrels. According to Aschwanden et al. (2005), accessibility of voles, which depends on vegetation structure, was more important for the selection of hunting habitats than prey abundance. However, at bogs and clear cuts in my study area, the vegetation cover is low at the time of kestrel arrival in spring. It therefore seems likely that the total amount of vole scent marks at the time of arrival was a main factor for nest box selection.

I found that kestrels selected nest boxes with a larger proportion of developed areas and inhabited houses in 2005, but not in 2006 and 2007, indicating that they hunted closer to developed areas and inhabited houses when voles were scarce. In Finland, kestrels moved away from agricultural fields in a poor vole year, and searched for alternative prey, such as birds, lizards, shrews and insects, in forests and marshlands (Valkama et al. 1995). During low vole years, kestrels indicatively increased their preference for ruderals (Riegert et al. 2007). In Trysil, kestrels probably selected the most productive habitats, i.e. the same environmental conditions that also humans prefer, when there were few voles to hunt. Interestingly, when all buildings were included in the analysis in 2005, there was no significant result. This means that the large number of holiday cottages, which in the Trysil region are often located in low-productive areas at higher elevations, were not important for nest box selection that year.

Village (1990) found that nest boxes were more likely to be used if they were situated at least 200 m from places frequently used by humans. This is not supported by my study, but on the other hand, only a few nest boxes in Trysil were situated closer than 200 m from buildings. In 2007, kestrels preferred nest boxes with few buildings in the surroundings, indicating that they avoided areas where they are frequently disturbed by people. The threshold for human disturbance may vary between years, depending on competition for nest boxes and food availability. In contrast, kestrel significantly preferred high percentage of developed areas when all years were pulled. This was probably because of the apparent preference for areas with inhabited houses in 2005. When looking at used versus not used nest boxes in 2006 an 2007, there was no preference for either percentage developed area or inhabited houses, neither was there any significant preference when looking at time of hatching in 2007.

It is possible that the presence of humans is actually favorable for kestrels in low vole years, because refinement of land through agriculture may increase alternative prey numbers. Also human gardening, setup of nest boxes for passerines, and feeding of birds may increase prey abundances. Metropolitan kestrels in Berlin have even been reported anthropogenic food in their pellets, such as cutlet bones, chicken bones and sausage skins (Kübler et al. 2005).

Microhabitat analyses

I found no preference for nest box height. The mean height was 6.8 m both for nest boxes used and those not used when data from all three years were pulled together. This could reflect that all nest boxes were situated above a minimum threshold for height. If so, this potential threshold must be somewhere below 4 m in my study area, since all nest boxes were put up above this height. Village (1990) concluded that nest boxes are more likely to be used if they are put up at least 3 m above the ground. In Israel, kestrels laid their eggs five days earlier in large nest boxes (50 cm * 75 cm) situated 2.5–3 m above the ground than in smaller nest boxes (50 cm * 30 cm) situated 5–6 m above the ground (Charter et al. 2007). In this study, nest box size was regarded to be more important than nest box height.

In Britain, kestrels avoided to use lower nests of both carrion crow (*Corvus corone*) and magpie (*Pica pica*) (Shrubb 1993). The mean height of magpie nests used by kestrels was 7.65 m, and the mean height of carrion crow nests used was 9.85 m (Shrubb 1993). Approximately 70% of the carrion crow nests used by kestrels were found above 8.1 m, even though nests situated so high were used by less than 45% of the carrion crows themselves (Shrubb 1993). Approximately 60% of the magpie nests used by kestrels were found above 6.1 m, whereas approximately 25% of these nests were used by magpies themselves (Shrubb 1993). Although no differences in predation rates were found in nests of different height (Shrubb 1993), the results indicate that kestrels have a strong preference for height when it comes to nest site selection, at least when using stick nests.

It is possible that nest box height is less important when kestrels nests in artificial boxes, which probably give better protection than corvid nests. Predation pressure on kestrels was probably negligible in my study area. There were only two known cases of predation in 2007, which is a predation rate of less than one percent. This is in accordance with earlier nest box studies on kestrels in Finland (Valkama and Korpimäki 1999). However, nest site preferences are likely to reflect adaptations to reduce predation risk in evolutionary time, and strong preferences may thus exist even in areas where the predation risk appears to be low today. The high occupancy of nest boxes in Trysil indicates that these nest sites were selected before stick nests, which is in accordance with the kestrels' general preference for hidden nesting places (Olsen 2007). A significant decrease in the use of stick nests, and a compensatory increase in the use of sites in tree cavities, has been observed through most of Britain (Shrubb 1993). This happened despite a simultaneous threefold increase in the abundance of carrion crow, which formed 83% of the stick nests used by kestrels (Shrubb 1993). Eggs are probably more difficult to spot in nest boxes than in open stick nests, and nest boxes may be more difficult to rob than stick nests. In Britain, most kestrel nest sites (54%) were in trees, but buildings were most commonly used in urban areas, although strong regional differences in the occupancy of sites were found (Shrubb 1993). Predation was highest in stick nests and lowest in buildings, with an overall predation rate of 16% (Shrubb 1993).

I found no preferences for nest box orientation when comparing used and not used nest boxes, but in 2007, boxes with a southern orientation had earlier date of hatching than those with a northern orientation. According to Village (1990), nest boxes are most likely to be used if the entrance faces south or south-west. My result is also in accordance with what Selås (1997) found for the common buzzard and Rohrbaugh and Yahnerr (1997) found for the American kestrel (*Falco sparverius*). It may be favourable to have more solar radiation into the nest box in the early phase of the breeding, but it could also be important that snow accumulated in the nest box over the winter melts earlier with a southern orientation.

There was no significant selection for any specific nest box tree species, but in the analysis based on time of hatching, there was a preference for pine and conifers and avoidance of deciduous trees around the nest box. Coniferous trees give more cover than deciduous trees at the time when kestrels choice their nest site. In 2007, there also was a tendency for a higher number of branches below nest boxes used than below boxes not used. When all three years were pulled together, kestrels also preferred nest boxes situated in forests of higher cutting classes. In cutting areas, nest boxes were usually attached to a single tree, which was saved as a seed tree. In contrast, nest box trees on bogs usually had some neighbour trees of the same height. Although kestrels seemed to prefer openness in the macrohabitat plot, they apparently preferred some degree of shelter close to their nests. This will reduce the risk of being detected by predators and also shelter against unfavourable weather conditions.

In 2006 there appeared to be a preference for bogs also in the microhabitat. However, this was probably because nest boxes put up in bog microhabitats also had more bogs close by than boxes put up in cutting areas and forests. Bogs are usually located in flat terrain, and especially larger bog areas with a lot of moisture in the ground cannot persist over time if there is a high angle of gradient. This is also confirmed by the correlation between the two variables (Appendix 1).

Nest box traits

The only significant results with regard to nest box traits was that nest boxes used had smaller entrance holes than those not used, both entrance area and entrance breadth, in 2006. In 2007 there was an almost significant preference for longer nest boxes, a variable which correlated with area entrance hole (Appendix 1). Nest box breadth was also almost significant this year, and strongly correlated with entrance hole breadth (Appendix 1). The entrance hole breath was in most cases similar to the width of the nest box. Kestrels may prefer nest boxes that matches the standard size of most of the nest boxes in the study area. Valkama and Korpimaki (1999) found that nest boxes of an intermediate size (base: 34 * 35 cm = 1190 cm^2) were selected before small boxes (base: 25 * 27.5 cm = 687.5 cm^2). The average nest box base size in Trysil was 978 cm^2 in 2007. Only 11 nest boxes had an internal size ≤ 700 cm^2. For these boxes, the proportion used was almost the same as for the entire sample of boxes in 2006 and 2007, but interestingly, none of them were used in 2005, when there was a lower number of breeding kestrels and probably less competition for nest boxes.

I did not find any preferences for nest box size, and in 2006, even the smallest nest box (414 cm^2) was used. Although nest box size was not important for kestrels' nest box selection in Trysil, I regard the standard nest box used, with breadth 34 cm, length 30 cm, height 28 cm and entrance width 34 cm and 15 cm height, to be a good standard. This size provides enough room for the nestling also in years when clutch sizes are large. Nevertheless, I will recommend making the entrance smaller than the nest box breadth, according to the analysis based on time of hatching in 2007, were kestrels preferred lower entrances before higher. I think 12 cm is sufficient and that there is no need for using higher entrance holes than 15 cm. Small entrances may shelter against unfavourable weather conditions, and kestrels may also feel safer when they are less visible.

The best model for kestrels nest box selection in the period

In 2005, percentage developed area was the only variable obtained in the model with the best AIC-value, indicating that this was the most important model for nest box selection this year. In 2006, the best model was given by the variables "nesting 2005" and "area entrance hole", indicating that previous use of the nest box was a very important factor. The other factor was the need of cover, as kestrels preferred small entrance holes before large.

The best model in 2007 included four variables; nest boxes within 3 km, buildings per nest box, bog percentage and nest box breadth. Vole populations peaked this year and density dependent factors probably affected kestrels' choice of nest site, as kestrels selected nest boxes with fewer occupied nest boxes in their surroundings. Kestrels also favoured fewer buildings in their macrohabitat, suggesting that they avoided human disturbance. Kestrels further selected higher percentage of bogs in their macrohabitat, which probably reflected favourable vole hunting habitats. Kestrels preferred small nest box breadth, probably because of the strong correlation with entrance hole breadth (Appendix 1).

The best model for the three-year period was given by the variables: year, nest box age, nest boxes within 3 km, angle of gradient, percentage developed area, percentage developed area*year, average laser and cutting class. Year intercept the different vole population level between years, and point out the importance of developed area in 2005 when crossing the two variables year and percentage developed area. There also were density dependent factors when all years were pulled. A preference for lower angle of gradient probably reflects the strong correlation with the variables bog percentage and average laser (Appendix 1). Cutting class was the only significant microhabitat variable in the model for the whole period, and this was not revealed in the single year analyses. Close to the nest, kestrels preferred higher cutting classes before smaller.

When analysing the time of hatching in 2007, the best model included the variables compass point, pine around nest box, nesting 2006 and entrance hole height. Again nesting in the previous year and not too large entrance holes were important for kestrels nest box choice. Interestingly, boxes with a south oriented entrance hole were selected before those with north oriented entrance hole. Kestrels also seemed to prefer to have several pines in the microhabitat.

Kestrels nest box selection divided in three different categories

Kestrel nest box selection in Trysil could be divided into the following three categories:

1. General preference over time
2. "Year effect" – preference depending on vole abundance
3. Early arrival preference

The general preference over time was mostly macrohabitat features given by the variables: nest boxes within 3 km, angle of gradient, average laser meters, bog percentage and nest box age. In addition, the microhabitat variable cutting class was included. Bog percentage is also included even though it was not included in the best model. This is because of the strong correlation with both angle of gradient and average laser (Appendix 1). For kestrels' general preference over time I also emphasize the importance of nest boxes with relatively small entrance holes, due to the importance of this factor in both 2006 and 2007. There was no information about nesting in the previous year in 2005, and therefore this variable was not included in the test for all three years combined. Kestrels selected nest boxes used in the previous year in 2006, and in 2007 when analysing for time of hatching. This means that the general preference for kestrels over time includes selection of older and previous used nest boxes in open and flat terrain in the macrohabitat, and better cover in the microhabitat, provided by a higher cutting class around the nest boxes and smaller entrance holes. There were also density dependence matters, affecting nest box selection when there were more than seven nest boxes within 3 km from a nest box.

The "year effect" was probably linked to vole abundance. When the vole abundance is low, such as in 2005, kestrels may prefer nest boxes situated in areas with a higher percentage of developed areas. This probably reflects that areas inhabited by humans are often productive and thus favourable for hunting alternative prey, especially birds.

"Early arrival preference" is assumed to be what the first arrivals, and thus the fittest individuals, select when they can choose from several empty boxes. Selection for microhabitat features appeared mainly in the hatching date analyses. The variables that appeared to be most important according to the best model for time of hatching 2007 were compass point, nesting in the previous year, number of pine trees around the nest box and entrance hole height. This means that kestrels selected south facing nest boxes used in the previous year, and with some tree cover within the 0.1 ha quadrate. A preference for small height in the nest box entrance hole may also reflect a need for cover.

Conclusions

Kestrels in Trysil selected nest boxes in open, flat habitats surrounded by bogs and clear-cuts when voles were abundant, whereas boxes closer to human settlements were selected when voles were scarce. Hence, prey availability appeared to be the most important factor for nest site selection. In addition, nest boxes used in the previous year were selected, and there was also density dependence in years with increasing and peaking vole numbers. Kestrels also preferred south facing nest boxes and some degree of cover in close proximity to the nest box, and not too big entrance holes. I conclude that analyses of used versus not used nest boxes is an appropriate method for testing for nest site preferences, but that time of hatching may give additional information when the proportion of occupied nest boxes is high. For further and similar studies I will also recommend to distinguish between micro- and macrohabitat analyses, in order to reveal preferences for both nest site and hunting habitats. I advise to not empty nest boxes for old droppings and prey remains, as this could be essential information for the kestrel's choice in the following year. Based on my results, I recommend ornithologist to put up nest boxes also in habitats where kestrels easier can find alternative prey when vole numbers are low, because this may contribute to maintain a more stable kestrel population between years.

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Appendix 1

Relationships between some important selected macro- and microhabitat continuous variables of nest boxes used from 2005 - 2007. Unfortunately I could not present all the variables because the totals of variables were too many. The lower part of the table gives the correlation coefficients (r) and the upper right part the P-values (N = 260).

	Average laser	Percentage bog	Percentage developed area	Angle of gradient	Nest box within 3km	Area entrance hole	Entrance hole breadth	Entrance hole height	Nest box breadth	Nest box length
Average laser		<0.001	0.268	<0.001	0.446	0.516	0.034	0.297	0.005	0.163
Bog percentage	0.49		0.317	<0.001	<0.001	0.147	<0.001	0.158	0.001	0.005
Percentage developed area	-0.07	-0.06		0.959	0.192	0.481	0.892	0.315	0.986	0.034
Angle of gradient	-0.26	-0.58	<0.01		0.006	0.118	0.178	<0.001	0.010	0.005
Nest box within 3km	0.05	0.33	-0.08	-0.17		0.402	0.422	0.737	0.379	0.4553
Area entrance hole	0.04	0.09	-0.04	0.10	0.05		<0.001	<0.001	0.009	0.002
Entrance hole breadth	0.13	0.22	<0.01	-0.08	0.05	0.64		0.023	<0.001	0.004
Entrance hole height	-0.06	-0.09	-0.06	0.22	0.02	0.66	-0.14		<0.001	0.250
Nest box breadth	0.17	0.20	<0.01	-0.16	0.05	0.16	0.46	-0.26		0.278
Nest box length	0.09	0.17	-0.13	-0.18	0.05	0.20	0.18	0.07	-0.07	