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Where to go to take what prey? Range use, habitat selection and prey capture in Tengmalm's owl (*Aegolius funereus*) males as revealed by simultaneous radio tracking and video surveillance at the nest

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Abstract

The home range use and habitat selection of four providing male Tengmalm's owls (*Aegolius funereus*) were studied by using radio telemetry, and simultaneously recording prey deliveries by a video camera positioned inside the nest box of each nest. The camera allowed prey identification and made it possible to assign prey deliveries to locations in the field, i.e, the last observation fix before a delivery. 100% MCP home ranges averaged 219.4 ha, whereas 95% kernel home ranges had a mean size of 310 ha, and decreased with increasing proportion of high productivity areas in the home range. Owls did not shift hunting areas from one night to the next, but rather changed it gradually over time. Habitat selection was estimated by calculating the distance from each observation fix (N=458) and from each random plot (N=480) to the nearest patch of each habitat class, and testing for differences using logistic regression. The owls showed a particularly strong selection for hunting in forest age class I (clear-cuts and plantations), which is the primary habitat of their main prey, *Microtus* voles. They hunted closer to areas of medium and high productivity, and farther from areas of low productivity and impediment than expected by random. This may be related to abundance and availability of prey animals which select areas of dense vegetative cover. Bogs did not seem to be selected, but due to the low proportion in two of the nests, the results were inconclusive. Male owls both hunted and captured prey closer to the nest than expected by random. Additionally, prey captures were located closer to high productivity and farther from areas of impediment than expected by random. Shrews were captured closer to areas of high productivity than expected by random, which is in accordance with other findings that suggest that the density of shrews increases with productivity. Shrews seemed to be excluded from certain habitats by *Microtus* voles because captures of shrews were located farther from forest age class I than captures of *Microtus* voles. Although the profitability of transporting prey items back to the nest in theory is related to prey size and distance from the nest, the larger *Microtus* voles were not transported to the nest from longer distances than the smaller shrews. An owl returned to the area where it captured the last prey more often than expected by random. Thus, the owls utilized a win-stay strategy. The present study is the first to combine radio tracking and video monitoring to determine habitat specific prey capture in Tengmalm's owl and highlight the importance of habitat productivity for hunting owls.

Sammendrag

Hjemmeområdet og habitat seleksjonen til fire Perleugle (*Aegolius funereus*) hanner ble studert ved bruk av radio telemetri, samtidig som byttedyrleveringer ble registrert av et videokamera plassert inni reir-kassen til hvert reir. Kameraopptakene tillot identifikasjon av byttedyr og gjorde det mulig å koble byttedyrleveringer til lokasjoner i felt, i hovedsak siste observasjon før levering. 100% MCP hjemmeområ der hadde en gjennomsnittlig størrelse p2̃19.4 ha, mens 95% kernel hjemmeområder hadde en gjennomsnittlig størrelse p3̃10 ha, og minket med økende andel av områder med høy produktivitet i hjemmeområdet. Perleuglene byttet ikke jaktområ de for hver natt, men skiftet jaktområ de gradvis over tid. Habitatseleksjon ble estimert ved åkalkulere avstanden fra hver observasjon (N=458) og fra hvert random plot (N=480) til nærmeste område av hver habitatkategori, for deretter åteste om det var signifikante forskjeller mellom disse ved bruk av logistisk regresjon. Perleuglene viste en spesielt stor seleksjon for skog i aldersklasse I (hogstflater og plantasjer), som er primærhabitatet for Perleugles hovedbyttedyr, *Microtus*. I tillegg jaktet de nærmere områder med medium og høy produktivitet, og lenger fra områder av lav produktivitet og impediment enn forventet av tilfeldig valg. Dette henger muligens sammen med tallrikhet og tilgjengelighet av byttedyr som foretrekker tett vegetasjonsdekke. Myrområder så ikke ut til å bli selektert, men grunnet lav tilgjengelighet i to av reirene var resultatene tvetydige. Hannene jaktet og fanget byttedyr nærmere reiret enn forventet ved tilfeldig valg. I tillegg var fangster av byttedyr lokalisert nærmere områder med høy produktivitet og lengre fra områder med impediment enn forventet ved tilfeldig valg. Spissmus ble fanget nærmere områder med høy produktivitet enn forventet ved tilfeldig valg. Dette stemmer overens med andre funn som indikerer at tettheten av spissmus øker med økende produktivitet. Spissmus så ut til å bli ekskludert fra enkelt habitat av *Microtus* fordi fangstpunkter av spissmus var lokalisert lengre fra aldersklasse I enn fangstpunkter av *Microtus*. Selvom lønnsomheten ved å transportere byttedyr tilbake til reiret er relatert til byttedyrstørrelse og avstand fra reiret, ble ikke *Microtus* transportert lengre enn spissmus til tross for forskjeller i størrelsen. Uglene returnerte oftere til forrige fangstomrde oftere enn forventet ved tilfeldig valg. Med andre ord utnyttet Perleuglene en ”vinn-bli” strategy. Dette studiet er det frste til å kombinere radio peiling og video overvåkning til å fastslå habitat-spesifikk byttedyr fangst hos Perleugle og belyser viktigheten av habitat produktivitet for jaktende ugler.

Contents

1 Introduction

Foraging predators can be expected to alter foraging behaviour in relation to the distribution of prey (Therrien et al. 2011), habitat characteristics (Tomé et a. 2011) and availability of prey (Baker & Brooks 1981, Bechard 1982). Animals should preferably forage in habitats which maximize feeding intake, but also minimize risk of predation and interspecific competition (Barnard 2004). Different habitats may provide animals with different amounts of resources both spatially (Garratt et al. 2011) and temporally (Nybo & Sonerud 1990, Jacobsen & Sonerud 1993). Hence, habitat selection may be a good predictor of habitat quality for different species (Sunde et al. 2001), and a species spatial behaviour is important knowledge in order to understand its biology and population dynamics (Sunde et al. 2009). Additionally, knowledge on the spatial behaviour of a species may improve the effectiveness of conservation measures (Mellone et al. 2013).

Habitat fragmentation and alternating land use by humans is the leading cause of present species decline (Andrén 1994), and understanding species response to alterations in their main habitat may be vital in order to predict future population trends of species (Sunde et al. 2009). In Europe, intensification of agricultural areas have caused declines of several species related to farmland habitats (Benton et al. 2003, Garrat et al. 2011). In the boreal forest region, forest fragmentation resulting from timber harvesting is the driving force in altering habitat (Widén 1994, Östlund et al. 1997, Strøm & Sonerud 2001, Jansson & Andrén 2003). Therefore, understanding species response to modern forestry practices is of vital importance (Sonerud 1997, Strøm & Sonerud 2001).

One group of animals that may be particularly affected by modern forestry are forest-dwelling birds of prey (Niemi & Hanowski 1997, Sonerud 1997, Strøm & Sonerud 2001). Clear-felling involves clearing large areas of mature forest and removing timber, hence leaving large open areas which may be suitable habitats for mammalian prey, but may lack natural perches from which predators can hunt (Widén 1994). Forestry practices may benefit species associated with open areas (Holt 1997, Sonerud 1997, Sulkava & Huhtala 1997), but limit abundance of species associated with mature forests (Widén 1997, Mazur et al. 1998, North et al. 1999, Strøm & Sonerud 2001).

Conventionally, studies of forest dwelling birds of prey have been limited to tracking studies focusing on habitat use versus availability (Sonerud et al. 1986, North et al. 1999, Strøm & Sonerud 2001, Sunde et al. 2001, Santangeli et al. 2012), but fewer studies have estimated prey capture rates in different habitats. Studies focusing on prey capture rate have usually been studied by direct observation and have been limited to predators hunting in open habitats (Wakeley 1978, Sonerud 1986, Preston 1990, Sonerud 1992a , Garratt et al. 2011). Classical theory suggests that predators should forage in areas of abundant prey, i.e, prey hotspots, whereas other models suggest that predator distributions should reflect the distribution of the resources of their prey (Roth & Lima 2007). However, studies have suggested that raptors instead forage in areas of low vegetative cover, rather than high prey abundance (Baker & Brooks 1981, Bechard 1982), indicating high prey availability due to lack of protective cover for ground dwelling prey (Preston 1990). This is particularly important for predators searching by visual cues (Andersson et al. 2009).

Observational studies are less feasible in forested areas, but recent advances in video surveillance (Steen 2009) may make such studies feasible. By constantly monitoring prey deliveries at the nest of predators feeding nestlings, and simultaneously tracking of parent birds it may be possible to assign prey deliveries to the last known fix before delivery, i.e, the probable capture site.

The Tengmalm's owl (*Aegolius funereus*) is a small, cavity-nesting, nocturnal predator which depends heavily on small mammals as their main food source (Korpimäki & Hakkarainen 2012). Tengmalm's owls utilize auditory prey location and hunt with a sit-and-wait strategy, perching at low branches (Norberg 1970, Bye et al. 1992). *Microtus* voles constitute the main prey of Tengmalm's owls, while bank voles (*Myodes glareolus*), shrews (*Soricidae*) and birds constitute alternative prey sources (Korpimäki 1988a). Tengmalm's owls are considered as vole specialists (Korpimäki 1994), and the abundance of voles have profound influences on behaviour (Hakkarainen & Korpimäki 1994, Eldegard & Sonerud 2009, Santangeli et al. 2012) and survival of owls (Hakkarainen et al. 2002).

Voles and shrews are inconspicuous prey which occur in a wide variety of habitats (Hansson 1977, Sonerud 1986, Hanski & Kaikusalo 1989, Ims 1991, Ecke et al. 2002), but abundance may differ with habitat productivity (Hanski & Kaikusalo 1989, Jedrzejewski & Jedrzejewska 1996) and vegetative cover (Ecke et al. 2002). High productivity facilitates vegetative growth and thus availability of food (Jedrzejewski & Jedrzejewska 1996), whereas cover increases protection from predators searching by visual cues (Rice 1983, Ecke et al. 2002, Andersson et al. 2009). Vegetative cover may limit prey availability for predators searching by visual cues (Sonerud 1992a, Andersson et al. 2009), predators searching by auditory cues or utilizing both senses may be less constrained (Rice 1983, Bye et al. 1992, Andersson et al. 2009, Tomé et al. 2011). Thus, by utilizing low perches (Tomé et al. 2011) Tengmalm's owls may hunt in areas covered by dense vegetation cover which may be unsuitable for other predators. If so, Tengmalm's owls may use cues regarding prey abundance, i.e, auditory clues, when selecting foraging areas.

Microtus voles are predominantly found in open habitats dominated by graminoids and forbs (Henttonen et al. 1977, Sonerud 1986, Nybo & Sonerud 1990, Ims 1991), and where the density of the field layer is high (Hansson 1977). The density of field cover increases with productivity, but decreases with volume of Norway spruce (*Picea abies*, Hedwall et al. 2013). Hence, clear-cuts and areas of high productivity may be important factors in determining *Microtus* vole abundance, and hence prey capture by Tengmalm's owls.

Shrews are considered habitat generalists, but abundance increases with increasing productivity (Hanski & Kaikusalo 1989). Therefore, similar to *Microtus* voles, habitat productivity may be important in determining occurrence of shrews. Shrews are subordinate to the larger *Microtus* voles (Hanski et al. 1991), which may affect shrew abundance. Thus, productivity and avoidance of the larger *Microtus* vole may determine shrew capture by Tengmalm's owls. Because productivity is related to moisture (cf. Fremstad 1997), prey capture by Tengmalm's owls may be related to the occurrence of rivers and streams.

According to theories on central-place foraging, profitability of foraging close to the nest is related to prey size (Andersson 1981, Olsson et al. 2008), and for single-prey loaders it is preferable to selectively transport larger prey items to the nest (Sonerud 1989). Travelling to and from the nest incurs costs, hence larger prey items provide a greater net energy gain per delivery than smaller items (Andersson 1981). *Microtus* voles are three times as heavy as shrews (G. A. Sonerud, pers. comm.), and it may therefore be predicted that shrews are captured closer to the nest than *Microtus* voles.

If abundance of prey is higher in certain habitats than to others, it may be preferable to focus foraging effort on patches that have yielded prey before (Roth & Lima 2007). When hunting for clumped prey, a central-place foraging animal may increase foraging efficiency by returning to the same patch as it has previously caught prey (Wakeley 1978, Sonerud 1985a). Hence, Tengmalm's owls may optimize foraging by returning to the same foraging area following nest provisioning, i.e, win-stay foraging (Sonerud 1985a). Using this strategy, animals can reduce time spent foraging by utilizing patches with high prey availability (Grundel 1992), but profitability of continued forage in the same patch may depend on predator vigilance in prey (Roth & Lima 2007, Valeix et al. 2011).

Consequently, the following predictions may be made on foraging Tengmalm's owls: 1) Tengmalm's owls will change foraging area between nights if they are subject to resource depression following increased prey vigilance. 2) Tengmalm's owl forage more in clear-cuts than other habitats due to the high abundance of the main prey, *Microtus* voles. 3) Tengmalm's owl are due to hunting by ear not much restricted by vegetative cover and will utilize areas with dense vegetation cover, indicated by high productivity. 4) Providing Tengmalm's owls hunt more in the vicinity of the nest than expected by random. 5) Both *Microtus* voles and shrews are more often captured in areas of high productivity than expected by random. 6) Shrew are less often captured in the primary habitat of *Microtus* voles, i.e, clear-cuts. 7) Shrews provided to the nestlings have been captured closer to the nest than *Microtus* voles. 8) Providing Tengmalm's owls will return from the nest to the same area as the last capture more often than expected by random.

2 Methods

2.1 Study area

The study was conducted in the boreal forest region Hedmark county, Norway (Figure 1). Of the four nests monitored, three were located in Hamar municipality (I, II and III, 60°56' N, 11°08'E, 550-600 m elevation), and one was located in Elverum municipality (IV, 60°59' N, 11°46'E, 350-400 m elevation).

The study area is dominated by coniferous forests intensively used for timber production (Sonerud 1986), and consists of forest fragments of various age and structure (Figure 2). Additionally, the forest surrounding nests II and III were mixed with bogs (Figure 3), and was also used as summer pastures for sheep and cattle. In contrast, nest I and IV were located closer to permanent human settlements, with several agricultural fields scattered in the surrounding area (Figure 3). Norway spruce is the dominating tree species, while bilberry (*Vaccinium myrtillus*) and mosses are important in the field layer (Selås et al. 2013).

The field work was conducted between 29 May and 4 July in 2013, which was an increase year of the vole cycle (Geir A. Sonerud, unpublished data). The most common mammalian prey species in the study area are field vole (*Microtus agrestis*), bank vole (*Myodes glareolus*), wood lemming (*Myopus schisticolor*), and common shrew (*Sorex araneus*).

2.2 Trapping, tagging and tracking

During the nestling phase of Tengmalm's owl, the male is the sole provider of the nestlings (Eldegard & Sonerud 2012). The male hunts for prey, while the female is responsible for feeding, warming and guarding the nestlings (Korpimäki & Hakkarainen 2012). Therefore, only the male at each of the four nests were fitted with a radio transmitter (Type PIP3, Biotrack, UK).

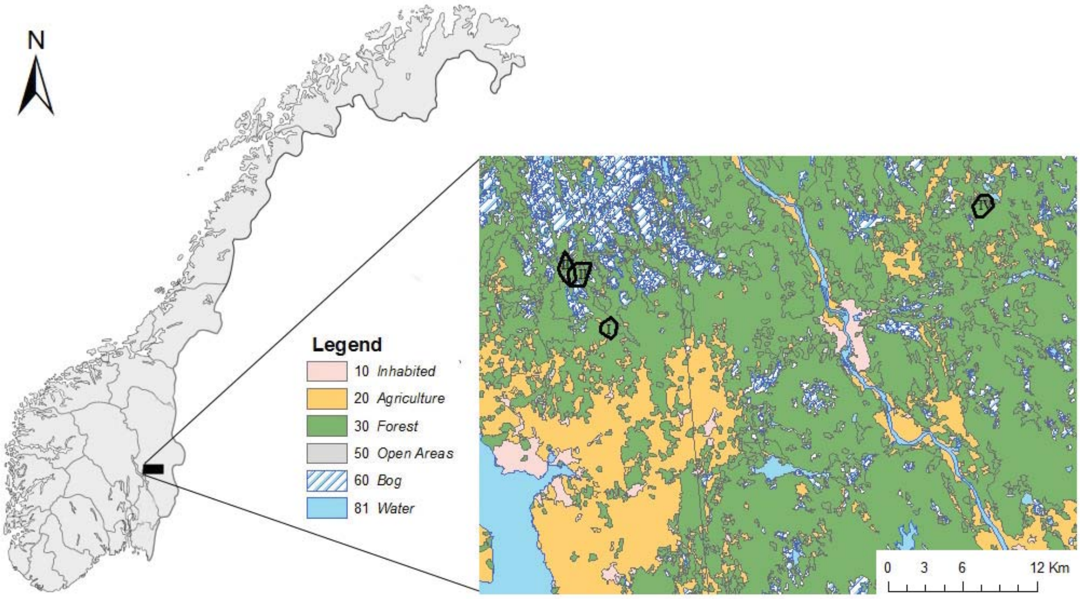

Figure 1: Map of Norway showing the study area and the home ranges of the four Tengmalm's owls studied. Numbers inside the home ranges refers to each nest. General habitat types are listed in the legend.

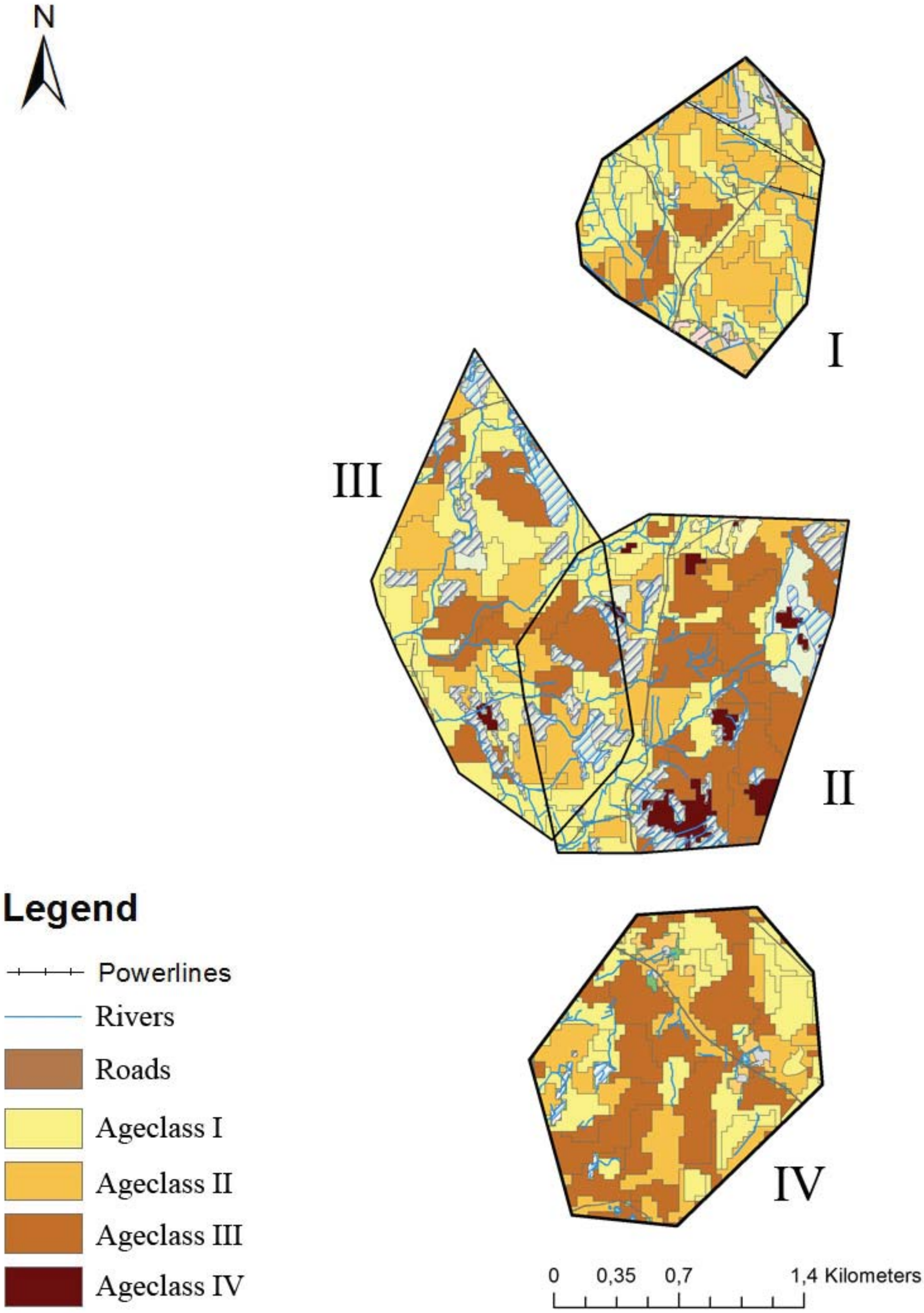

Figure 2: Individual home ranges of four male Tengmalm's owls, with the distribution of forest age classes and the occurrence of rivers, roads and powerlines. Capital letters next to the home ranges refer to nest ID. Blank (white) areas refers to non-forested areas, i.e. as not suitable for timber production. Age classes I, II, III and IV refer to forest patches with a minimum age between $0-15$, $16-30$, $31-60$, and >60 years, respectively.

The males were trapped using a tunnel trap mounted on the entrance of the nest box. The males could enter via a swing door, which could only be entered in one direction. Hence, once a male had entered the nest box, it could not exit. The male was thereafter removed from the nest

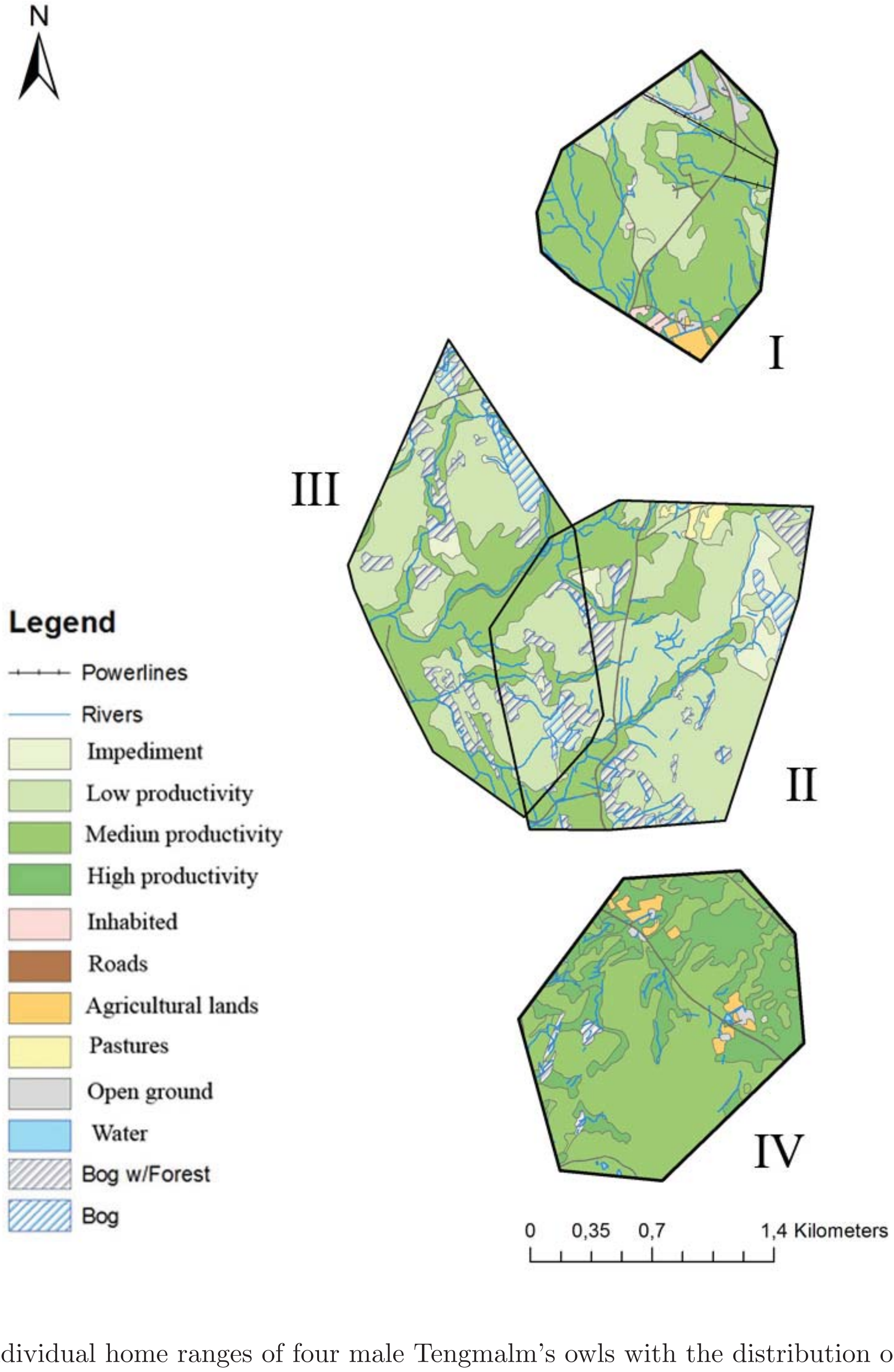

Figure 3: Individual home ranges of four male Tengmalm's owls with the distribution of habitats and occurrence of rivers, roads and powerlines. Capital letters next to the home ranges refer to nest ID. Areas of impediment, low, medium and high productivity are mainly forested habitats.

box and fitted with a radio transmitter. The transmitter was fitted as a backpack harness using tebular teflon tape (Bally Ribbon Mills, Pennsylvania, USA). For details of fitting, see Eldegard & Sonerud (2009). The owls were tracked on foot using a portable receiver (Televilt, Sweden) and a hand-held, three-element Yagi-antenna (Televilt, Sweden).

Habitat characteristics were measured when the owl was either observed directly, signals were strong, (i.e, indicating that the owl was close by), or when the observers noted a shift in signal towards the nest (i.e., indicating that the male had returned to the nest). Direct observations were assigned the letter A, strong signals were assigned the letter B, while all other observations were given the letter C, in order to distinguish between them. Additionally, UTM coordinates obtained from a handheld GPS receiver were noted for each observation. If the male was observed perching, the perch height and perch type was registered. Perch height was measured using reference material, by either comparing the height of the perch in relation to an object with a known length, i.e, either an observer or the Yagi-antenna.

Using the minimum convex polygon (MCP) method, 95% and 100% MCP home ranges were estimated for each nest with the ”mcp”-function in R 3.0.2 (Calenge 2006, R Core Team 2013). Additionally, kernel home ranges were constructed using the ”kernelUD”-function in R 3.0.2 (Calenge 2006, R Core Team 2013). Kernel home ranges provide a density estimate than can be interpreted as a utilization distribution (Seaman et al. 1999). Sample sizes were >50, and therefore sufficient to estimate kernel home ranges (Seaman et al. 1999). During the fieldwork, male owls were often seen perching close to small streams and creeks. Therefore, whether or not a fix was located <10 m from a stream was measured in the field.

2.3 Daily home ranges

Home-range size for each single night was determined using the 100% MCP method. The number of fixes obtained per owl per night varied from 8 to 38, with a mean of 16.6 ± 1.4. A total of 27 nights were included in the analysis. Three nights of tracking were excluded because the tracking was aborted early due to heavy rain or problems with the receiver. In order to test if the owls hunted in the same area during consecutive nights, overlap (O) between utilized areas was calculated for each pair of nights using the ”Tabulate Intersection” function in ArcMap. Percentage overlap between night A and B was then calcultated using the formula:

$$O = \frac{2(A \cap B)}{A + B}$$

where $A \cap B$ denotes the area common to A and B (Sonerud et al. 1986). The relationship between the overlap between the pair of two home ranges and the number of days elapsed between these two home ranges was tested using a linear mixed-effect model in R 3.0.2 (Pinheiro et al. 2013, R Core Team 2013), where nest ID was added as a random variable.

2.4 Video monitoring

In order to monitor prey deliveries at the nest, a GoPro (Hero 3 White edition) camera was fitted to the underside of a specially made roof that fitted all four nest boxes. The camera was connected to an external MC-battery (12 V) to extend the running time of the camera. An infrared (IR) lightsource, which illuminated the nest box without disturbing the breeding owls, was connected to the external battery. The original camera lens was removed, and a lens with no IR filter was installed, which made the camera better able to receive infrared light.

The camera was fitted with a 32 GB SD memory card, and filmed continuously throughout the night. The memory card allowed filming for 7 - 12 hours, depending on the quality (i.e, amount of detail in the picture frame). Therefore, given the short summer nights at the high latitudes of the study area, the camera could film continuously throughout the night.

In order to minimize the risk of missing events, we chose to film continuously throughout the night (see Reif & Tornberg 2006). Given the limited storage capacity of the memory cards fitted, this meant that the camera had to be removed from the nest box after each night. However, this was not expected to be a significant problem because Tengmalms owl are not shy and easily habituate to human observers (Eldegard & Sonerud 2012). In order to minimize the risk of abandonment, cameras were first fixed when the oldest nestling had an age of at least nine days.

Fitting the camera involved climbing the nest tree with a ladder, removing the lid of the nest box, placing the special lid with the GoPro pre-attached, and then fitting the battery on top of the lid. This usually took less than five minutes. The brooding female usually exited the nest box when the nest tree was touched (cf. Sonerud 1985b), and usually perched in a nearby tree <10 m from the nest during the camera fitting. She returned to the nest as soon as the observers left.

Video cameras have been used to document nest behaviour and prey deliveries since the early 1970s (Temple 1972). Early studies focused on filming nesting behaviour, but due to limitations with the camera, prey identification was often difficult (Booms & Fuller 2003, Reif & Tornberg 2006). However, GoPro cameras have the possibility to film in HD and are therefore ideal for prey identification. Unfortunately, given this level of detail, large amounts of storage is necessary. In order to limit storage use and cut time in examining data, studies have opted to use movement sensors to trigger filming (Steen 2009). Instead of using such pre-filming sensors, a computer software program was used post-filming in the present study. This allowed automatic detection of movements in the entrance of the nest box, and created separate slow motion video-files. Most of these included prey deliveries and simplified prey identification.

2.5 Prey deliveries and identification

Because Tengmalms owls are single prey loaders (cf. Sonerud 1992b), it is possible to assign each prey delivery to a specific habitat in which the prey was caught if the owls are tracked continuously. Hence, by comparing the time at which a prey was delivered to the last known fix of the owl before the delivery, as obtained from radio tracking, it was possible to assign a habitat to the prey delivered. Therefore, plots which were followed by a prey delivery were assigned as capture sites.

Prey delivered at the nest was identified as type, i.e. whether it was a shrew (*Sorex sp.*), *Microtus* vole (field vole or root Vole (*Microtus oeconomus*)), bank vole , wood lemming, or birch mouse (*Sicista betulina*). If prey identification to any of these types were difficult, prey was assigned to the category rodent, or as small mammal if they were difficult to separate from shrews. Additionally, avian prey were identified to species if possible.

Unfortunately, when trying to connect an extra external camera to the battery, the IR-light malfunctioned. This resulted in a night in which the recordings contained completely dark pictures. However, prey deliveries were still identifiable by the sound of the male entering the nest box and the nestlings begging. On the next night, prey deliveries were recorded by two observers positioned close to the nest. The prey type of these deliveries were assigned as unknown. Additionally, on three occasions during radio tracking, the owl was seen capturing prey. On one of these occasions, the owl was confirmed not to deliver the prey at the nest. However, on the other two, whether or not the prey was delivered could not be verified, but the plots were still assigned as plots were prey had been captured.

On the last night of tracking of the male in nest III, the nestlings had already fledged when the camera was fitted to the nest. However, tracking was still performed that night. On three occasions, the male was heard calling in the vicinity of the nest after he had been out hunting. In one of these cases, the male was observed handling prey only ten minutes prior to calling. Therefore, this calling behaviour was considered as prey delivery. All three deliveries were added to the unknown prey category.

2.6 GIS

I uploaded the UTM coordinates of all fixes into ArcMap 10.2, where I added an area resource map (AR5) provided by the The Norwegian Mapping Authority (Bjørkelo et al. 2009), and a forest resource map (SAT-SKOG) provided by The Norwegian Forest and Landscape Institute (Gjertsen & Jensen 2012).

First, I used the area resource map to extract information on habitat classes in and around the home ranges. By using the ”select by attributes” function in ArcMap, I selected each habitat feature and created separate shapefiles containing only one habitat class. The habitat features I chose were agricultural land (area resource codes 21, 22 and 23), bog with trees (area resource code 60 and tree codes 31, 32, 33), bog without trees (area resource code 60 and tree code 39), road (area resource code 12), and open ground (area resource code 50). Open ground included open areas with a firm soil which could not be classified as agriculture, forest, inhabited areas and roads (Bjørkelo et al. 2009). This was included because nest I was located close to a large car park and skiing stadium. Additionally, private court yards and gardens were included in this category.

Second, in order to test if Tengmalms owl prefer to hunt close to rivers and streams, I chose to add a shapefile containing line information about rivers and lakes. Additionally, I added line information about power lines in the area. Third, 120 random plots were created within the 95% MCP home range and within the 100% MCP home ranges for each nest (totalling 960 plots). Fourth, to assess the habitat preferences, by considering random plots as habitat availability and observation plots as habitat use I calculated the distance from each plot, both observation plots and random plots, to the nearest polygon of each habitat class.

Additionally, in order to assess the importance of productivity I calculated the distance from each plot to each of four different productivity classes (i.e. impediment, low, medium and high). Information were extracted from the area resource map. Impediment is defined as areas with a growth rate of 0.1 m^3 per 0.1 ha per year. For low, medium and high productivity the corresponding figures are 0.1 - 0.3 m^3, 0.3 - 0.5 m^3, and 0.5 - 1.0 m^3 per 0.1 ha per year, respectively (Bjørkelo et al. 2009).

From the forest resource map, I extracted information on the age of each forest polygon and created four shapefiles. Each forest polygon in the forest resource map contained information on age of the forest within each polygon. Therefore, I grouped forest polygons into one of four minimum age categories, i.e. minimum age between 0 – 15, 16 – 30, 31 – 60 and >60 years. Then, I created a shapefile for each of these age categories. Finally, I calculated the distance from each plot to each of the four forest age categories.

2.7 Statistics

In order to investigate habitat preferences of the Tengmalm's owls, I used logistic regression modelling to test for differences between observed habitat use and habitat availability. Logistic regression is suited for testing for relationships between a categorical outcome variable, and several continuous predictor variables (Manly et al. 1992, Peng et al. 2002). Hence, using whether a plot was an observation plots or a random plots as the outcome variable, and the distance to each habitat as predictor variables, I tested whether there was a significant difference in distance to habitat between random plots and observation fixes.

In essence, logistic regression predicts the logit (i.e. log odds) of the dependent variable from each predictor variable (Peng et al. 2002). Therefore, it is possible to estimate the likelihood of a plot being either a random plot or observation fix at any given distance from a habitat feature.

By fitting the data to the logistic regression formula:

$$\ln(\frac{\gamma}{1-\gamma}) = \alpha + \beta_1 X_1 + ... + \beta_x X_x$$

where, γ is the probability of the event, α is the Y intercept, βs are regression coefficients, and Xs are predictor variables (Peng et al. 2002), I was able to estimate the slope of the selection curve, i.e., whether the probability of use was increasing or decreasing with increasing distance from a habitat. By fitting random points as "1" and observation points as "2", a negative estimate of β indicated a preference for that particular variable. In other words, the probability of a plot being random was higher at increasing distances from the given habitat. If the habitat was avoided, the estimate would be positive.

A general linear mixed model (GLMM) was created using the "glmer" function in R version 3.0.2 (Bates et al. 2013, R Core Team 2013). The model was fitted by a maximum likelihood (ML) method. Given the range of my dataset, I was able to test for habitat differences in three different scenarios. First, I tested for differences between general habitat use and habitat availability. Second, I tested for habitat differences between prey capture sites and available habitat. Third, I tested for differences between capture sites and non-capture sites.

To find variables with significant effect, I used backward selection based on p-values. In essence, I ran the model which included all variables, examined the results, removed the variable with the highest p-value, and ran the model again. This was repeated until all variables were significant ($p < 0.05$). Estimates are given as mean ± SE. Parameter estimates for all models are summarized in the appendix.

2.7.1 Habitat selection

The tracking resulted in 138, 118, 74 and 128 fixes for nest I, II, III and IV, respectively. Out of the 458 fixes, 312 where A fixes, 89 where B fixes, and 57 where C fixes. I generated a GLMM which included all observations (A, B and C) of all males. These observations were tested against the 120 random points created in each 95% MCP and 100% MCP, i.e. two separate tests were run. In total, twelve habitat variables were added as predictor variables. These were the calculated distances to forest age classes I, II, III and IV, bog without trees, bog with trees, agricultural land, open areas (see above for description), road, river, powerline, and finally distance to the nest. The latter was used to control for any higher activity close to the nest than farther away. Tengmalms owl ID was added as a random variable to control for individual differences.

Initial analysis showed that there was a significant avoidance of powerline, but closer inspection of the data showed that this avoidance was based on the relative distribution of random points versus observation points within the home ranges, given that nest I was the only nest with a powerline within the home range. Therefore, distance to powerline was excluded from all analysis.

Additionally, to test if Tengmalms owl preferred certain productivity classes I generated a separate GLMM, where distance to each of the four levels of productivity classes was used as predictor variables. The productivity classes was extracted from the area resource map (AR5).

2.7.2 Individual habitat selection

To test the effect of the variation in habitat availability between the home ranges of the four males, a separate analysis was performed where the habitat selection for each male was estimated individually. Therefore, the observation fixes from each individual was tested against the relevant 100% MCP random plots using the statistics software JMP 10. Using the same procedure as above, the habitat selection for each male was estimated individually.

2.7.3 Habitat specific hunting success

In order to test if prey were captured disproportionally in certain habitats, capture points were tested towards both sets of random points. Therefore, I generated a GLMM which included only the capture sites and random variables. This GLMM contained the same eleven variables as the first analysis. A separate GLMM was generated to test for differences in productivity classes between prey capture sites and random points. Additionally, similar models were generated which included only capture sites of shrews or *Microtus*-voles.

To test for differences between shrew capture fixes and *Microtus* vole capture fixes, I generated a separate model which included whether the prey was a shrew capture fix or a *Microtus* vole capture fix as response variable, and distance to the eleven habitat types as explanatory variables. Because the male in nest II did not capture any shrews, the data on this male was excluded from the test. Additionally, a model was run which included only distance to nest as explanatory variable to test if there was a difference in transport distances for shrews and *Microtus* voles, which may be expected due to differences in energy gains based on their size (cf. Sonerud 1992b).

2.8 Success dependent habitat selection

Sonerud et al. (1986) suggested that Tengmalms owl utilize a win-stay strategy when hunting. Win-stay theory predicts that a central-place foraging predator will more often return to the area where it has previously caught prey than expected by random (Sonerud 1985a). Therefore, following a successful prey capture, the male owl may return to the same area as the previous prey was captured. Given that the video monitoring in this study allowed for control of prey deliveries, it was possible to investigate if an owl returned to the area where it caught the previous prey. Based on the initial capture fixes and the following prey delivery, I checked all the fixes after each delivery to investigate where the owl had foraged after prey delivery.

To avoid the use of inappropriate fixes, the fixes where the owl had delivered more than one prey between the capture fix and the following fix where excluded. Hence, of the 100 capture fixes, 52 where used in the win-stay analysis. The distribution of fixes on nest was seven, ten, seven and 28 for nest I, II, III and IV, respectively. Additionally, each fix following after a delivery was included until the owl either captured a new prey or tracking was terminated. This resulted in 167 post-delivery hunting fixes, with mean 3.9 ± 0.3 $(1 - 17)$ fixes per delivery.

Sonerud et al. (1986) estimated whether or not an owl returned to the same area by dividing the total home range size by the number of fixes where prey delivery was assumed. Hence, the home range was divided into several equal-sized areas, depending on the number of appropriate fixes. Then, Sonerud et al. (1986) tested whether the male returned to the same area after prey delivery.

I calculated similar areas for each nest separately. For each nest, a buffer (circular area) was created in ArcMap. For nest I, II, III and IV, the radius of the buffer was 269, 307, 327 and 154 m, respectively, i.e, the respective areas were 22.8, 27.3, 33.6 and 7.5 ha. Thereafter, whether the owl returned to within the buffer was analysed manually using ArcMap.

3 Results

3.1 Home range use and hunting behaviour

3.1.1 Home range use

Based on all fixes, the 100% MCP was on average 219.4 ± 23.9 ha (range 159.6 – 273.4 ha, while 95% MCP was on average 160.3 ± 23.2 ha (range 105.9 – 199 ha). The cumulative home range levelled of for nest III and IV, whereas it did not for nest I and II. This indicates that the amount of tracking performed was enough to estimate the total home range for nest III and IV, but not for nest I and II (Figure 4). Unfortunately, the male in nest III crossed the Flagstadelva-river on three occasions, and the observer was unable to follow. Hence, the home range of nest III was slightly underestimated. The 100% MCP home-ranges of nest II and III overlapped with a total of 66.1 ha, while the 95% MCP home ranges overlapped with 54.2 ha. The maximum distance recorded between the owl and the nest was 1168 m, 1649 m, 1709 m, and 1569 m, while the average distance between the fixes and the nest was 514 ± 22, 644 ± 37, 660 ± 49, and 439 ± 26 for nest I, II, III, and IV, respectively.

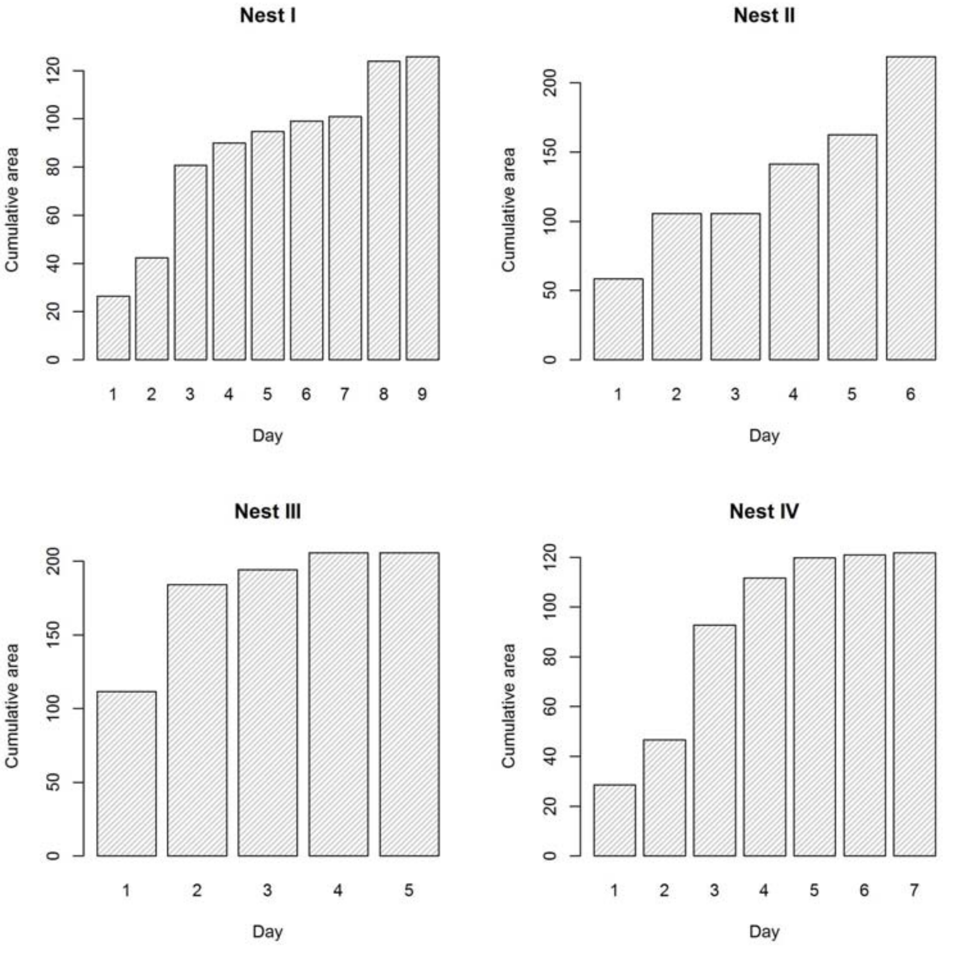

Figure 4: Cumulative home range (100% MCP) of each of the four Tengmalm's owl males in relation to number of nights of tracked.

3.1.2 Kernel home range estimates

95% kernel home range estimates averaged 310 ± 62.7 (189.3 - 419.5) ha. The size decreased significantly with increasing proportion of high productivity in the 100% MCP home range, and increased significantly with increasing proportion of impediment. The results were similar for all levels of the kernel estimates, but the sample size was small. The size of the 95% kernel home range increased significantly with increasing proportion of both bog types pooled (Table 1, Figure 5). Forest age classes were excluded because habitat productivity was considered a more robust predictor of prey abundance.

Kernel estimates revealed that the core areas for hunting males were in close vicinity of the nests (Figure 6). Plots were often clustered close to small rivers and creeks. For nest II and III the core areas (25%) did not overlap, but all other kernel zones did. Unfortunately, the area resource map (AR5) was insufficient for estimating the abundance of rivers in the vicinity of nest IV, because at least three creeks observed in the core area were not present in the AR5-map. Between 2006 - 2012 the mean monthly precipitation for May and June in the study area averaged 56 ± 7 mm, whereas for 2013 the mean monthly precipitation averaged 109 ± 11 mm. Therefore, because 2013 was a particularly rainy breeding season, the presence of streams in the AR5-map was probably underestimated. Timing of snow melt may also have affected this. The male in nest IV was often seen hunting <10 m from three of these creeks, and caught several prey close by. Therefore, these discrepancies may have biased the results slightly by masking a possible preference for rivers and streams.

3.1.3 Hunting behaviour

Perch height ranged from 0.2 - 10 m, and was on average 2.9 ± 0.092 (N=*286*. Spruce was by far the most common perch tree (63% of perches), followed by birch (13%, Figure 7). In total, the owls were perching in the top of the tree in 20% of the recorded cases and <10 m from rivers and streams in 37.4% of all cases (N=312). Foraging bouts, estimated as time between consecutive deliveries at the nest lasted for 36 ± 3 (range: 3 - 289) min (N=153) for all nests pooled. Length of foraging bouts was 38 ± 5 min, 58 ± 13 min, 40 ± 5 min, and 24 ± 3 min for nest I, II, III, and IV, respectively. The data was slightly biased for male II because on one occasion, he delivered a prey item at 04:50 in the morning, 289 minutes after the previous delivery. Given that this prey was delivered after sunrise it is likely that the owl did not forage for the entire time between the two the deliveries. If this was excluded, the mean length of foraging bouts was 47 ± 8 min for nest II.

Table 1: Effect of availability of four levels of productivity on the size of each kernel zone. 25%, 50%, 75% and 95% refer to kernel zones. With increasing coverage of low producitivity, impediment and bog the home range size increased. With increasing coverage of medium and high productivity the home range size decreased. - denotes insignificant tests.

	25%			50%			75%			95%		
	F	R^2	P	F	R^2	P	F	R^2	P	F	R^2	P
Bog	–	–	–	–	–	–	–	–	–	42.15	0.95	0.023
Impediment	25.08	0.96	0.038	32.83	0.94	0.029	112.73	0.98	0.0088	1615.29	0.99	0.0006
Low prod	47.93	0.96	0.020	47.35	0.96	0.020	23.82	0.92	0.039	–	–	–
Medium prod	–	–	–	–	–	–	–	–	–	21.01	0.91	0.044
High prod	360.31	>0.99	0.0028	616.33	>0.99	0.0016	105.47	0.98	0.0093	25.95	0.93	0.036

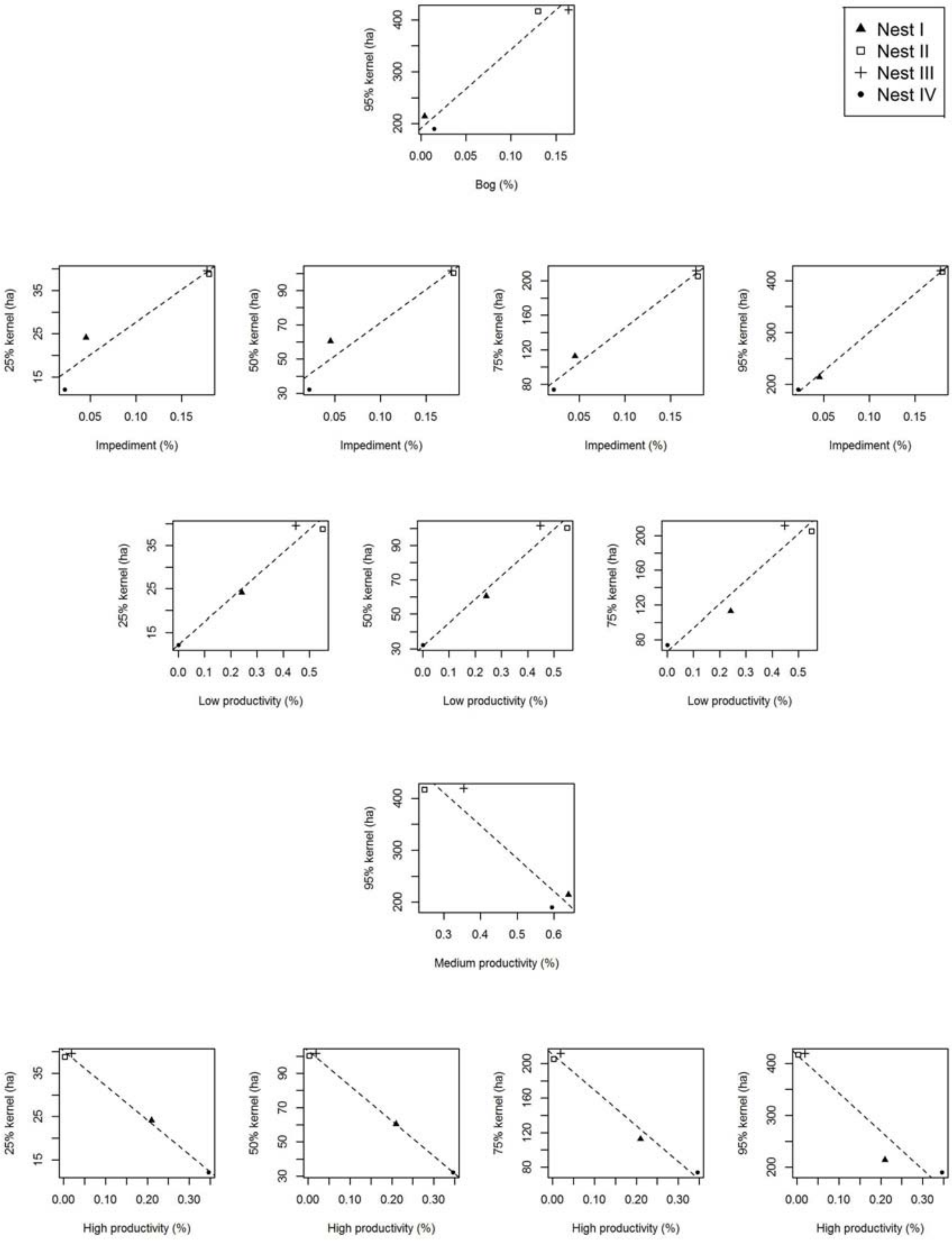

Figure 5: Slopes of linear regression from significant models of kernel home range size as function of proportion of bog (both types pooled) and proportion of different forest productivity categories in the 100% MCP home range.

3.1.4 Overlap between nights

The amount of overlap between each pair of single-night home-ranges of an owl was on average 35.4 ± 2.2 (range 0 – 81.7) % (Figure 8), and decreased significantly with increasing number of days elapsed between the tracking nights ($P = 0.034$). In order to test if overlap was related to

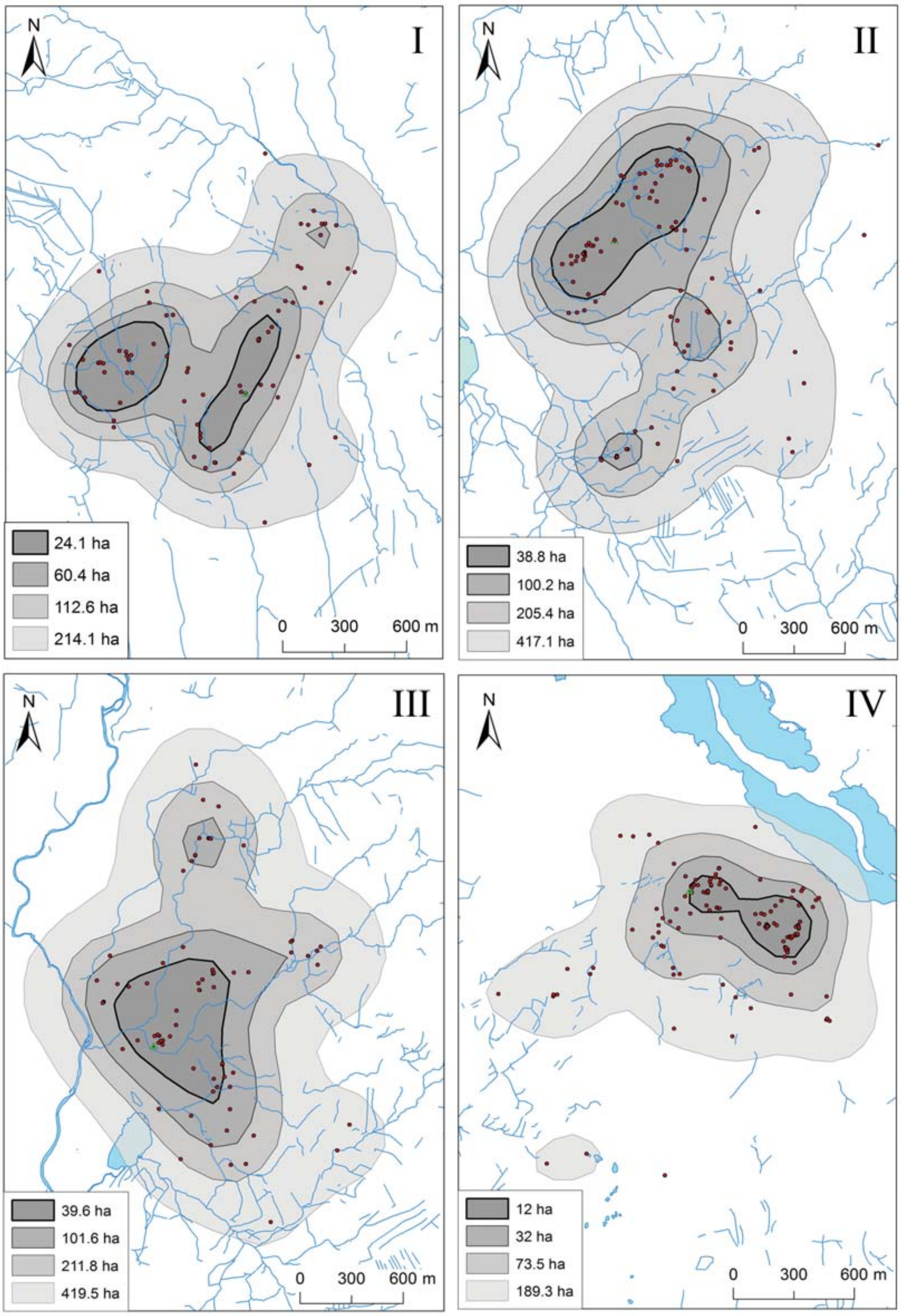

Figure 6: Kernel estimates for the four home ranges. The darkest areas show core areas, whereas the lightest show less utilized areas. Kernel densities are 25%, 50%, 75% and 95%, with 25% being the darkest, and 95% being the lightest. Green pyramids illustrate the individual nests, whereas red dots illustrate owl fixes. Numbers in boxes denote the size of each cumulative kernel zone. Number in picture refer to nest ID.

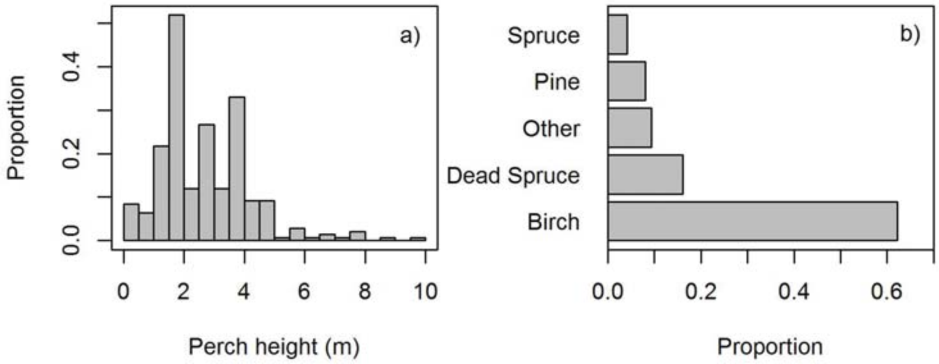

Figure 7: Distribution of perch height (a) and perch type (b) for four individuals of Tengmalm's owl (N=286).

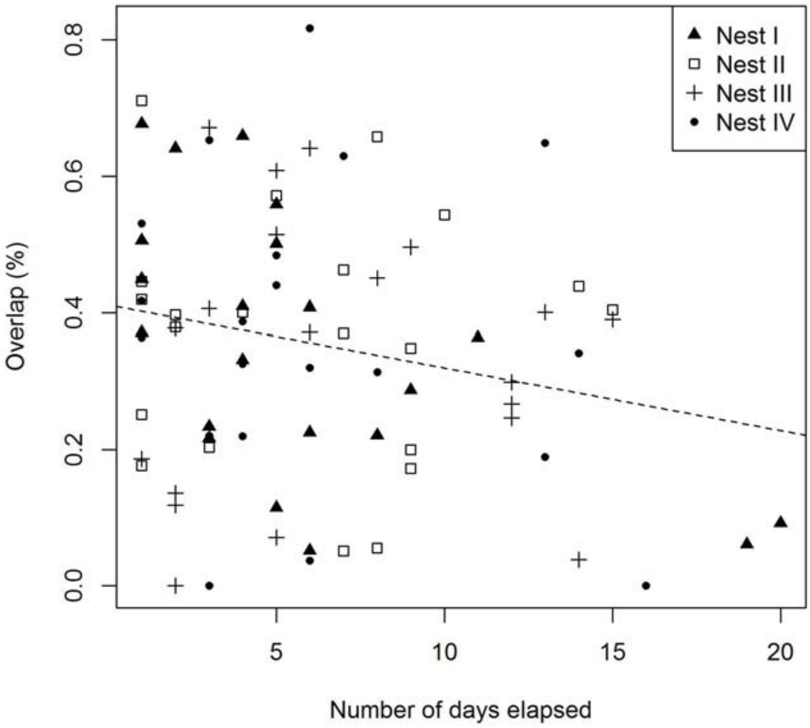

Figure 8: Relationship between the amount of overlap between each pair of single night home ranges for a Tengmalm's owl and the number of days elapsed between the two nights of tracking. The line shows the regression line ($y = 0.42 - 0.010x$).

hunting success, a correlation test was run between amount of overlap between two consecutive nights, and the amount of prey mass (g/h) delivered the first night. Among the ten cases that were suitable for analysis, there was no relationship between overlap between two consecutive nights and hunting success (Linear regression, $y = 0,461647 - 0,0029275x$, R^2=0.051 P=0.53).

Table 2: Prey deliveries at the Tengmalm's owl nests as recorded on video. For each nest the upper row shows number of prey captures *(N)*, and the lower row shows percentage total prey.

Nest	*Microtus*	Shrews	Wood lemming	Bank vole	Birch mouse	Small rodents	Small mammals	Birds	Unknown	Total
I	21	5	4	7	5	8	0	2	5	57
	36.84	8.77	7.02	12.28	8.77	14.04	0	3.51	8.77	100
II	18	0	1	4	0	3	0	2	0	28
	64.29	0	3.57	14.29	0	7.14	0	7.14	3.57	100
III	13	6	12	1	0	1	1	0	0	34
	38.24	17.65	35.29	2.94	0	2.94	2.94	0	0	100
IV	16	39	0	1	0	7	0	0	2	65
	24.62	60	0	1.54	0	10.77	0	0	3.08	100
Total	68	50	17	13	5	19	1	4	7	185
	36.96	27.17	9.24	7.06	2.72	10.33	0.54	2.17	3.80	100.00

3.2 Prey capture

3.2.1 Video monitoring

In total, the camera recorded 184 prey deliveries based on 168 h of filming. Additionally, six prey deliveries were added to the sample based on observations at the nest, making a total of 190 prey recorded as delivered. *Microtus* voles was the most frequently caught prey type (37%), followed by shrews (27%), unidentified rodents (10%), wood lemmings (9%) and bank voles (7%, Table 2). There were substantial differences between the males; the male from nest IV captured the most prey, with 65 prey deliveries during 35 h of filming. Hence, he delivered 1.87 prey per hour recorded, which was substantially more than the other three males from nest I, II and III, who delivered 0.98, 0.72, and 0.93 prey per hour, respectively.

Males showed individual differences in prey capture. The male from nest I was the only male to deliver birch mouse, whereas the male from nest III caught a substantial number of wood lemmings, and the male from nest IV caught the majority of all shrews (Table 2).

3.3 Habitat selection

The average distance from fixes to each habitat varied considerably, with the shortest mean distances and highest number of plots with the habitat for forest age class I (Table 3). Even though 33.1% of the available habitat was made up of forest age class I, 59.8% of observations were made in this habitat. Forest age class II, III and IV comprised 22.9%, 28.6% and 1.9% of the available habitat, while 22.5%, 11.1% and 0.22% of observations were made in these habitat categories, respectively (Figure 9). Of prey, 52.2%, 20.9%, 20.3% and 0% were captured in age classes I, II, III, and IV, respectively (Figure 9). Random plots fitted the overall habitat availability (Figure 9). The majority of observations were located in areas of medium productivity, which was used in proportionally to availability (Figure 10).

When all fixes were compared with 95% MCP random points, distance to forest age class I and III, bog with trees, bog without trees and open ground were included as significant variables (Table 4). The probability of a plot being an owl fix decreased with increasing distance from age class I, III, bog without trees and open ground. In contrast, the probability of a plot being an owl fix

Table 3: Distance (m) from fixes of the four Tengmalm's owl males tracked to each habitat. I, II, III, and IV refer to the forest age classes. Bog n/trees refer to bogs without trees. *N* refer to number of fixes which were located in the given habitat. By default, minimum distances are 0, i.e, in the habitat. *Value refer to number of fixes <10 m from rivers. †Value refer to number of fixes <100 m from the nest.

	Habitat type										
	Forest				Bog		Agriland	Open ground	Road	Water	Nest
	I	II	III	IV	n/trees	trees					
Mean	26	73	91	508	606	382	555	627	217	90	550
SE	3	4	4	15	15	13	17	22	9	4	16
Max	465	564	499	1540	1594	1020	1591	1903	755	326	1709
N	274	103	51	1	1	8	2	6	12	85*	32†

increased with increasing distance from bog with trees (Figure 11). Thus, the four former habitat types seemed to be preferred, while the latter was avoided.

A separate analysis on productivity revealed that the probability of a plot being an owl fix increased with increasing distances from impediment and areas of low productivity (Figure 11). In contrast, the probability of a plot being an owl fix decreased with increasing distance from areas of high productivity (Figure 11). Thus, the owls preferred high producitivity and avoided areas of low productivity and impediment.

When comparing the observation fixes with random plots created within the 100% MCP home range, the resulting significant variables was slightly different than the one for 95% MCP. The significant variables included were distance to forest age class I, II, III, and IV, as well as bog without trees, bog with trees and distance to nest (Table 4). The probability of a plot being an owl fix decreased with increasing distance from forest age class I, II, III, and IV, as well as bog without trees, and the nest (Figure 12). In contrast, the probability of a plot being an owl fix increased, with increasing distance from bog w/trees (Figure 12). The separate analysis of productivity included impediment, medium productivity and high productivity as significant variables. The probability of a plot being an owl fix decreased with increasing distance to areas of medium and high productivity (Figure 13). In contrast, the probability of a plot being an owl fix increased with increasing distance to areas of impediment (Figure 13). Thus, the owls preferred all forest age classes, bog, and vicinity of the nest, as well as medium and high productivity, and avoided bog with trees and areas of impediment.

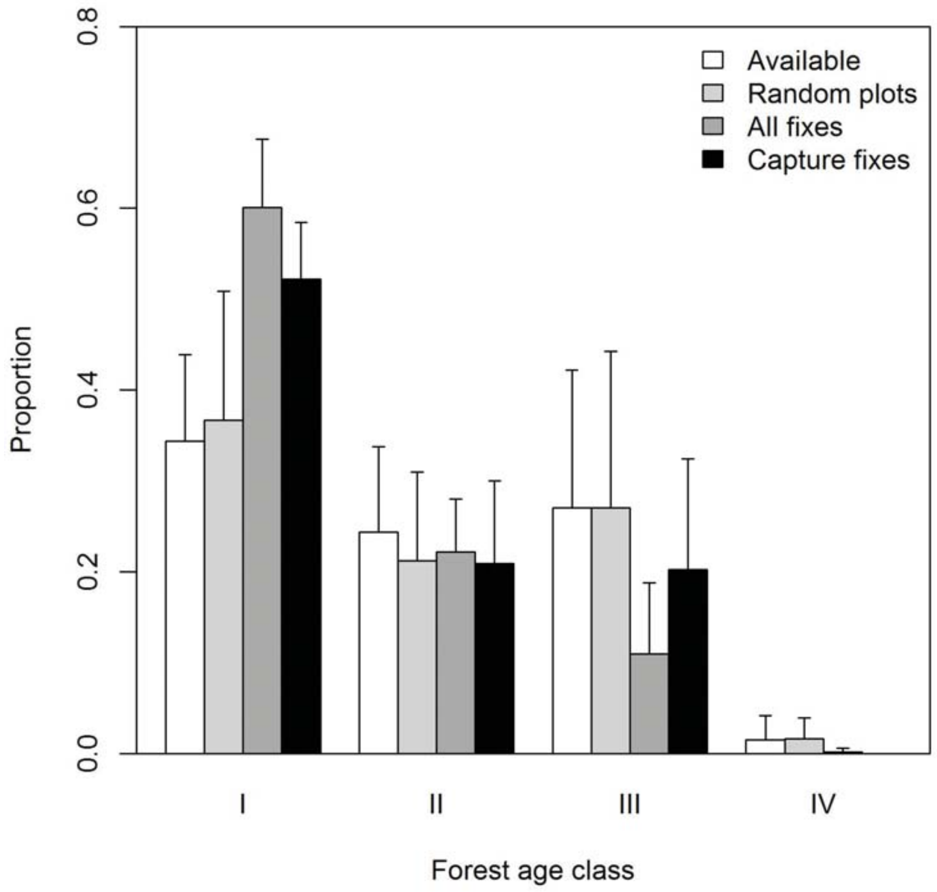

Figure 9: Habitat availability and use of forest age classes by four male Tengmalm's owls. Availability is calculated by dividing the total area of one age class in the home range by the total area of the home range. Random plots, all fixes and capture fixes are calculated as total number of each plot type in each age class, divided by total number of each plot type. Error bars show standard deviation (N=4)

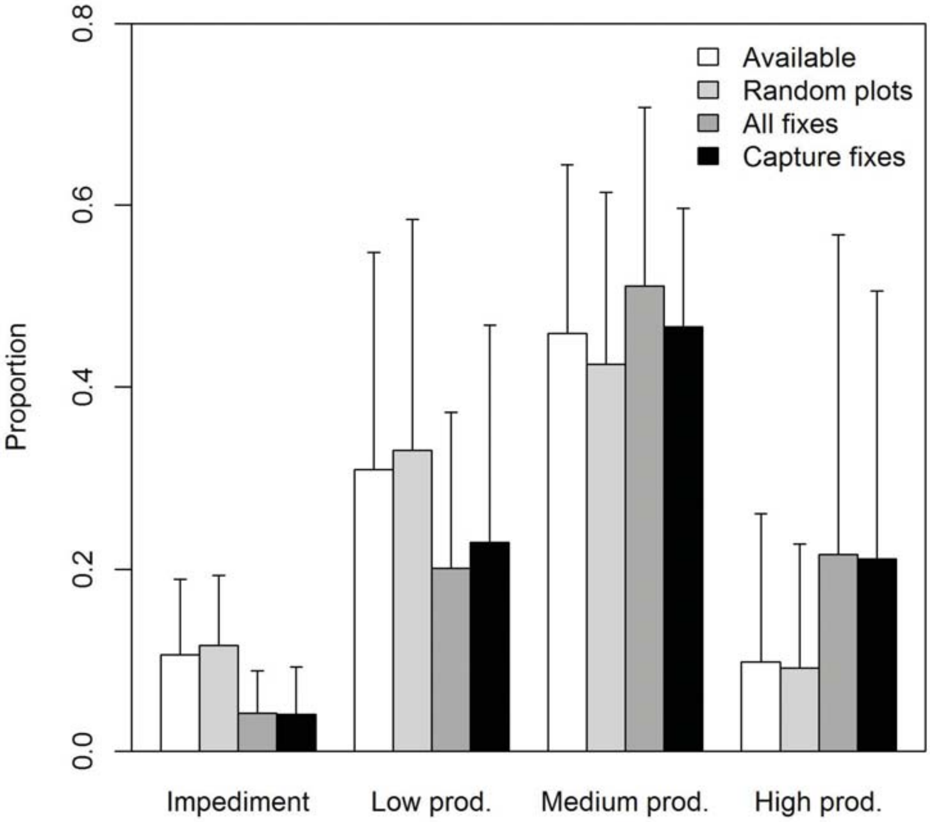

Figure 10: Availability of and use of habitat productivity classes by four male Tengmalm's owls. Availability is calculated by dividing the total area of one productivity class in the home range by the total area of the home range. Random plots, all fixes and capture fixes are calculated as total number of each plot type in each productivity class, divided by total number of each plot type. Error bars show standard deviation (N=4)

Table 4: P-values of the significant variables from the best fitted models for tests of habitat selection by the four Tengmalm's owls. For test types, letter refer to the data set tested, whereas the number denote which set of random plots that was used. O = Observation fixes. C = All capture fixes. M = *Microtus* vole capture fixes. S = Shrew capture fixes. C/CN refer to capture fixes tested against non-capture fixes, and M/S to *Microtus* vole capture fixes tested against shrew capture fixes.

	Test type									
Explanatory variable	O95	O100	C95	C100	C/NC	M95	M100	S95	S100	M/S
Forest age class I	0.023*	<0.0001*	–	–	0.0018*	–	–	0.036*	–	0.033*
Forest age class II	–	0.025*	–	–	–	–	–	–	–	–
Forest age class III	0.043*	0.0067*	–	–	–	–	–	–	–	–
Forest age class IV	–	0.0011*	–	0.027*	–	0.109	0.00067*	–	–	0.0016*
Bog	0.0052*	0.0002*	–	–	–	–	–	–	–	–
Bog with trees	0.012*	<0.0001*	–	0.003*	–	–	0.0085*	–	–	–
Agriculture	–	–	–	–	–	–	–	–	–	–
Open Ground	0.023*	–	0.03*	–	–	–	–	–	–	–
Road	–	–	–	–	0.024*	–	–	–	–	–
Water (line)	–	–	–	–	–	–	–	–	–	–
Nest	–	<0.0001*	–	0.0024*	–	–	0.021*	–	0.0015*	–
Impediment	0.0096*	<0.0001*	–	0.041*	–	0.021*	0.0025*	–	–	0.0020*
Low Prod.	0.044*	–	<0.0001*	–	–	–	–	0.012*	–	0.00045*
Medium Prod.	–	0.0083*	–	–	0.022*	–	–	–	–	–
High Prod.	0.0007***	<0.0001*	–	0.0099*	–	–	–	0.014*	0.002*	–

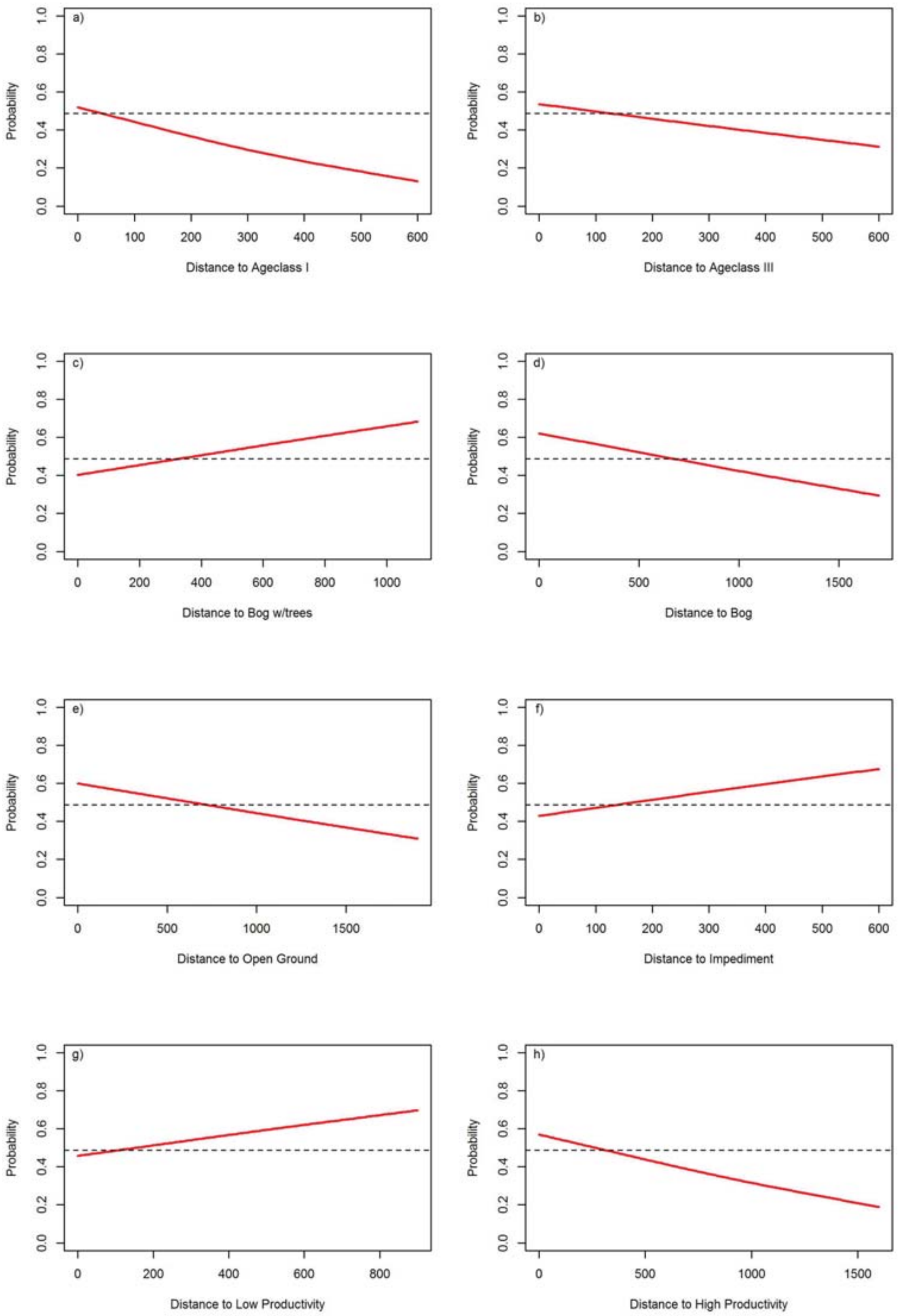

Figure 11: Probability of a plot being either a random plot or a Tengmalm's owl fix with the curve describing the logistic regression model for forest age class I (a), III (b), bog with trees (c), bog without trees (d), open ground (e), areas of impediment (f), low productivity (g) and high productivity (h). The dotted line represents the distribution expected if habitat selection is random. The area below the dotted line is represented by the owl fixes, while the area above the dotted line represents the random plots.

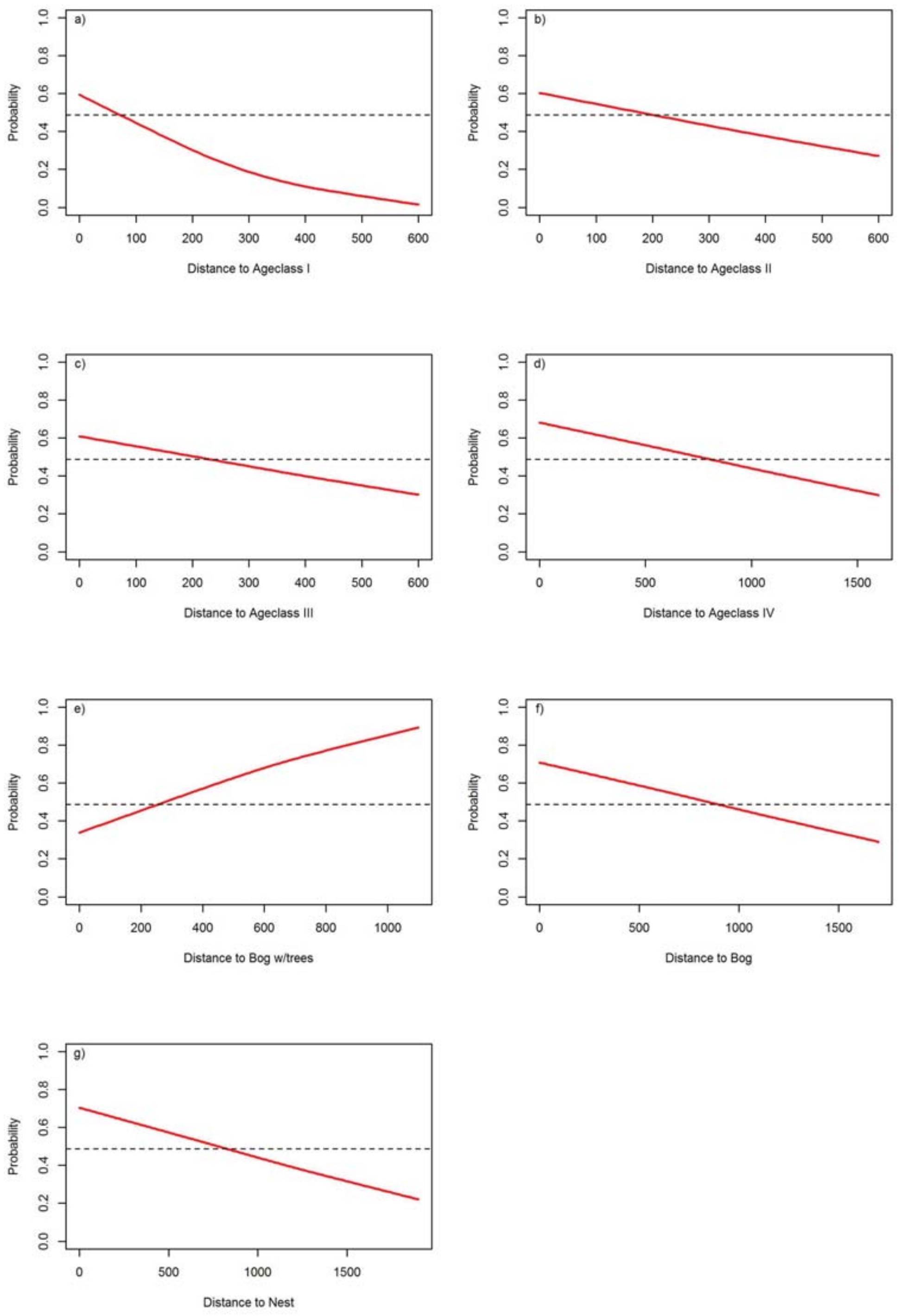

Figure 12: Probability of a plot being a Tengmalm's owl fix rather than a random plot with the curve describing the logistic regression model for forest age class I (a), II (b), III (c), IV (d), bog with trees (e), bog without trees (f) and nest (g). Area below dotted line indicates owl fixes, whereas area above dotted line indicates 100% MCP random plots.

3.4 Individual habitat selection

The owls showed variation in their habitat selection (Table 4). Forest age class II, agricultural land, open ground and road were never significant for any male. Forest age class III was avoided by three males, and not significant for the remaining male.

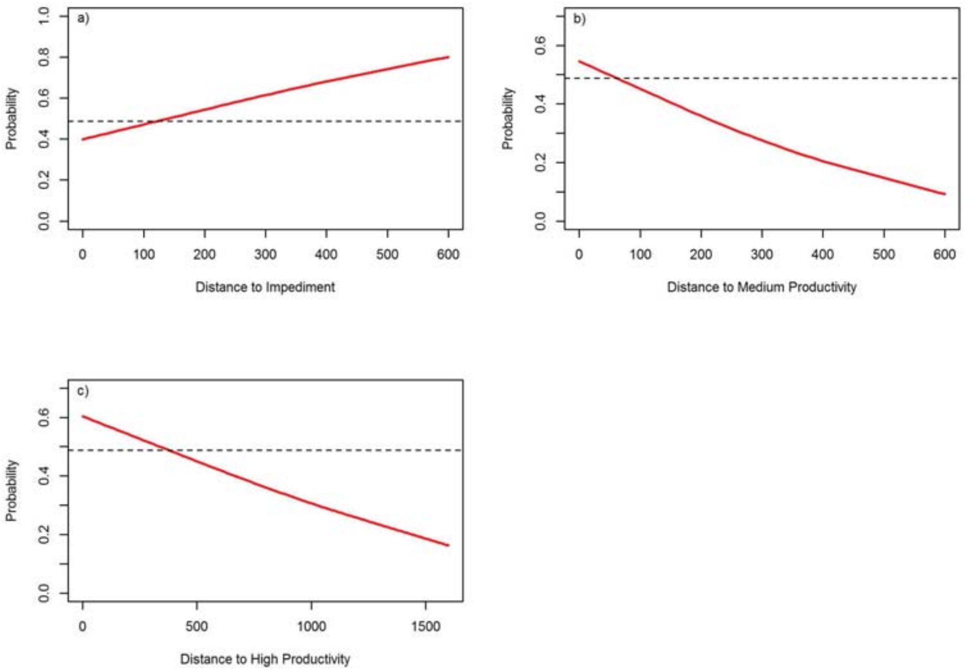

Figure 13: Probability of a plot being either a random plot or a Tengmalm's owl fix in relation to productivity with the curve describing the logistic regression model for areas of impediment (a), medium productivity (b) and high productivity (c). Area below dotted line indicates owl fixes, whereas area above dotted line indicates 100% MCP random plots.

Table 5: Parameter estimates for the best fitted model of four individual male Tengmalm's owls when habitat selection was tested individually for each owl. Estimate refer to the slope of the selection curve, i.e, negative values indicate preference for hunting within the habitat or in the vicinity of it, whereas positive values indicate avoidance for hunting in the vicinity of the habitat. *P* represent the *P*-value of each significant variable. Non-significant values are denoted by -.

	Male I		Male II		Male III		Male IV	
	Estimate	*P*	Estimate	*P*	Estimate	*P*	Estimate	*P*
Age class I	–	–	–	–	−0.023	0.0008	–	–
Age class II	–	–	–	–	–	–	–	–
Age class III	0.0078	<0.0001*	0.0059	0.0028*	–	–	0.0091	0.0068*
Age class IV	–	–	0.0035	0.0019*	–	–	−0.0050	0.0393*
Bog without trees	–	–	0.0053	<0.0001*	0.0025	0.012*	–	–
Bog with trees	0.0025	0.0013*	0.0044	0.0051*	–	–	–	–
Agricultural lands	–	–	–	–	–	–	–	–
Open ground	–	–	–	–	–	–	–	–
Roads	–	–	–	–	–	–	–	–
Water	−0.011	0.0002*	–	–	–	–	0.0050	0.0090*
Nest	−0.0017	0.011*	–	–	–	–	−0.0021	<0.0001*
Impediment	–	–	0.0072	<0.0001*	–	–	0.0056	<0.0001*
Low productivity	–	–	–	–	–	–	–	–
Medium productivity	−0.016	–	–	−0.013	0.0035*	–	–	
High productivity	–	–	−0.0020	<0.0001*	–	–	−0.030	<0.0001*

3.5 Habitat-specific prey capture

Out of the 191 prey delivered, I was able to assign a capture fix to 98. Of these, 36 were *Microtus*-voles (36.7%), 32 were shrews (32.6%), ten were unidentified small rodent (10.2%), and 20 were other types of prey (20.5%). Two fixes was added to this dataset, where the male had been observed catching prey, but prey delivery had not been recorded due to malfunction of the video equipment. The distance from the nest to the prey capture site was 572 ± 61 m (range 47 – 924 m, N = 19) for male I, 736 ± 99 m (105 – 1649 m, N = 19) for male II, 604 ± 84 m (69 – 1289 m, N=18) for male III, and 499 ± 49 m (38 – 1569 m, N = 44) for male IV.

When prey capture fixes were compared with the 95% MCP random plots, distance to open ground was the only significant variable ($P = 0.03$, Table 4). The corresponding separate analysis of productivity included only distance to low productivity ($P < 0.0001$, Table 4). The probability of a plot being a capture fix decreased with increasing distance to the nearest open ground (Figure 14). In contrast, the probability of a being a capture fix increased with increasing distance to areas of low productivity (Figure 14).

When prey capture were compared to the 100% MCP random plots the results were quite different. The significant variables included were distance from age class IV ($P = 0.027$), bog with trees ($P = 0.0030$) and nest ($P = 0.0024$, Table 4). The separate analysis with productivity (Table 4) included distance to areas of impediment ($P = 0.041$) and high productivity ($P = 0.0099$). The probability of a plot being a capture fix increased with increasing distance from bog with trees and with increasing distance from areas of impediment (Figure 15). In contrast, the probability of a plot being a capture fix decreased with increasing distance from the nest, and with increasing distance from areas of high productivity (Figure 15).

A separate analysis was performed to test for differences between capture fixes and non-capture owl fixes. The best fitted model included only distance to age class I ($P = 0.0018$) and road ($P = 0.024$) as significant variables, whereas the separate model for productivity included only distance to areas of medium productivity ($P = 0.022$, Table 4). The probability of a plot being a capture fix increased with increasing distance from age class I and increasing distance from areas of medium productivity, but decreased with increasing distance from road (Figure 16).

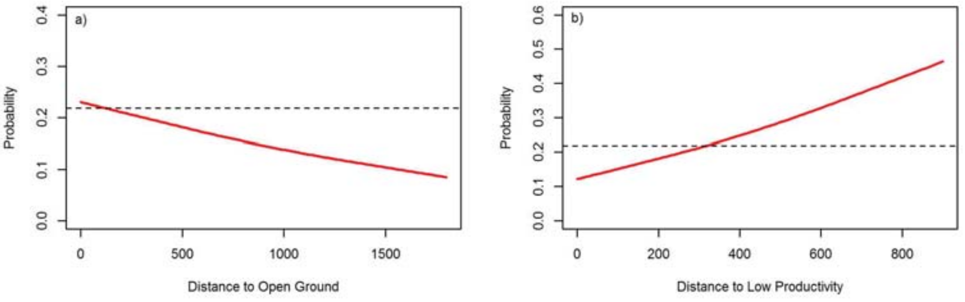

Figure 14: Probability of a plot being either a random plot or a capture fix with the curve describing the logistic regression model for open ground (a) and areas of low productivity (b). Area below dotted line indicates owl fixes, whereas area above dotted line indicates 95% MCP random plots.

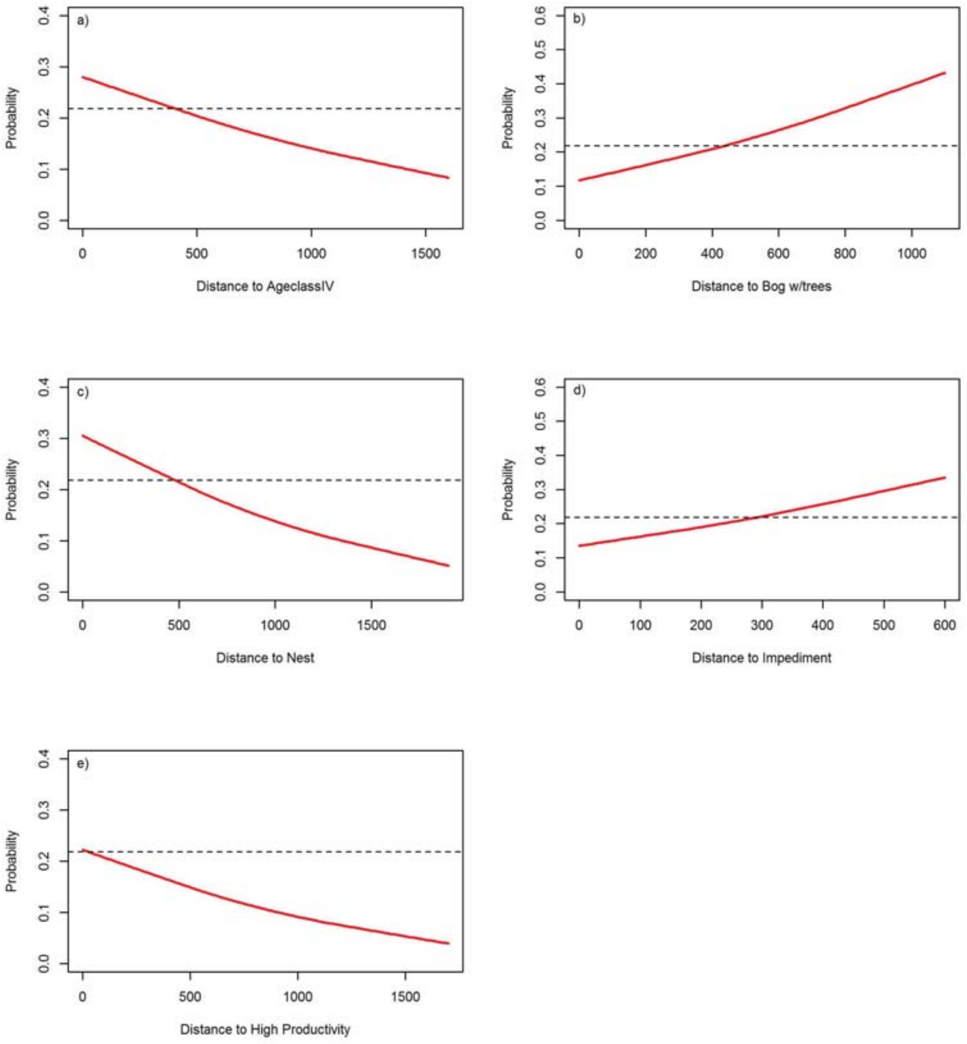

Figure 15: Probability of a plot being either a random plot or a capture fix with the curve describing the logistic regression model for forest age class IV (a), bog with trees (b), nest (c), areas of impediment (d) and high productivity (e). Area below dotted line indicates owl fixes, whereas area above dotted line indicates 100% MCP random plots.

3.5.1 Captures of *Microtus* voles

Given that 36 of the capture fixes concerned *Microtus* voles, a separate analysis was performed for this prey group. *Microtus* voles were captured on average 605 ± 49 (range 47 – 1397) m from the nests. When *Microtus* vole capture fixes were tested towards 95% MCP random plots no significant variables were included. However, in the separate analysis of productivity (Table 4), distance to areas of impediment turned out to be significant ($P = 0.021$). Hence, the probability of a plot being a *Microtus* vole fix increased with increasing distance from impediment (Figure 17).

In the analysis where the *Microtus* vole capture fixes were tested against the 100% MCP random plots the significant variables included distance to forest age class IV ($P = 0.00067$), bog with trees ($P = 0.0085$) and nest ($P = 0.021$) as significant variables (Table 4). The productivity analysis

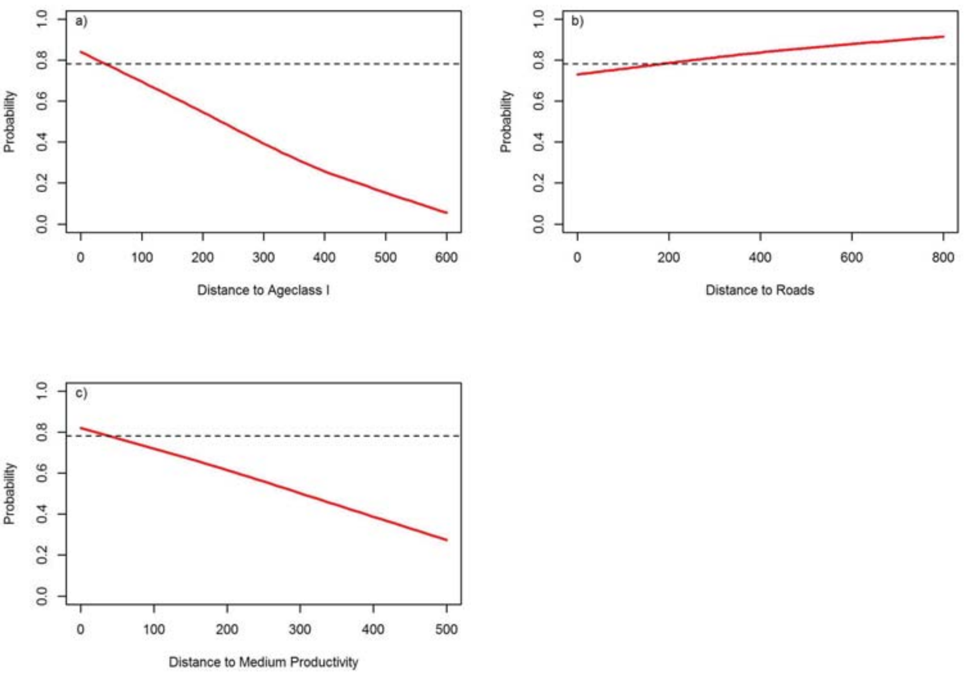

Figure 16: Probability of a plot being either a capture fix or a non-capture owl fix with the curve describing the logistic regression model for age class I (a), road (b), and areas of medium productivity (c). Area below dotted line indicates non-capture owl fixes, whereas area above dotted line indicates capture fixes.

included distance to impediment ($P = 0.002$) as a significant variable (Table 4). The probability of a plot being a *Microtus* vole capture fix decreased with increasing distance to age class IV and the nest (Figure 17) and decreased with increasing distance from bog with trees and distance from areas of impediment (Figure 17).

3.5.2 Captures of shrews

A separate analysis was performed to test for differences between shrew capture fixes and random plots. The 32 shrews for which a capture fix could be assigned were captured on average 493 ± 55 (range 109 – 1569) m from the nests. When testing the shrew capture fixes against the 95% MCP random plots, distance to ageclass I was the only significant variable ($P = 0.036$, Table 4). In the productivity analysis, the significant variables included were distance from areas of low productivity ($P = 0.012$) and high productivity ($P = 0.014$, Table 4). The probability of a plot being a shrew capture fix increased with increasing distance from age class I and areas of low productivity (Figure 18). In contrast, the probability of a plot being a shrew capture fix decreased with increasing distance from areas of high productivity (Figure 18).

In the analysis including the shrew capture fixes and 100% MCP random plots, distance to nest was the only significant variable ($P = 0.0015$, Table 4), while distance to areas of high productivity was the only significant variable in the productivity analysis ($P = 0.002$, Table 4). The probability of a plot being a shrew capture fix decreased with increasing distance from the nest and areas of high productivity (Figure 18).

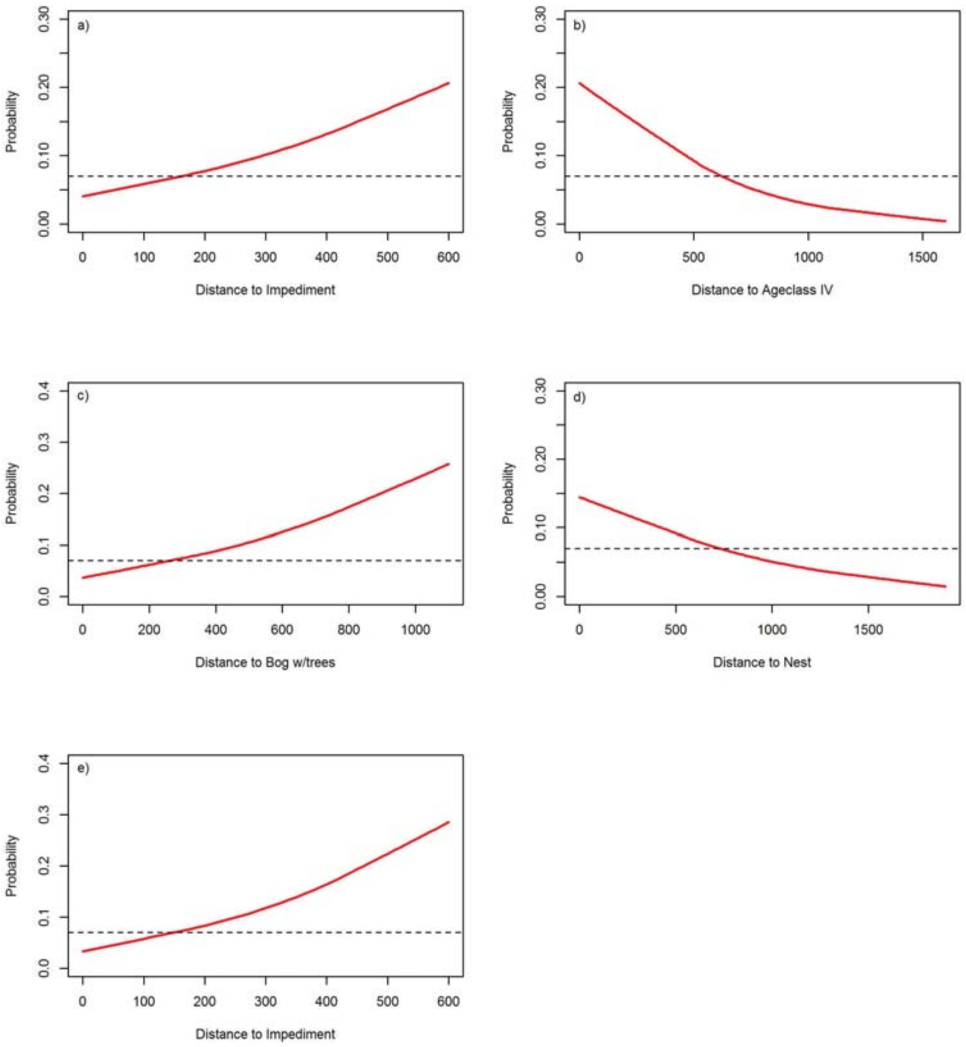

Figure 17: Probability of a plot being either *Microtus* vole capture fix or a random plot with the curve describing the logistic regression model for areas of impediment (a), age class IV (b), bog with trees (c), nest (d) and impediment (e). (a) are tested against the 95% MCP random plots, whereas (b-e) are tested against the 100% MCP random plots. Area below dotted line indicates *Microtus* vole capture fixes, whereas area above dotted line indicates MCP random plots.

3.5.3 Differences between captures of shrews and *Microtus* voles

Based on the 32 shrew capture fixes and 25 *Microtus* vole capture fixes from the three males were also shrews were delivered, a separate analysis was performed to test for differences in capture habitat between these two prey groups. The significant variables was only distance from forest age class I (P = 0.033, Table 4). The significant productivity variables included distance to areas of impediment (P = 0.0020) and low productivity (P = 0.00045, Table 4). The probability of a plot being a shrew capture fix rather than a *Microtus* vole capture fix increased with increasing distance from age class I and areas of low productivity (Figure 19), and decreased with increasing distance to impediment areas (Figure 19). No significant difference were detected between transport distances of *Microtus* voles and shrews (P=0.44). The maximum distance at which a shrew was caught (1569

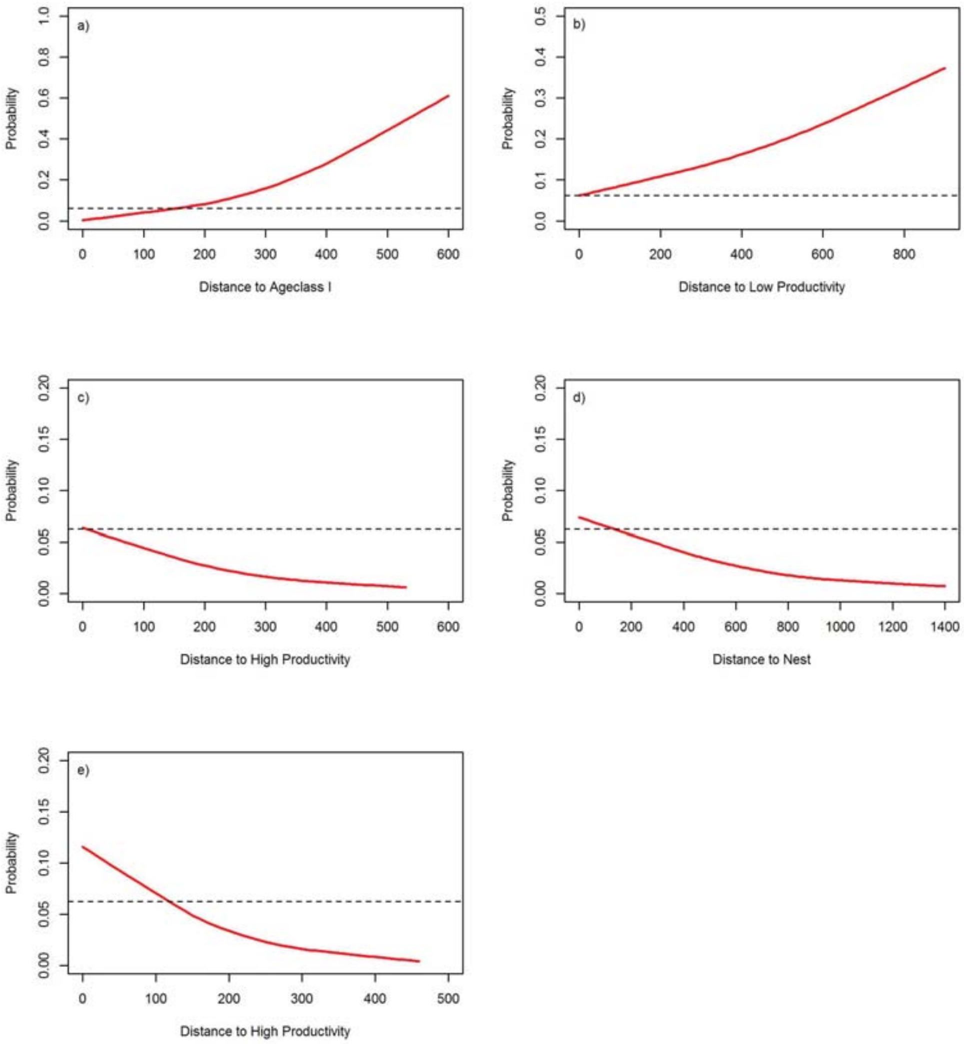

Figure 18: Probability of a plot being either shrew capture fix or a random plot with the curve describing the logistic regression model for forest age class I (a), areas of low productivity (b), high productivity (c), nest (d) and high productivity (e). (a), (b), and (c) are tested against the 95% MCP random plots, whereas (d), and (e), are tested against the 100% MCP random plots. Area below dotted line indicates owl fixes, whereas area above dotted line indicates MCP random plots.

m) was farther from the nest than the maximum distance for *Microtus* voles fixes (1397 m).

3.6 Success dependent habitat selection

The males from nest I, II, III and IV returned to the same area following a successful capture in 2, 4, 2 and 13 cases, respectively. The males from nest II and IV returned to the same area more often than expected by random (Table 6), whereas male I and III did not. A Fischer combined probability test revealed that when pooled, males returned to the same hunting area more often than expected by random (Table 6).

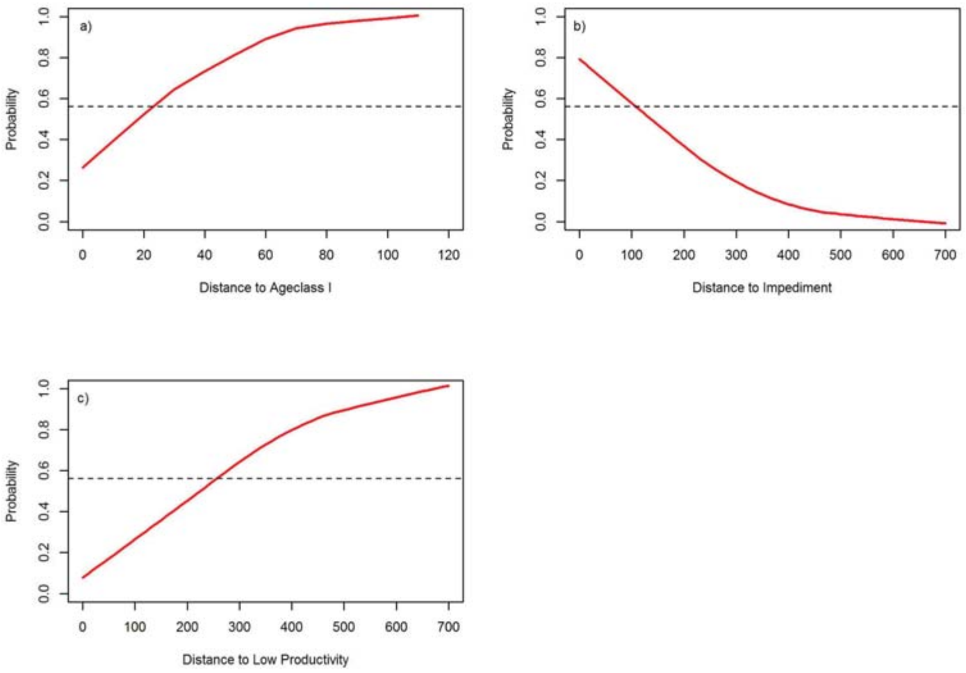

Figure 19: Probability of a plot being either a *Microtus* vole capture fix or a shrew capture fix with the curve describing the logistic regression model for forest age class I (a), areas of impediment (b) and low productivity (c). Area below the dotted line indicates shrew-fixes, whereas area above the dotted line indicates *Microtus* vole capture fixes.

Table 6: The number of times each Tengmalm's owl male returned from the nest to the area of the previous capture (Same area) rather than to somewhere else in the home range (Different area). †refer to the Fischer combined probability test.

Nest	Same area	Different area	Capture fixes	χ	diff.	P
I	2	5	7	1.17	1	0.28
II	4	6	10	10.00	1	0.0016*
III	2	5	7	1.17	1	0.28
IV	13	15	28	149.33	1	<0.0001*
Total	21	31	52	41.10†	8†	<0.0001*†

4 Discussion

4.1 Home range use and hunting behaviour

4.1.1 Home range use

The four owls had a mean home range of 219 ha estimated by the 100% MCP method. The home range estimates are in accordance with other home range estimates for Tengmalm's owl. Sonerud et al. (1986) reported a home range of 205 ha (100% MCP) for one male within the same study area as the present study, while Korpimäki & Hakkarainen (2012) found a mean home range of 151 (range 54 - 268) ha (100% MCP) for nine males in Finland. In contrast, Lane et al. (1997) estimated a mean home range size of 1202 ha (range: 742 to 1444) for four males in Minnesota, USA.

Using the 95% kernel home range estimation method, the home ranges in the present study had a mean size of 310 ha. Santangeli et al. (2012) estimated a mean home range of 114 (range: 49 to 293) ha for 15 males within the same area as Korpimäki & Hakkarainen (2012), while Hayward et al. (1993) found a mean home range size of 1182 ha in Idaho, Montana and Wyoming, USA.

The reason for these continental differences may be that Tengmalm's owls in north America have to rely on less profitable foraging areas (Korpimäki & Hakkarainen 2012). Additionally, Lane et al. (1997) used diurnal roost sites collected over several years to estimate the home range, while Hayward et al. (1993) tracked owls for longer than a single breeding season. In contrast, the Scandinavian studies were restricted to a single nesting season (Sonerud et al. 1986, Korpimäki & Hakkarainen 2012, Santangeli et al. 2012). Therefore, the owls in the American studies were not restricted to the area surrounding the nest when they were tracked and may have been free to range over a larger area. Also, Lane et al. (1997) detected a difference between selection of nesting habitat and selection of roosting and foraging habitats. Whereas owls selected mature, upland, mixed forests for nesting, they selected homogeneous lowland conifer forests for roosting and foraging (Lane et al. 1997). In other words, they may have had to travel longer distances between the nest and preferred hunting habitats than their Scandinavian counterparts, given that the shortest known distance between prey capture and the nest in my study was less than 40 m.

Cumulative home ranges revealed that the present tracking effort was not sufficient to accurately estimate the home ranges. Similarly, in other studies the cumulative home range of three out of four males did not level off, despite a high tracking effort (Sonerud et al. 1986, Jacobsen & Sonerud 1987). Given that the tracking by Korpimäki & Hakkarainen (2012) lasted for only 2 - 4 days, whereas the home ranges by Santangeli et al. (2012) were estimated from a minimum of 32 fixes per owl, the home ranges in these studies are presumably underestimated. Thus, continental differences may also be related to a lower tracking effort in European studies.

The mean maximum distance between the nest and the hunting male was 1523 m, and the owls hunted at a mean distance of 550 m from the nest. Santangeli et al. (2012) found that males hunted at an average distance of 644, and up to 2880 m from the nest, which fits with the findings of my study. Korpimäki & Hakkarainen (2012) speculated that this distance would increase with decreasing prey availability, based on their failed attempts to track two males in a year of low vole abundance, when the males regularly hunted 2-3 km from the nest (Korpimäki & Hakkarainen 2012). However, the male tracked by Sonerud et al. (1986) was tracked during a low vole year, but the mean nightly maximum distance from the nest (1198 m) did not differ substantially from the present study (1523 m), and was in fact shorter.

In Finland, Tengmalm's owl home ranges increased with decreasing proportion of spruce forest in the home range (Santangeli et al. 2012). However, in the present study area, independent of forest age, spruce was by far the dominating tree species and presumably not a limiting factor for breeding Tengmalm's owls. However, size of home ranges was related to area of productive habitats. As proportion of impediment and low productive areas increased, so did the home ranges. This is presumably related to prey abundance. Kouba et al. (2013) found that the home range size of dependent juveniles was larger during a year of low prey availability, compared to a year with high prey availability. Thus, home range sizes are presumably related to prey availability.

4.1.2 Hunting behaviour

In the present study, owls perched at a mean height of 2.9 m, and spruce was by far the most common perch tree (63%), followed by birch (13%). Similarly, Norberg (1970) reported a mean perching height of 1.7 m, whereas Bye et al. (1992) reported a mean perch height of 3.1 m. Additionally, Hayward et al. (1993) found that Tengmalm's owl perched at an average height of 4.0 m. These perch heights are presumably optimal for predators searching for concealed prey using auditory clues (Bye et al. 1992, Andersson et al. 2009).

4.1.3 Overlap between nights

The males in the present study did not seem to shift hunting areas from one night to the next, but instead shifted hunting areas gradually over more nights. In contrast, Sonerud et al. (1986) found that a male owl tended to avoid hunting in the same areas for consecutive nights. This shift may be due to a resource depression (Sonerud et al. 1986), if the owls activity increases prey vigilance, and hence decreases prey detectability (Nilsson et al. 1982, Kotler 1992). Such a response is considered to be common among avian prey, but less so for mammalian prey (Nilsson et al. 1982). However, Kotler (1992) found that two species of gerbils (*Gerbillus allenbyi* and *G. pyramidum*) reduced their activity following exposure to a live barn owl (*Tyto alba*), and stayed more vigilant for two to five days following the exposure (Kotler 1992). Additionally, Hendrie et al. (1998) found that social voles (*Microtus socialis*) spent more time in the burrow following exposure to tawny owl (*Strix aluco*) vocalizations.

Tengmalm's owls are silent hunters (Norberg 1970), and provide few clues of their whereabouts to potential prey. However, considering that both northern hawk owls (*Surnia ulula*) and Tengmalm's owls regularly fail in prey capture attempts (Bye et al. 1992, Sonerud 1992), an increased prey vigilance can be expected after failed attempts. It may be beneficial to change hunting areas, but considering that field voles have a mean daily home range of 0.11 ha for males, and 0.05 ha for females during the breeding season (Borowski & Owadowska 2010), the decreased prey detectability may not affect habitat selection on the scale at which it was studied here. In contrast, because the study of Sonerud et al. (1986) was conducted during a low vole year in which the owl probably had to hunt more avian prey, the increased prey vigilance may have been substantial enough to facilitate a change in hunting area. Alternatively, the shift in hunting area may be due to a low hunting success the first night (Sonerud et al. 1986). However, there was no support for this in the present study.

4.2 Habitat selection

4.2.1 Importance of clear-cuts

Male Tengmalm's owl in the present study preferred hunting closer to all forest age classes and bogs without trees, than expected by random. This was particularly strong for forest age class I, i.e, clear-cuts and plantations. Additionally, approximately 60% of all fixes were located in this habitat, as opposed to an availability of approximately 35%. Similarly, Jacobsen & Sonerud (1993) found that males hunted in clear-cuts more often than expected by random when the ground was snow-free, as it was also when the present study was conducted. In contrast, Korpimäki & Hakkarainen (2012) found that Tengmalm's owl in Finland avoided clear-cuts and agricultural areas, and rather hunted in forested habitats. Presumably, the avoidance of clear-cuts in Finland may be related to an increased risk of predation from larger birds of prey, including Ural owls (*Strix uralensis*), goshawks (*Accipiter gentilis*, Korpimäki & Hakkarainen 2012) and tawny owls (Vrezec & Torne 2004). This prediction is supported by several studies revealing that survival and lifetime reproductive success of Tengmalm's owls males in Finland increase with cover of old forest in the home range (Laaksonen et al. 2004, Hakkarainen et al. 2008), presumably because these habitats work as refuges from larger avian predators (Hakkarainen et al. 2008). However, this is probably not the case in the present study area because neither Ural owl nor tawny owl occur in the study area (Sonerud 1994, Solheim et al. 2009), and goshawks are temporally segregated (Mönkkonen et al. 2007). Korpimäki & Hakkarainen (2012) grouped clear-cuts and agricultural areas into one category when estimating resource selection. This is problematic, given that agricultural areas, as opposed to many clear-cuts, lack elevated perches from which Tengmalm's owls may search for prey. Also the study of (Korpimäki & Hakkarainen 2012) was conducted in an area with a relatively high amount of agricultural fields, in contrast to the present study.

Sonerud et al. (1986) found that a male Tengmalm's owl hunting in the vicinity of the present study area, preferred hunting in mature forests, and avoided clear-cuts. The study was conducted in a low vole year (Geir A. Sonerud, pers. communication), and the male may therefore have had to utilize alternative prey groups for food, i.e, avian prey, which are more abundant in forests than in clear-cuts (Jansson & Andren 2003).

Several studies have emphasized the importance of clear-cuts in maintaining large populations of prey animals, particularly *Microtus* voles for birds of prey (Sonerud 1986, Ims 1991, Jacobsen & Sonerud 1993, Hakkarainen et al. 1996, Hakkarainen et al. 1997, Ecke et al. 2002). The relatively high availability of clear-cuts has come about as a result of modern forestry practices (Sonerud 1997), which have altered the habitat characteristics by creating habitat patches of evenly aged forest stands (Östlund et al. 1997), and by increasing the total volume of standing wood (Östlund et al. 1997, Hedwall et al. 2013). The current practice of clear-felling creates large areas of grassland habitat (Hedwall et al. 2013), which are suitable habitats for *Microtus* voles (Sonerud 1986, Ims 1991, Ecke et al. 2002) and were readily used by hunting males in the present study.

The density of graminoids in clear-cuts increases with habitat productivity, but decreases with forest age (Hedwall et al. 2013). Therefore, clear-cuts may serve as prey hotspots in the first years following clear-felling as graminoids dominate the field layer (Hakkarainen et al. 1996). Hakkarainen et al. (1996) found that Tengmalm's owl pairs produced more fledglings in territories with high (>30%) proportions of clear cuts, as opposed to those with lower proportions of clear-cuts. This was attributed to a higher density of *Microtus* voles in large clear cuts. However, the prey availability in clear-cuts may be reduced by either high vegetation (Sonerud et al. 1986), lack of perches (Widén 1994) or snow cover (Sonerud 1986).

For predators searching by visual cues, prey detection can be expected to decrease with increasing vegetation and density (Andersson et al. 2009). Bechard (1992) found a negative correlation between plant cover and foraging in Swainson's hawk (*Buteo swainsoni*) and attributed this to a greater prey availability in areas of low vegetative cover, despite a lower prey abundance. Similarly, the distribution of foraging red-tailed hawks (*Buteo jamaicensis*) and rough-legged buzzard (*Buteo lagopus*) was affected by vegetative cover (Baker & Brooks 1981). However, although dense vegetation limits prey detectability by visual clues, it may be less constraining for animals hunting by auditory clues (Norberg 1970, Rice 1983, Bye et al. 1992, Andersson et al. 2009). Therefore, the presence of dense field vegetation does not necessarily reduce prey availability enough to cause an avoidance of habitats dominated by grasses and forbs.

In especially dense vegetation stands, prey detection may only be possible from directly above (Andersson et al. 2009). Little owls (*Athene noctua*) reduced their perch height with increasing vegetation cover, indicating that they may have focused on the area directly beneath the perch (Tomé et al. 2011). Faced with dense vegetation, this mainly visually hunting owl may have included auditory clues to detect prey concealed in vegetation (Tomé et al. 2011). Also, hen harriers (*Circus cyaneus*), which utilizes both hearing and sight when hunting, had a lower search height than raptors searching only by visual cues (Rice 1983). Similarly, Tengmalm's owls may reduce perch height in habitats with denser vegetation to facilitate detection of concealed prey in dense habitats (cf. Rice 1983).

The lack of perches in clear-cuts has been emphasized as a factor limiting habitat suitability of clear-cuts for raptors (Widén 1994), especially for raptors searching by visual cues given that these more often prefer higher perches (Sonerud 1992a, Andersson et al. 2009). However, Tengmalm's owl prefer lower perches and readily use small saplings and other plants as perch posts. Therefore, the presence of perches is presumably not a limiting factor but may exclude owls from parts of the clear-cut.

Sonerud (1986), Nybo & Sonerud (1990) and Jacobsen & Sonerud (1993) have emphasized the importance of snow cover for prey availability on clear-cuts. When clear-cuts are snow covered the prey availability of *Microtus* voles are low in clear-cuts, due to the protective snow cover, while prey availability of bank voles may be greater because these are generally more active over the snow layer (Jacobsen & Sonerud 1993). It may therefore be beneficial for Tengmalm's owls to forage in forested habitats while the ground is snow-covered (Sonerud 1986, Jacobsen & Sonerud 1993). As spring precedes, the snow in clear-cuts will generally melt quicker than in forested areas due to a higher solar radiation. Thus, Tengmalm's owl shifted from hunting in forested habitats to clear-cuts when the latter became partially snow-free (Jacobsen & Sonerud 1993). Therefore, the high utilization of clear-cuts by male Tengmalm's owls in the present study may thus have only been a temporary utilization.

4.2.2 Selection of forested habitats

A preference for hunting closer to all forest age classes than expected by random was only evident in the analysis including 100% MCP random plots, whereas only ageclass I and III were included in the test containing 95% MCP random plots. However, when comparing number of observations per habitat to availability, it was revealed that owls used age class III less than what was available. When the habitat selection of each owl was tested individually, three of the four males preferred hunting farther from age class III than expected by random. These results highlight that it may be problematic to pool observations from several individuals when testing for habitat selection, even though individual ID is modelled as random factor. Pygmy owls (*Glaucidium passerinum*) foraged less in intermediate age classes than what was proportionally available (Strøm & Sonerud 2001).

Depending on the local productivity, intermediate age classes tend to be quite dense, and given that Tengmalm's owls are relatively small, dense forested habitats may act as shelter from larger predators (Hakkarainen et al. 2008). However, this remains untested in the present study population. Dense forest stands may however be used more frequently as roost sites (cf. Bye et al. 1992). There is a lower abundance of small mammals in low and intermediate age classes, especially those that have not been thinned (Sullivan et al. 2001). Additionally, there was a reduced biomass of herbaceous plants in forest patches that had not been thinned (Sullivan et al. 2001), probably related to the shadowing effect of dense spruce stands.

Male owls in the present study were found to hunt closer to age class IV (i.e, mature stands) than expected by random. Similarly, Korpimäki & Hakkarainen (2012) found that males preferred hunting in mature stands more often than expected by random. The importance of mature stands has been emphasized for a number of owl species and seem especially important for northern spotted owls (*Strix occidentalis*, North et al. 1999). Similarly, pygmy owls foraged more in mature age stands than expected by random (Strøm & Sonerud 2001). Mature forests constitute the main habitat type of bank voles (Sonerud 1986, Jacobsen & Sonerud 1993, Gorini et al. 2011), and may serve as source areas from which prey disperse to surrounding areas (Ecke et al. 2002). However, given the low availability and high average distance to age class IV in the present study, the result seems to rather be an effect of the relative spatial location of observation fixes versus random plots, than an actual preference of mature forests. It is also noteworthy that in the individual analysis, age class IV was only significant for the two males that had little or nothing of the given habitat in their home range.

4.2.3 Other habitat categories

In the analysis based on 95% random plots, the owls were found to hunt closer to open ground than expected by random. This is unlikely given the lack of prey in these habitats, and the result is probably biased due to low availability of this habitat types in three of the four nests.

I found that male Tengmalm's owls preferred hunting closer to bogs without trees, and farther from bogs with trees than expected by random. This may be explained by an increased availability of shrews (cf. Hanski & Kaikusalo 1989) and bank voles (Gorini et al. 2011) in these habitats . However, the results were inconclusive based on the high average distances between observation plots and the two habitat types. This may be due to the relatively low occurence of both types of bogs in the home ranges of the males from nest I and IV, which may have biased the results. This is supported by data from the individual models, where males II and III were found to hunt farther from bogs without trees than expected by random, whereas male I and II were found to hunt farther from bogs with trees than expected by random. Korpimäki (1988) found that the probability of a Tengmalm's owl territory being occupied decreased with increasing amount of bog in the territory. Similarly, the owls in the present study had to forage over wider areas with increasing proportion of bogs in their home range.

Male Tengmalm's owl hunted more often in the vicinity of the nest than expected by random in my study. Theories on central place foraging predict that foraging animals will hunt more thoroughly close to the nest than farther away from it, because the cost of carrying the captured prey to the nest increases with increasing distance from the nest (Andersson 1981). Andersson (1981) found that whinchats (*Saxicola rubetra*) decreased their search effort with increasing distance from the nest, searched more close to the nest than farther away, and took more of the available food near the nest than farther from it. Similarly, half of all little owl fixes were recorded within 125 m from the nest (Sunde et al. 2009), whereas hen harriers tended to hunt more often in the vicinity of the nest than expected by random (Thirgood et al. 2003). The core areas of the owls I studied, as shown by kernel home ranges, were located close to the nest, this confirms that the males preferred hunting in the vicinity of the nest, presumably in order to minimize costs of travelling.

4.2.4 Importance of habitat productivity

When each owl was tested individually, males I and IV hunted significantly to the nest than expected by random. Additionally, the core kernel area was considerably smaller for these two males than for the other two males. This size difference in core areas may be related to a difference in productivity between habitats, given that these two males had a higher abundance of medium and high productivity areas than the other two males. This is supported by the results showing that the males preferred hunting close to areas of medium and high productivity, and avoided areas of impediment and low productivity.

Dense vegetation in the field layer is important for the abundance of voles (Hansson 1977, Ecke et al. 2002). Therefore, areas of high productivity may be favoured as hunting habitat by Tengmalm's owl, given that these areas provide a higher amount of available prey than low productivity areas. Productivity tends to follow a gradient with decreasing productivity with increasing altitude, i.e, productivity is higher in valley floors than on hill-tops (cf. Fremstad 1997). This relationship is also related to a moisture gradient, with increasing amount of productivity in moist areas such as along streams (Fremstad 1997).

Distance to water proved insignificant in all models, which was surprising, given that the owl was regularly observed close to small rivers during the tracking. The surroundings of small rivers are important habitat for *Microtus* voles (Gorini et al. 2011). Unfortunately, due to the weakness in the data retrieved from the area resource map concerning rivers, my results may be biased and hampered a detection of selection. The individual analysis revealed that male IV preferred hunting farther from rivers and streams than expected by random, whereas male I preferred hunting closer to rivers and streams than expected by random. Due to the lack of several brooks and small streams in the area resource map, the avoidance of this habitat by male IV was probably a result of a biased dataset.

4.3 Habitat-specific prey capture

I found that male Tengmalm's owls captured prey closer to age class IV than expected by random. This is probably related to biased data resulting from the habitats low availability in the study area (see above). Also, prey was captured closer to areas of high productivity than expected by random. Jedrzejewski & Jedrzejewska (1996) analysed several long-term studies (>5 years) of rodent abundance and found that mean densities of rodents were related to productivity of ground vegetation. Similarly, Bechard (1982) found that vole density was correlated with the total dry weight of vegetation. Presumably, high productivity of vegetation allows faster renewal of food resources after grazing, which in turn, enhances rodent survival (Jedrzejewski & Jedrzejewska 1996). For shrews, home ranges decrease (Wang & Grimm 2007) and densities increase (Hanski & Kaikusalo 1989) with increasing productivity, indicating a higher resource availability. Apparently, the level of productivity is an essential factor in determining prey abundance for Tengmalm's owls.

This is strengthened by the result that prey were captured further from areas of impediment than expected by random. Due to the low productivity of plant material in areas of impediment, the small mammal densities are presumably low and the distribution of potential owl prey dispersed. Therefore, the frequency of prey capture is reduced in areas of low productivity. Male Tengmalm's owls captured prey farther from bog with trees than expected by random. Bog with trees are classified as areas of impediment, and the lack of prey capture (and hunting) in the vicinity of this habitat probably results from a lower density of prey than in other habitats (see Henttonen et al. 1977, Korpimäki 1988).

Capture fixes were located closer to the nest than expected by random. This may result from an increased search effort closer to the nest than farther from it (cf. Andersson 1981). Animals are expected to make different foraging decisions on different spatial scales (Ortego & Diaz 2004), and most hunting should occur in patches yielding the greatest net energy gain (Thirgood et al. 2003). Given the reduced energy expenditure of travelling closer to the nest (Sonerud 1992b), a higher search effort closer to the nest will likely result in an increased probability of prey capture.

4.3.1 Differences between foraging effort and success

By comparing capture fixes with non-capture fixes, it was possible to determine if certain habitats provided higher probabilities of prey capture than other. Habitats closer to roads seemed to be important foraging areas because they yielded relatively high rate of capture fixes compared to the effort put into foraging there. Roadside vegetation can be very diverse due to the repeated disturbances and abundance of light (Fremstad 1997), creating a grass rich habitat utilized by small mammals, particularly field voles (Henttonen et al. 1977). Therefore, such human-altered landscapes may serve as valuable foraging areas for birds of prey. Martinez et al. (1998) reported that short-eared owls (*Asio flammeus*) regularly hunted along roads, utilizing wooden fence posts as perches. In the present study, male I was seen perching on small saplings in the roadside particularly often. On one occasion, he was seen perching <5 m from the road, seemingly unaffected when a car passed by. Shortly after, he captured a *Microtus* vole after perching for approximately three minutes.

Forest age class I provided relatively fewer prey captures than would be expected based on the utilization of this habitat. Similarly, the proportion of capture fixes located in age class I was lower than the proportion of observation fixes in the same habitat. Because prey abundance was not estimated in the present study, it can not be ruled out that the lower capture rate was due to a relatively low prey availability. However, it is presumably more likely a result of the relatively high search effort in age class I.

Similarly, capture fixes were located farther from areas of medium productivity than non-capture fixes, indicating that despite the high level of search effort, the owls were unable to catch the number of prey that could be expected based on the utilization. Whereas age class I was the most frequently used habitat, medium productivity was the most frequently used productivity class.

4.3.2 Captures of *Microtus* voles

Microtus vole capture fixes were located closer to age class IV than expected by random. Hansson (1977) predicted that two factors govern habitat selection in *Microtus* voles. First, cover is the primary factor by which *Microtus* voles select their habitat, and litter or vegetation should cover at least 80% - 90% of the ground (Hansson 1977). This cover should facilitate tunnelling and provide shelter (Hansson 1977). Second, the primary food of *Microtus* voles, are graminoids and forbs, and should be plentiful to provide enough food (Hansson 1977). *Microtus* voles are particularly abundant in clear-cuts (Henttonen et al. 1977, Sonerud 1986, Nybo & Sonerud 1990, Ims 1991, Ecke et al. 2002), and Hansson (1977) predicted that they would be less abundant in forested areas.

Therefore, the result that male Tengmalm's owls captured *Microtus* voles closer to age class IV than expected by random is surprising. Given the habitat requirements of *Microtus* voles, patches of age class IV do probably not work as source areas from which to disperse. The result may rather stem from biases resulting from the low availability of age class IV in the study area (see above). For example, all but one of the *Microtus* voles captured by male IV was located in the same clear-cut located east of the nest. The closest patch of age class IV to these fixes were located approximately 300 m north-east, just outside the home range. Whereas these fixes were spatially concentrated, the random plots were more spread out and the majority located farther to the south-west, i.e, farther from the patch of age class IV. Therefore, the probability of being closer to the patch of age class IV was higher for fixes than random plots, but it did not reflect any selection of age class IV.

Microtus vole fixes were located closer to the nest than expected by random. There may be several explanations for this result. First, owls may selectively choose to transport captured *Microtus* voles to the nest, depending on the distance from the nest (cf. Sonerud 1992b). Sonerud (1989) predicted that single-prey loaders would selectively transport larger prey items to the nest, and that the strength of this selection would increase with increasing distance from the nest. Therefore, male Tengmalm's owls may have selected to consume small prey captured far from the nest themselves, and only feed the nestlings with the ones captured closer to the nest. On one occasion, the male in nest II was seen capturing a vole approximately 1300 m from the nest. The prey was not transported to the nest, rather the male continued hunting in the same area. This observation may indicate that the prey was too small to be worth transporting to the nest. However, given that on this particular night, the male only delivered two prey items to the nest,the male may have chosen to eat the prey for self-maintenance due to an energy deficiency.

Second, owls may have had a generally higher search effort closer to the nest, resulting in increased tendency to capture *Microtus* voles closer to the nest than expected by random. Alternatively, it may also be due to a higher proportion of suitable habitat closer to the nest than farther from it (cf. Ortego & Diaz 2004), given that nest boxes were erected in what was assumed to be suitable habitat. However, this remains to be tested in detail.

Capture fixes of *Microtus* voles were located farther from bogs with trees and areas of impediment than expected by random. *Microtus* voles can be abundant in eutrophic and mesotrophic bogs (Henttonen et al. 1977), but the bogs located in the study area are rather poor in nutrients and prey availability are presumably very low. Given the availability of perches in forested bogs, and due to the low vegetation, the owls should presumably have a high detection rate. Therefore, bog with trees should be an acceptable foraging habitat if the abundance of prey allows it. Therefore, the rather low usage of these areas probably stems from low levels of prey in forested bogs. However, forested bogs may be a particularly suitable habitat in peak years when production of small mammals is high in surrounding habitats. In peak years, subordinate voles may be forced into unsuitable habitat such as forested bogs (see Hansson 1977, Koivunen et al. 1998, Meri et al. 2008), which will make these habitats suitable foraging habitats for Tengmalm's owls. Therefore, in peak vole years it could be expected that hunting Tengmalm's owls could use forested bogs to a greater extent.

4.3.3 Capture of shrews

Shrews are highly opportunistic generalists (Hanski & Kaikusalo 1989), with a high mass-specific metabolic rate (Saarikko 1989). Thus, shrews are highly active and alternate between foraging and sleeping in turns of approximately 1 hr (Saarikko & Hanski 1990). Shrews have poor eyesight, and hunt arachnids and insects, primarily by touch and smell (Barnard & Baker 1981). Additionally, both sexes are highly territorial and defend their territories ferociously (Saarikko 1989, Wang & Grimm 2007), whereas subordinate individuals who fail to obtain a territory either starve to death, or are forced to disperse (Hanski et al. 1991). Additionally, shrews are more prone to take risks while foraging when the need for food is large, i.e, energy deficient (Barnard & Baker 1985). The high activity levels (Saarikko & Hanski 1990) and territoriality (Saarikko 1989, Wang & Grimm 2007) may make shrews highly detectable for Tengmalm's owls.

Captures fixes of shrews were located closer to the nest than expected by random. Throughout all tests, the effect of distance to nest was significant only when the 100% MCP random plots were included. Hence, a higher capture rate of shrews closer to the nest than expected by random may primarily be caused by a higher search effort in these areas compared to areas farther from the nest. It is presumably not based on specific size-based allocation of search effort and transportation.

Shrews were captured farther from forest age class I than expected by random. Shrews occur in a wide variety of habitats, but abundance has been found to be lower in clear-cuts than spruce forests (Hanski & Kaikusalo 1989). Hanski & Kaikusalo (1989) reported that dominance of common shrew over other species of shrews increased following clear-felling, but the abundance decreased. Similarly, in the same area as my study area, shrews made up a smaller proportion of the prey base in clear-cuts compared to other habitats (Jacobsen & Sonerud 1993). Hence, the low capture rates of shrews in age class I may thus be a result of a generally low abundance of this prey type here.

Capture fixes of shrews were located closer to areas of high productivity and farther from areas of low productivity than expected by random. Hanski & Kaikusalo (1989) found that, in Finland, larger species of the genus *Sorex* inhabited more productive habitat, and that the density of common shrews increased with increasing productivity. Therefore, densities in productive habitats may be high, yielding profitable foraging areas for Tengmalm's owls. In the present study, 78% of all shrews were delivered at nest IV, which is presumably related to a higher abundance of this species given the generally higher proportion of productive areas around this nest. A higher capture rate in productive areas may indicate that owls select prey by availability, rather than selecting specific prey types.

4.3.4 Differences between prey groups

Microtus vole capture fixes were located closer to forest age class I than shrew capture fixes. *Microtus* voles are found predominantly in clear-cuts (Henttonen et al. 1977, Sonerud 1986, Nybo & Sonerud 1990, Ims 1991, Ecke et al. 2002), while shrews are less abundant in the same habitat (Hanski & Kaikusalo 1989). Therefore, the predominance of *Microtus* voles over shrews among prey captures closer to forest age class I presumably reflects a higher abundance. The reduced abundance of shrews may be related to competition with the larger field vole (cf. Hanski et al. 1991).

Capture fixes of *Microtus* voles were located closer to areas of low productivity and significantly farther from areas of impediment than shrew capture fixes. This is in congruence with results from each prey group individually.

The profitability of transporting prey back to the nest depends on the distance from the nest and the size of the prey (Andersson 1981). Sonerud (1989) observed that central-place foraging great grey shrikes (*Lanius excubitor*) and Eurasian kestrels (*Falco tinnunculus*) transported larger prey back to the nest, whereas smaller prey where consumed at the capture site. Self-consumption of smaller prey would presumably increase at larger distances from the nest (Andersson 1981, Sonerud 1992b). Shrews are smaller (approximately 10 g) than *Microtus* voles (approximately 30 g). Accordingly, one could expect that *Microtus* voles delivered to the nest have been captured farther from the nest than shrews (cf. Sonerud 1992b). However, no such relationship was discovered in the present study. The reason may be that both shrews and *Microtus* voles were sufficiently large to be worth transporting back to the nest. This is supported by the fact that both species groups were captured closer to the nest than expected by random.

4.4 Success dependent habitat selection

Male Tengmalm's owls returned to the area in which they had captured the previous prey more often than expected by random. This behaviour is predicted for central-place foraging animals searching for clumped prey (Wakeley 1978, Sonerud 1985a). If prey is clumped, time between visits to the capture site should be minimized (Sonerud 1985a), because several prey may be located in the vicinity of the previous capture site. However, if prey is uniformly distributed (Sonerud 1985a) or subject to depletion (Sulikowski & Burke 2007), a predator would benefit from switching hunting areas. Sulikowski & Burke (2007) found that the omnivorous noisy miner (*Manorina melanocephala*) shifted patches after foraging on nectar, whereas after foraging on insects, no such relationship was found. Similarly, after hen harriers had caught a grouse chick, they rarely returned to the same brood to catch another (Redpath 1992).

Mountain chickadees (*Poecile gambeli*), a single prey loading species, returned to the area where they had made the previous capture more often than expected by random (Grundel 1992). Returning to the previous capture site reduced search time, but chickadees stopped returning when search time increased (Grundel 1992). Similarly, male IV in the present study had the shortest duration of foraging bouts, and returned to the same patch more often than the others. Hence, the lack of return in hen harriers (Redpath 1992) may be due to grouse broods either being difficult to locate in the first place, or because of grouse broods relocated following predation (cf. Sonerud 1985a). The profitability of returning to the same capture sites for predators searching for grouse broods probably decreases with increasing distance to the nest, because increased time spent travelling increases the time made available for grouse broods to relocate.

Ferruginous hawks (*Buteo regalis*) returned to the same area as the previous capture site following 52% of all captures (Wakeley 1978). Norberg (1970) observed a Tengmalm's owl catching several nestlings in succession from the same nest, whereas Korpimäki & Hakkarainen (2012) observed a male Tengmalm's owl first delivering a male chaffinch (*Fringilla coelebs*) to the nest, and thereafter several nestlings. Hence, Tengmalm's owl have the ability to remember specific spatial locations in relation to food availability. Sonerud et al. (1986) estimated that a male Tengmalm's owl returned to the same hunting area in six out of eight cases, but lacked proper verification that prey capture and prey delivery had taken place.

Voles and shrews are neither randomly nor uniformly distributed, and abundance depends on habitat structure, i.e, vegetative cover (Hansson 1977, Henttonen et al. 1977, Ims 1991, Ecke et al. 2002) and productivity (Hanski & Kaikusalo 1989). Thus, in particularly productive habitats densities are higher, making the overall distribution clumped (Hanski & Kaikusalo 1989). Therefore, quick prey detection may be used by foraging Tengmalm's as a cue to return to the capture site.

5 Conclusion

Tengmalm's owls did not shift hunting areas from one night to the next, but rather changed hunting areas gradually with increasing time. The nest of all four owls were located within the core area, as estimated by kernel home range estimates. Additionally, logistic regression analysis revealed that owls hunted more in the vicinity of the nest, but made infrequent foraging trips farther from the nest. Increased foraging effort closer to the nest is in line with predictions of optimal central-place foraging.

As predicted the breeding male Tengmalm's owls hunted more often closer to age class I than expected by random. Although not specifically tested in the present study, age class I presumably provided suitable habitat for *Microtus* voles, which were readily available for hunting owls. Additionally, since density of the field layer increases with site productivity (Hedwall et al. 2013), Tengmalm's owl did not seem to be restricted by vegetative cover in any significant degree because male owls hunted more in high productivity sites than expected by random. Tengmalm's owls may have compensated for the lack of prey visibility with auditory clues and hunting from low perches.

As predicted, captures of shrews were related to productivity, with most captures occurring in productive habitats. However, high productivity was not related to *Microtus* vole capture fixes as expected, only an avoidance of impediment was apparent. Results indicate that the shrews may be excluded from certain habitats by the larger *Microtus* voles, because *Microtus* voles were more often captured in age class I. Thus, the population cycles of *Microtus* voles may have profound effects on the distribution of shrews as predicted by Hanski et al. (1991).

Although it may be beneficial to transport larger prey items to the nest, I found no such relationship between shrews and *Microtus* voles in the present study. The lack of difference may be because both prey groups were captured quite close to the nest. However, male Tengmalm's owls may show a different pattern in years of low vole abundance, when owls presumably forage over a larger area, and may choose to differ between prey groups when the distances to the nest increase.

According to predictions, male Tengmalm's owls returned to the same foraging more often than expected by random, and the selection was particularly strong for the male in nest IV. This may be related to the shorter foraging bouts in male IV, similar to other species (Grundel 1992).

The combined use of radio telemetry and nest surveillance by video recordings is a new method in ecological research. The present study show that it is possible to record the time and prey type of deliveries at the nest, and relate these to a spatial location. Thus, this method allow detailed studies of habitat specific hunting success which to date have been difficult to study. VHF tags present one drawback because the number of capture fixes will be affected by observer experience and species studied. Tengmalm's owls are not shy and is a suitable study species for this design, whereas other more evasive species which are harder to track may be less suitable. For larger species, GPS transmitters may provide a suitable alternative, which will not depend on observers, but rather the number of signals sent per time unit. Thus, current technology is restricted by battery limitations, but the technological advancement may mitigate this limitation.

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A Appendix

Appendix 1: Parameter estimates for the significant variables based on backward selection on p-values when Tengmalm's owl observation fixes were tested against 95% MCP random plots.

	Estimate	SE	z value	P
(Intercept)	0.71	0.39	1.83	0.07
Ageclass I	-0.0032	0.0014	-2.28	0.023
Ageclass III	-0.0015	0.00076	-2.020	0.043
Bog	-0.00079	0.00028	-2.80	0.0052
Bog w/trees	0.0010	0.00042	2.50	0.012
Open Ground	-0.00063	0.00028	-2.27	0.023

Appendix 2: Parameter estimates for the significant variables based on backward selection when Tengmalm's owl observation fixes were tested against 95% MCP random plots for differences in relation to productivity.

	Estimate	SE	z value	P
(Intercept)	-0.21	0.26	0.82	0.41
Impediment	0.0017	0.00065	2.59	0.0096
Low Productivity	0.0011	0.00055	2.01	0.044
High Productivity	-0.0011	0.00031	-3.39	0.00070

Appendix 3: Parameter estimates for the significant variables based on backward selection on p-values when Tengmalm's owl observation fixes were tested towards 100% MCP random plots.

	Estimate	SE	z value	P
(Intercept)	1.60	0.32	5.00	<0.0001
Ageclass I	-0.0065	0.0015	-4.30	<0.0001
Ageclass II	-0.0023	0.0010	-2.24	0.025
Ageclass III	-0.0021	0.00078	-2.71	0.0067
Ageclass IV	-0.00099	0.0003	-3.26	0.0011
Bog	-0.0010	0.00027	-3.73	0.00019
Bog w/trees	0.0024	0.00041	5.88	<0.0001
Nest	-0.0011	0.00022	-4.83	<0.0001

Appendix 4: Parameter estimates for the significant variables based on backward selection on p-values when Tengmalm's owl observation fixes were tested against 100% MCP random plots for differences in relation to productivity.

	Estimate	SE	z value	P
(Intercept)	-0.018	0.26	-0.071	0.94
Impediment	0.0029	0.00067	4.39	<0.0001
Medium Productivity	-0.0040	0.0015	-2.64	0.0083
High Productivity	-0.0012	0.00032	-3.91	<0.0001

Appendix 5: Parameter estimates for the significant variables based on backward selection on p-values when capture fixes were tested against 95% MCP random plots.

	Estimate	SE	z value	P
(Intercept)	-1.19	0.25	-4.71	<0.0001
Open Ground	-0.00065	0.00030	-2.17	0.030

Appendix 6: Parameter estimates for the significant variables based on backward selection on p-values when capture fixes were tested against 95% MCP random plots for differences in relation to productivity.

	Estimate	SE	z value	P
(Intercept)	-1.93	0.15	-12.84	<0.0001
Low Productivity	0.0020	0.00049	4.08	<0.0001

Appendix 7: Parameter estimates for the significant variables based on backward selection on p-values when capture fixes were tested against 100% MCP random plots.

	Estimate	SE	z value	P
(Intercept)	-0.92	0.39	-2.37	0.018
Ageclass IV	-0.0009	0.00041	-2.21	0.027
Bog w/trees	0.0015	0.00052	2.97	0.0030
Nest	-0.0011	0.00035	-3.03	0.0024

Appendix 8: Parameter estimates for the significant variables based on backward selection on p-values when capture fixes were tested agianst 100% MCP random plots for differences in relation to productivity.

	Estimate	SE	z value	P
(Intercept)	-1.57	0.25	-6.34	<0.0001
Impediment	0.0020	0.00096	2.04	0.041
High Productivity	-0.0011	0.00043	-2.58	0.0099

Appendix 9: Parameter estimates for the best fitted model based on backward selection of p-values when the capture fixes were tested against the non-capture owl fixes.

	Estimate	SE	z value	P
(Intercept)	1.14	0.32	3.58	0.00035
Ageclass I	-0.0066	0.0021	-3.13	0.0018
Roads	0.0017	0.00075	2.25	0.024

Appendix 10: Parameter estimates for the significant variables based on backward selection of p-values when the capture fixes were tested against the non-capture owl fixes for differences in productivity.

	Estimate	SE	z value	P
(Intercept)	1.45	0.25	5.73	<0.0001
Medium Productivity	-0.0048	0.0021	-2.28	0.022

Appendix 11: Parameter estimates for the significant variables based on backward selection on p-values when *Microtus* vole capture fixes were tested against 95% MCP random plots.

	Estimate	SE	z value	P
(Intercept)	-2.17	0.30	-7.31	<0.0001
Ageclass IV	-0.00093	0.00058	-1.60	0.11

Appendix 12: Parameter estimates for the significant variables based on backward selection on p-values when *Microtus* vole capture fixes were tested against 95% MCP random plot for differences in relation to productivity.

	Estimate	SE	z value	P
(Intercept)	-3.10	0.30	-10.20	<0.0001
Impediment	0.0020	0.00049	2.30	0.021

Appendix 13: Parameter estimates for the significant variables based on backward selection on p-values when *Microtus* vole capture fixes were tested against 100% MCP random plots.

	Estimate	SE	z value	P
(Intercept)	-1.20	0.55	-2.19	0.028
Ageclass IV	-0.0025	0.00073	-3.40	0.00067
Bog w/trees	0.0019	0.00074	2.63	0.0085
Nest	-0.0013	0.00054	-2.31	0.021

Appendix 14: Parameter estimates for the significant variables based on backward selection on p-values when *Microtus* vole capture fixes were tested against 100% MCP random plots for differences in relation to productivity.

	Estimate	SE	z value	P
(Intercept)	-3.24	0.30	-10.61	<0.0001
Impediment	0.0039	0.0013	3.02	0.0025

Appendix 15: Parameter estimates for the significant variables based on backward selection on p-values when shrew capture fixes were tested against 95% MCP random plots.

	Estimate	SE	z value	P
(Intercept)	-4.06	0.90	-4.49	<0.0001
Ageclass I	0.0076	0.0036	2.10	0.036

Appendix 16: Parameter estimates for the significant variables based on backward selection on p-values when shrew vole capture fixes were tested against 95% MCP random plots for differences in relation to productivity.

	Estimate	SE	z value	P
(Intercept)	-2.61	0.45	-5.75	<0.0001
Low Productivity	0.0024	0.00094	2.50	0.012
High Productivity	-0.0052	0.0021	-2.45	0.014

Appendix 17: Parameter estimates for the significant variables based on backward selection on p-values when shrew capture fixes were tested against 100% MCP random plots.

	Estimate	SE	z value	P
(Intercept)	-2.43	0.90	-2.71	0.0067
Nest	-0.0021	0.00065	-3.18	0.0015

Appendix 18: Parameter estimates for the significant variables based on backward selection on p-values when shrew vole capture fixes were tested against 95% MCP random plots for differences in relation to productivity.

	Estimate	SE	z value	P
(Intercept)	-1.91	0.38	-4.97	<0.0001
High Productivity	-0.0077	0.0025	-3.09	0.0020

Appendix 19: Parameter estimates for the significant variables based on backward selection of p-values when *Microtus* vole capture fixes were tested against shrew capture fixes.

	Estimate	SE	z value	P
(Intercept)	-3.19	1.11	-2.88	0.0040
Ageclass IV	0.0039	0.0012	3.15	0.0016

Appendix 20: Parameter estimates for the significant variables based on backward selection of p-values when *Microtus* vole capture fixes were tested against shrew capture fixes to test for differences in productivity.

	Estimate	SE	z value	P
(Intercept)	-0.85	0.53	-1.59	0.11
Impediment	-0.010	0.0033	-3.07	0.0021
Low Productivity	0.010	0.0026	4.06	<0.0001

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