

Home range and area use of female Eurasian kestrels (*Falco tinnunculus*) in the boreal forest during the breeding season

Hjemmeområde og arealbruk hos hunner av tårnfalk (*Falco tinnunculus*) i boreal skog i hekkesesongen

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“The wild things that live on my farm are reluctant to tell me, in so many words, how much of my township is included within their daily or nightly beat. I am curious about this, for it gives me the ratio between the size of their universe and the size of mine, and it conveniently begs the much more important question, who is the more thoroughly acquainted with the world in which he lives?”

- Aldo Leopold, “A Sand County Almanac”

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To my parents, Lutgard Van der Spiegel and James Cunningham: Thank you for instilling in me a respect for nature and an inquisitive mind. To my sister, Eevi Cunningham: Thank you for listening. To my late grandmother, Elisabeth de Troch: Thank you for being a strong woman in my life. Last, but not least, to my partner, Odd Petter Nord Slyngstad: Thank you for your dedication and devotion. You were with me every step of the way, and you know the measure of my gratitude.

ABSTRACT

I studied home range and area use of the female Eurasian kestrel (*Falco tinnunculus*), in the boreal forested area of Trysil municipality (61°00' - 61°41'N, 11°44' - 12°52'E) in the breeding season of 2011, a peak vole year. Six females were tagged and radio-tracked using VHF telemetry in the pre-fledging period, and two of these females were additionally followed in the early post-fledge period. Females were located between 49 and 141 times in the pre-fledging period ($\bar{x} = 98 \pm 13$ SE), totaling 589 observations, which allowed the investigation of area use questions using the Minimum Convex Polygon (MCP) and fixed kernel h_{ref} methods. I found a large variation in home range size between females as measured by the overall 100% MCP (range 0.69 - 6.16 km², median = 0.94 km², $\bar{x} = 1.84 \pm 0.87$ SE km²), and in the levels to which each home range was centered on the nest. Home range size was significantly positively correlated with the proportion of bog with forest (overall 95% kernel) and the proportion of forest of developmental stage 3 present (overall 95% kernel, and overall 100% MCP), and significantly negatively correlated with proportion of pooled developmental stage 4 and 5 (overall 95% kernel). A trend approaching significance was found for negative correlation with *Microtus* vole abundance (overall 95% kernel). A higher probability of being in the core foraging area (foraging 50% kernel) was associated with decreased distance to nest and decreased distance to bog, highlighting the importance of maintaining proximity to the nest site for the kestrel as a central-place forager, and the importance of proximity to open habitat. In addition, post-fledge tracking highlighted the importance of the nest in the early fledging period. My results indicate the importance of taking into account vegetation structure and how it relates to prey availability, when looking at the effect on home range size. I further suggest that the role of modern forestry practices should be investigated, with regards to the effects habitat fragmentation and patch size and shape may play on spatial and temporal area use by the female kestrel in boreal forest.

SAMMENDRAG

Jeg studerte hjemmeområde og arealbruk hos hunner av tårnfalk (*Falco tinnunculus*), i boreal skog i Trysil kommune (61°00' - 61°41'N, 11°44' - 12°52'Ø) i hekkesesongen 2011, et smågnagerår. Seks hunner ble radiomerket og peilet ved hjelp av VHF-telemetri i perioden før ungene var flygedyktige, og to av disse hunnene ble også fulgt tidlig i perioden etter at ungene ble flygedyktige. Hunnene ble lokalisert mellom 49 og 141 ganger i perioden før ungene var flygedyktige ($\bar{x} = 98 \pm 13$ SE), totalt 589 observasjoner, hvilket gjorde det mulig å studere spørsmål knyttet til arealbruk ved bruk av metodene Minimum Convex Polygon (MCP) og kernel sannsynlighetsanalyse med fastsatt referanseverdi (kernel h_{ref}). Jeg fant stor variasjon i størrelsen på hunnens hjemmeområde målt ved total 100 % MCP (variasjon 0,69 - 6,16 km², median = 0,94 km², $\bar{x} = 1,84 \pm 0,87$ SE km²), samt i hvor sentrert hvert hjemmeområde var rundt reiret. Størrelsen på hjemmeområdet var signifikant positivt korrelert med andelen av tresatt myr (total 95 % kernel) og med andelen av skog av hogstklasse 3 (total 95 % kernel, og total 100 % MCP), og signifikant negativt korrelert med andelen av skog av hogstklasse 4 og 5 samlet (total 95 % kernel). En trend ble funnet for negativ korrelasjon med forekomsten av *Microtus* smågnagere (total 95 % kernel). Tårnfalkene var mer sannsynlig i kjerneområdet for jakt (jakt 50 % kernel) når de var nærmere reiret og nærmere myr, hvilket viser at for tårnfalkhunnen er nærhet til reiret og nærhet til åpent habitat viktig. I tillegg viste radiopeilingen at reiret var viktig i den første tiden etter at ungene var flygedyktige. Mine resultater indikerer at det er viktig å ta hensyn til vegetasjonsstruktur og hvordan denne relaterer til tilgangen på byttedyr for å vurdere effekter på størrelsen på hjemmeområde. Jeg foreslår videre at rollen til moderne skogsbruk bør studeres videre, med hensyn på hvilken effekt habitatsfragmentering kan ha på arealbruk i tid og rom hos tårnfalk i boreal skog.

TABLE OF CONTENTS

ACKNOWLEDGEMENTS	iii
ABSTRACT	iv
SAMMENDRAG	v
1. INTRODUCTION.....	1
2. METHODS.....	4
2.1. Study area.....	4
2.2. Capture and tagging of the female kestrels	5
2.3. Tracking of the female kestrels	8
2.4. Variables measured	9
2.4.1 Tracking data.....	9
2.4.2 Additional data	9
2.5. Snap-trapping of small mammals.....	10
2.6. Analysis and statistics	10
2.6.1 Home range estimators.....	11
2.6.2 Habitat and forestry developmental stage variables	12
2.7. Core foraging area use.....	14
2.8. Nest centricity and distances	15
3. RESULTS.....	16
3.1. Tracking effort.....	16
3.2. Home range sizes.....	17
3.2.1. Overall.....	17
3.2.2. Home range overlap	19
3.2.3. Number of locations	21
3.2.4. Foraging.....	21
3.3. Variables that influenced home range size	22
3.4. Core foraging area use.....	25
3.5. Nest centricity and distances	31
3.6. Post-fledge.....	32
4. DISCUSSION	34
4.1. Home range	34
4.1.1. Estimator types	34
4.1.2. Tracking effort and time to independence.....	35
4.1.3. Home range size	36

4.1.4. Home range overlap	37
4.2. Variables that influenced home range size	38
4.3. Core foraging area use.....	41
4.4 Nest centricity and distances	43
4.5. Post-fledge.....	44
4.6. Limitations and thoughts for future research.....	45
5. CONCLUSION	47
REFERENCES.....	48
APPENDIX	56

1. INTRODUCTION

Animal area use questions have long fascinated researchers, and span from where an animal ranges to how it utilizes the space within its range. Burt (1943, p. 351) classically defined an animal's home range as the "area traversed by the individual in its normal activities of food gathering, mating, and caring for young", and described territory as the exclusive area of the home range that is defended against conspecifics. Home ranges have both a spatial and temporal aspect (Powell 2000; Börger et al. 2006b), and knowledge of home ranges can shed light on social structure, resource utilization, foraging, and habitat preferences (Powell 2000).

While there are a number of ways to delineate a home range (Worton 1987; Powell 2000), a common method utilizes the Minimum Convex Polygon (MCP) (Mohr 1947), in which the outermost observations made of an animal are joined to form a polygon. Although the MCP has received criticism (Worton 1987; Börger et al. 2006a), it is still a commonly employed estimator, and allows comparisons across studies. More recently, non-parametric kernel estimators (Worton 1987, 1989) have been used to look at home range size, by applying a smoothing parameter (h) to generate a utilization distribution (UD) based on the probability of an animal being at a particular location. UD's have the advantage in that they allow for analysis of more intensively used core areas within the home range (Samuel et al. 1985), and allow for more than one center of activity (Kenward 2001; Kernohan et al. 2001). The UD concept can also be extended to look at resource utilization, such as selection for specific habitat types within the home range (Marzluff et al. 2001).

Across species, variables such as habitat structure, prey availability, body mass (Schoener 1968), age, and sex (Harestad & Bunnell 1979), have been shown to affect home range sizes. Raptors in particular are well suited to studies investigating the different variables that influence home range size, due to the fact that they have large home ranges and live in heterogeneous habitat (Preston 1990), employ various hunting strategies, and are generalist predators (Peery 2000). Previous studies have shown that home range sizes of raptors are e.g. negatively correlated with prey availability, and positively correlated with body mass (Newton 1979).

The Eurasian kestrel (*Falco tinnunculus*, hereafter kestrel) is the most prevalent diurnal raptor found in the western Palearctic (Cramp & Simmons 1980), with distribution throughout Europe, Africa, and Asia (Village 1990). As in many other raptor species, the kestrel exhibits female-biased sexual size dimorphism, with the female typically larger than the male (Village 1990; Massemin et al. 2000). Females have a body mass of ca. 230 g, and weigh on average 15% more, and have a ca. 4% longer wing chord, than males (Cramp & Simmons 1980, Village 1990). The kestrel exhibits plumage dimorphism, the most striking feature of which is the adult female's brown head and back in comparison with the adult male's grey plumage (Village et al. 1980; Village 1990).

In Norway, the kestrel breeds primarily in the southern part, arriving in April from Spain via Denmark, and migrating south again in October (Tømmeraas 1994). The kestrel is a cavity nester, readily taking over tree hollows, and artificial nestboxes (Village 1990; Shrubbs 1993). Egg laying occurs in May to June (Tømmeraas 1994). A clutch will normally contain 3 to 6 eggs. The female assumes sole responsibility for incubation and brooding, during which time the male assumes provisioning duties. Eggs are incubated for 27 to 29 days (Cramp & Simmons 1980). Nestlings can thermoregulate at 7 to 10 days old (Village 1990), after which the female is free to hunt. During the pre-fledging period, then, the female kestrel is a central-place forager. Fledging occurs between 27 and 32 days after hatching, but the fledglings are dependent upon parental provisioning for up to 30 days post-fledging (Cramp & Simmons 1980; Bustamante 1994).

The kestrel is found primarily in open habitat (Village 1990), and utilizes agricultural areas (Valkama et al. 1995; Aschwanden et al. 2005), bogs, forests (Valkama et al. 1995), and clear-cuts (Sonerud 1986). As a generalist predator, the kestrel has a varied diet, feeding mostly on *Microtus* voles, followed by other small mammals, birds, invertebrates, reptiles, amphibians (Village 1982a; Korpimäki 1985; Costantini et al. 2005), bats (Negro et al. 1992), and occasionally carrion (Village 1990). In Fennoscandia, *Microtus* vole populations cycle between peak and trough years (Hansson & Henttonen 1985), and in Norway the kestrel has been shown to take mostly *Microtus* voles during years of high vole abundance, supplemented by *Myodes* voles, shrews (*Sorex* spp.), wood lemming (*Myopus schisticolor*), birds, lizards, frogs, and insects (Hagen 1952; Steen 2010; Steen et al. 2011b; Sonerud et al. 2013). The kestrel seems able to determine the abundance of *Microtus* voles in an area by detecting tracks of vole urine and feces with its ultraviolet vision (Viitala et al. 1995). The foraging tactics of

the kestrel are distinct, and varied. The kestrel hunts from perches, and strikes prey from the air when wind and thermal conditions are optimal, by hovering and soaring respectively (Village 1990).

Although the kestrel is a common and easily observed species, relatively few studies have been conducted to investigate its home range, and area use within. Male home range sizes have been documented in an Italian agricultural landscape (Casagrande et al. 2008), and male foraging ranges in an urban setting (Riegert et al. 2007). In coniferous forest landscapes, comparisons of home range sizes between breeding males have been looked at in Scotland (Village 1982b), and in Trysil, Norway (Løken 2009), and have employed the MCP method. In both of these cases, home range size was shown to be negatively correlated with *Microtus* vole abundance, as calculated by a snap-trapping index. However, to the best of my knowledge, no studies have investigated home range sizes of breeding female kestrels, in boreal forest regions. In addition, while Village's dataset was utilized by Börger et al. (2006a) to generate UD's based on the fixed kernel least squares cross-validation (h_{lscv}) (Worton 1989) and fixed kernel reference (h_{ref}) (Worton 1995) methods, the results were primarily used in a methodological analysis. Hence, no studies have investigated utilization distributions in breeding female kestrels, with core area use and resource selection in mind.

The aim of my study, then, was to investigate area use questions for a sample of breeding female kestrels in my study site, Trysil municipality. More specifically, I was interested in looking at the following topics: 1) How did home range size differ by type of estimator used? Did the potential exist for overlap between neighboring nests? 2) Did correlations exist between home range size and various factors, such as different habitat types, abundance of *Microtus* voles, and adult female age and size? 3) Did foraging female kestrels exhibit preference for (or avoidance of) different habitat types and forestry developmental stages in the core area, versus what was available in the home range? Could the probability of being in the core area be explained by distances from different habitat types and forestry developmental stages? 4) How were home ranges centered around the nests? What distances did females travel across their home ranges?

2. METHODS

2.1. Study area

The study was conducted in southeastern Norway, in Hedmark county, in the municipality of Trysil (61°00' - 61°41'N, 11°44' - 12°52'E) (Fig. 1), during June - July 2011. Trysil is characterized by a continental climate, and is dominated by the middle boreal and northern boreal vegetation zones (Moen 1998; Reiso 2005). The middle boreal zone is characterized by coniferous forest, and bog, with tree types dominated by spruce (*Picea abies*), pine (*Pinus sylvestris*) and birch (*Betula* spp.), whereas the northern boreal zone is characterized by bog, birch forest, and low-growing coniferous forest (Moen 1998). In Trysil, the coniferous forest is dominated by blueberry-spruce forest. Trysil occupies an area of 3,016 km², of which approximately 75% is forest, and 10% bog, and the majority of the municipality lies between 300 and 900 m a.s.l (Reiso 2005).

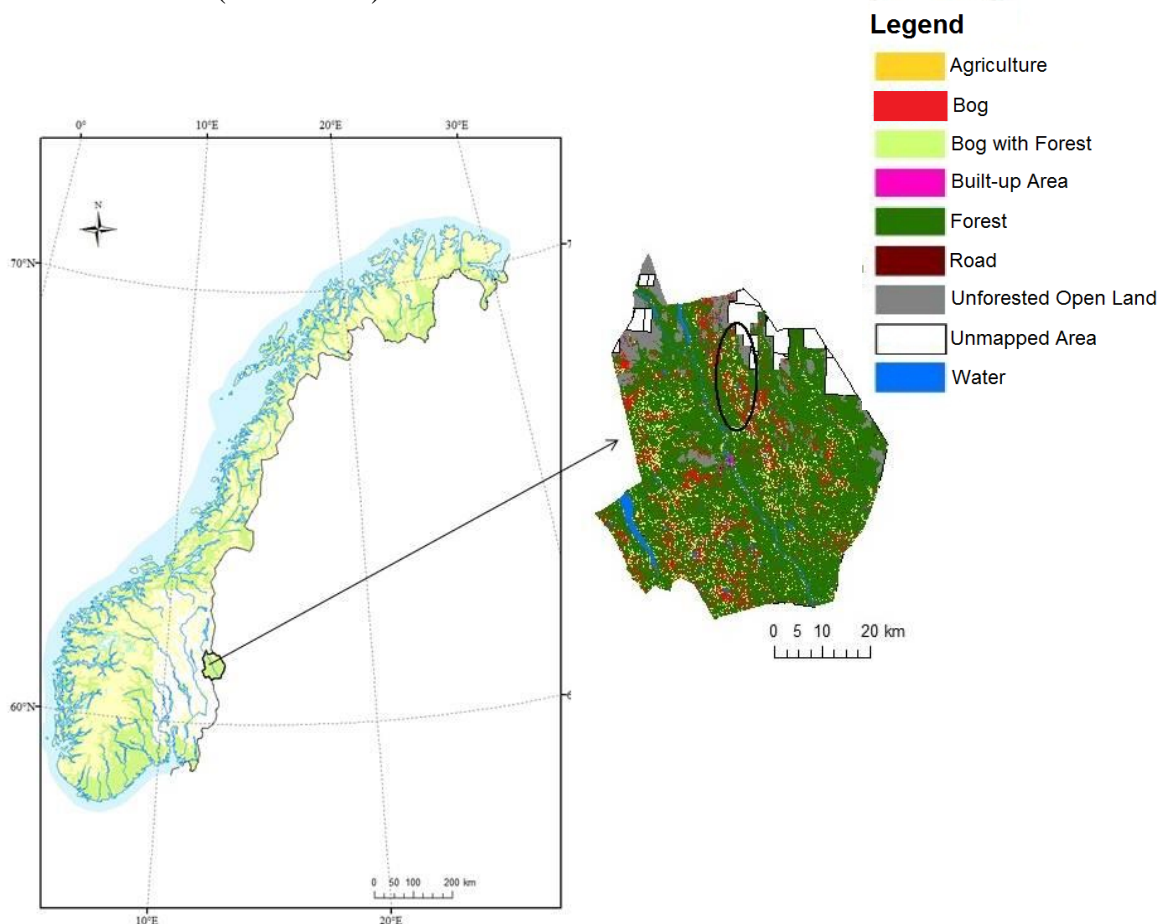


Figure 1. Study site area (Map base: Statens kartverk – Geodata AS). Trysil municipality is presented to the right with habitat classifications. The black oval circle indicates the general area of the six kestrel nests studied.

Under the initiative of local ornithologists, the study area had previously been equipped with over 300 artificial nestboxes, utilized by kestrels in the breeding season. Nestboxes in the area were checked frequently from mid-June onwards, and six inhabited ones were selected in the Flendalen valley, at a range of altitude from 502 to 762 m a.s.l. The sites will hereafter be referred to respectively, from north to south and with descending altitude, as Bryn Nord, Flenvoll, Husfliden, Tøråsen, Storflendammen, and Storfallet. Nestboxes were chosen with ease of accessibility in mind (both with location in relation to roads, and terrain that was relatively easy for trackers to traverse), and with consideration to the age of the nestlings. Therefore, the six sites chosen did not represent a completely random selection of the population. The nestboxes were situated on either bog (Bryn Nord), clear-cuts (Storfallet and Flenvoll), or young forest of developmental stage 2 (Tøråsen, Husfliden, and Storflendammen, see section 2.6.2 for definition). On five of the localities the nestboxes were mounted in pine trees, while at Husfliden the nestbox was mounted in a birch tree.

2.2. Capture and tagging of the female kestrels

Permission to perform data collection using VHF telemetry was provided by the Directorate for Nature Management, and the National Animal Research Authority of Norway. Accordingly, all rules and regulations governing the ethical treatment of animals used in this study were complied with. Nests were selected where the females were brooding nestlings no younger than 7 days old. Brood age at radio tagging ranged from 7 - 14 ($\bar{x} = 11 \pm 1$ SE, $n = 6$) days, from Tøråsen to Bryn Nord respectively. Capture was staggered over 2 weeks. The capturing and tagging of the kestrels was carried out by my advisors, Geir A. Sonerud and Ronny Steen. I assisted at Bryn Nord and Tøråsen, in particular with the mounting of the radiotelemetry unit. Females were captured using one of two approved trapping methods: either on the nestbox using a tunnel trap, or when foraging using a bal-chatri trap.

The tunnel trap consisted of a rectangular short box mounted over the nestbox entrance. A swing door was attached to the front of the trap, propped open by a stick (Fig. 2). A rope led from the stick to a camouflage tent near the nest, where surveillance of both the outside and inside of the nestbox took place. Video surveillance had been installed at each nest to record activity within the nestbox, using equipment as described in Steen (2009), and modified setup as described in Steen (2010). The tunnel trap was pulled shut behind the female when she

entered the nestbox to provision the nestlings, and her position within was noted. Constant surveillance ensured that the female was removed immediately upon capture. The tunnel trap was the most successful method, as it captured five of the six females, with the exception of Storfallet.



Figure 2. Tunnel trap mounted at Bryn Nord (*Photo credit: Odd Petter N. Slyngstad*).

The second capture method used was the bal-chatri trap, an approved method to capture raptor species described in Berger and Mueller (1959). The trap consisted of a double walled cage made of metal wire, with the inner cage baited with a live hamster. To comply with animal welfare regulations, six hamsters were used in rotation, with no one hamster caged for more than two hours at a time. Small hangman knot loops of nylon thread were attached to the outer cage, to ensnare the talons of the female kestrel as she attempted to capture the caged rodent. The cage was under constant surveillance, from a camouflaged tent. The bal-chatri trap had limited success, as it only captured the female at Storfallet. As the trap was set close to the nests, it is possible that the females were more interested in nest duties than foraging.

Upon capture, each kestrel was outfitted with a tail-mounted TW-4 radio transmitter from Biotrack Ltd. in England (Biotrack, Wareham, Dorset). Tail-mounts are an accepted and safe method for monitoring raptors (Kenward 1978), when the weight of the transmitter is less

than 2% of the bird's bodyweight (Kenward 2001). The TW-4 radio transmitter weighed close to 3 g. As a female kestrel averages 230 g (Cramp & Simmons 1980), this was 1.3% of the body mass, well below the 2% limit. The female was first hooded, to reduce stress, and banded with a regular steel ring on the left tarsus. The transmitter was attached according to Kenward (1978) to the base of the central rectrices using rapid drying glue (commercial brand Araldite), and the antenna sewn in place along the shaft (Fig. 3a, Fig. 3b). Neighboring feathers were used with the Flenvoll and Tøråsen females, as molting of the central rectrices had started. The transmitters included a posture-sensing circuit, based on a mercury tilt-switch, which oscillated between fast and slow pulse rates, depending on the kestrel's posture. A fast pulse rate indicated that the kestrel was in flight, while a slow pulse rate indicated perching. Battery life was estimated at 4 weeks.



Figure 3a. Tagging the Tøråsen kestrel.



Figure 3b. The tagged Bryn Nord kestrel
(*Photo credit: Odd Petter N. Slyngstad*).

2.3. Tracking of the female kestrels

Tracking started at the earliest the day after tagging, in order to allow females to acclimatize to their radio transmitters, and to exhibit normal behavior. Tracking was conducted between the hours of 06:00 - 20:00, as these were the times when the kestrels were assumed to be most active (Steen et al. 2011a). Tracking was halted during bouts of heavy rain, to avoid waterlogging the receivers, and as kestrels are not as active under these conditions (Cavé 1968; Village 1982b). Efforts were made to cover all times of day for all nests at least once, but there was some discrepancy between nests. The tracking was split into sessions of intensive, continuous monitoring that ranged from 2 - 10 ($\bar{x} = 5.92 \pm 0.35$ SE, $n = 26$) hours in length, in addition to opportunistic observations ($n = 11$). Tracking was done using Televilt RX-81 (Televilt AB, Sweden) and Telonics TR-2 (Telonics, Mesa, Arizona) receivers, in combination with 2-element and 4-element Yagi antennas. The homing-in technique was used (White & Garrott 1990), with trackers radiating outwards from the nest. In addition, one observer was located near the nest in a camouflaged tent or in a car, with a spotting scope.

The female at Tøråsen exhibited abnormal behavior for the first two tracking sessions. As the female did not tolerate our presence, the observer at the nest was removed, and I excluded the biased observations ($n = 36$) from future analysis. In addition, all nests were checked daily for signs of abandonment (no radio signal), and I regularly checked for indications that molting of the central rectrices had occurred (no change in pulse rate). Once molting occurred, I located the radio transmitter and retrieved it, when possible. At two of the localities, Storflendammen and Tøråsen, molting occurred after fledging. Post-fledge tracking was therefore done at these two nests, but analysis was limited due to a sample size of only two individuals. Tracking was terminated on Storflendammen when the radiotransmitter was shed. On Tøråsen, tracking had to be halted when the female flew over an electric fence used to keep brown bears (*Ursus arctos*) out of the sheep grazing range.

Although nests were chosen with ease of trackability in mind, Storflena River runs through the study area, which affected trackability at two sites to a certain extent. At Storflendammen the river could be crossed by bridge at only one location, and at Tøråsen a rubber boat with a rope pulley system was employed. There were indications that the female at Storfallet might have crossed the river as well, but this was not verified.

2.4. Variables measured

2.4.1 Tracking data

A number of behavioral and environmental variables were taken in the field. For each observation, a UTM coordinate was taken using a Garmin eTrex H handheld GPS (Garmin Ltd., Kansas), which had an accuracy of less than 10 m. The UTM zone used was 33N, in the WGS 1984 coordinate system. Plot quality was recorded, depending on the observation. If visual contact had been made, and the location was certain, it was characterized as “Absolute”. If visual contact had been achieved, but there was uncertainty as to the actual location of the kestrel (due to e.g. distance of the tracker from the kestrel), then the plot quality was “Range Visual”. If no visual contact had been achieved, then the plot was characterized as “Range Unseen”. The time of the observation was recorded, to the minute. In the event that an observer forgot to record time (pre-fledge $n = 8$, post-fledge $n = 2$), an estimated time was later assigned, by taking the average of the previous and successive observation times from the observer in question. As time was recorded to the minute only, observations taken within the same minute were spaced by ten second intervals (pre-fledge $n = 40$, post-fledge $n = 4$), which accounted for 6.8% of the total pre-fledge dataset.

If visual contact was achieved, kestrel behavior was listed as either Perch (and perch type and perch height recorded), Hover, Flight or Nest (prey delivery or otherwise at the nest site). Habitat type, density of vegetation, dominant tree type and forestry developmental stage information was taken at each location, within a 25 m buffered radius. However, as I extracted data from habitat and forestry maps for my analyses, these observations were mainly anecdotal.

2.4.2 Additional data

The wing chord length (mm) of each female was measured at capture, to be used as a proxy for body size. The age of the female kestrels was determined by Geir A. Sonerud and myself. A combination of photos taken at tagging, and stills from the video footage shot within nestboxes, were compared using a key (Blasco-Zumeta & Heinze 2012) and guidance on molting patterns (Village et al. 1980). The brood size was noted when tracking started, and I calculated the average brood age during each tracking period (Appendix 1).

2.5. Snap-trapping of small mammals

Snap-trapping was conducted by Geir A. Sonerud at all six locations, during the radio tracking period, in order to establish an index of prey abundance for each available small mammal type. At each location, 120 snap traps (commercial brand “Rapp”) were placed radiating out from the nest in the four cardinal directions, with one trap line in each direction. Each direction had 30 traps set out at intervals of ca. 10 m. When the further setting out of traps along a trap line was impeded, due to e.g. the presence of a lake or wet bog with plain *Sphagnum* spp. cover, the remaining traps were added to another trap line on the same nest. Average trap line length was 382 ± 23 SE (range 50 - 578) m. All traps were baited with coconut fat (commercial brand “Delfia”), prior to the setting out of the first 120 traps at the first location. At each location, traps were set out on one day, then checked, and reset if necessary on the second day, and collected on the third day. This led to a maximum of 240 trap nights per nest. I assisted with the collection of traps for one day at the Husfliden site.

A snap-trapping index was then calculated by Geir A. Sonerud for each prey species collected per location, as detailed in Steen (2010). At each nest, a correction factor was applied to the maximum trap nights ($n = 240$), to account for traps that did not trap the prey species in question (e.g. due to trap disappearance, trap that failed to release, or other prey species being trapped), and to account for trap saturation caused by the prey species in question. The four small mammal categories of interest were *Microtus* vole (comprised of field vole (*Microtus agrestis*), and tundra vole (*Microtus oeconomus*)), bank vole (*Myodes glareolus*), wood lemming (*Myopus schisticolor*), and total microtine rodents (comprised of the sum of the former three categories, plus a few lemmings (*Lemmus lemmus*), and grey-sided voles (*Myodes rufocanus*)) (Appendix 2a). Geir A. Sonerud also calculated an average snap-trapping index per small mammal by habitat type (clear-cut, forest, bog with forest, and bog) for *Microtus* vole, bank vole, wood lemming, and total microtine rodents (Appendix 2b).

2.6. Analysis and statistics

All basic statistical analyses were performed in R 2.15.1 (R Core Team 2012), by launching the Rcmdr (Fox 2005) and the plotrix (Lemon 2006) packages. Unless otherwise stated, statistical summaries were displayed as the mean \pm SE (standard error), with $n = 6$. Excel

(Microsoft 2010) was used for tables, figures, and simple calculations. I used ArcGIS Desktop 10.0 (ESRI 2010) to visualize and display the home range estimators, extract data from the locations (e.g. with regards to distances), and to display and manipulate the habitat and forestry maps.

2.6.1 Home range estimators

To estimate home range size for each locality, a 100% MCP and 95% MCP were constructed from all pre-fledge locations (range and absolute), when a minimum of 30 observations had been collected (Kenward 2001). This was done using the R packages `adehabitatHR` (Calenge 2006) and `rgdal` (Bivand et al. 2013). The 100% MCP denoted the overall total area used by each kestrel, whereas the 95% MCP provided a more conservative estimate, removing the 5% most extreme locations. In this way, the effect of outliers could be accounted for. The method was repeated on all pre-fledge foraging locations, where foraging was defined to be locations taken outside of a 100 m perimeter around the nest. Locations within this perimeter were assumed to represent provisioning and nest guarding duties (Geir A. Sonerud pers. comm.). Likewise, post-fledge 100% MCPs and 95% MCPs were calculated, for Tøråsen and Storflendammen, on all locations.

To generate overall and foraging home range sizes and utilization distributions, the fixed kernel method (Worton 1989) was employed, using the `adehabitatHR` and `rgdal` packages in R. The locations used were limited to only absolute observations, and kernels were calculated per locality when a minimum of 15 observations had been collected (Kenward 2001). The grid cell used was 20 m, and isopleths were constructed at the 95%, 75%, 50% and 25% levels. The overall 95% kernel was used as a home range size estimator, whereas the foraging 50% kernel was used as an estimator of core foraging area use. In both cases, the 75% and 25% kernels were generated for visualization purposes only. The fixed least squares cross validation method (Worton 1989) was first tried, but as the matrix failed to converge the fixed reference method (Worton 1995) was used instead.

As kernels can be sensitive to autocorrelation (Worton 1989; Gitzen et al. 2006), the dataset was tested for this, using Schoener's ratio (Schoener 1981). Schoener utilized the ratio of t^2/r^2 , where t^2 = the mean squared distance between relocations, and r^2 = the mean squared

distance between relocations and the arithmetic mean of all locations. Swihart and Slade (1985b) showed that independence between consecutive locations occurs when $t^2/r^2 = 2$, and autocorrelation when the ratio deviates from this value. Schoener's ratio was calculated in ArcGIS 9.3 (ESRI 2008), using the Home Range Tools (HRT) extension (Rodgers et al. 2007). The ratio was calculated for each locality, using the total number of pre-fledge observations per locality.

Time to independence (TTI) was defined, per locality, as the time it would take each kestrel to cross its home range (Kenward 2001). This was done by taking the two locations farthest apart of each overall 100% MCP, and calculating the resulting Euclidean distance between the two, to give the most extreme diameter of the home range. The time it would take to cross this diameter was calculated using the average directional flight speed of a kestrel in the field at 8.3 m/s (Videler et al. 1983). The resulting TTI, per kestrel, indicated the time interval needed between successive relocations in order to avoid temporal autocorrelation.

2.6.2 Habitat and forestry developmental stage variables

Habitat map

An AR5 habitat map (scale 1:5,000) for Trysil municipality was retrieved from the Norwegian Forest and Landscape Institute (2012), and uploaded into ArcGIS. I split the habitat map layers into Agriculture, Bog, Bog with forest, Coniferous forest, Deciduous forest, Mixed forest, Water, Road, Unforested open land, Built-up area, and Unmapped area, based on the classification scheme of Bjørndal and Bjørkelo (2006). I used the primary attribute of land type, in combination with the attribute for tree type where relevant, and associated code values (Appendix 3). In the case of Flenvoll, I further sectioned out mountain as a habitat type, based on a combination of interpreting the AR5 map and field observations, as advocated by Bjørndal and Bjørkelo (2006). When looking at the proportion of forest types present in the overall 100% MCP, 92.2% of the total forest area was coniferous. In addition, deciduous forest was only present at one locality (Tøråsen), accounting for only 6.1% of the forest at that locality. Mixed forest was not present at two of the localities, and overall accounted for 7.2% of the total forest area. Therefore, for the purposes of further analyses, forest type was pooled. This further reflected the usage of the general category of forest in the snap-trapping indices per habitat type (Appendix 2b).

Forestry developmental stage maps

I obtained access to paper versions of forestry developmental stage maps (scale 1:10,000) from Trysil Kommuneskoger (FORAN Norge AS 2007), which I then digitalized. The maps employed the standard Norwegian forestry developmental stage (in Norwegian, “hogstklasse”) system of 1 - 5, where 1 denotes clear-cuts to be regenerated, 2 denotes recently regenerated and young forest, 3 denotes young productive forest, 4 denotes older productive forest, and 5 denotes mature forest ready for logging (Fitje 1989; Landsskogtakseringen 2008). The paper maps were scanned to create PDF files, which I then converted to PNG files using Inkscape 0.48.2 r9819 (Canonical 2011). These PNG files were then uploaded into ArcGIS, and the “Georeferencing” tool used to assign UTM coordinates to each map, to create a spatial reference. Using the overall 100% MCPs derived for each locality as a minimum perimeter, a new shapefile was created per locality, and the two fields of “Developmental stage” and “Area” (km²) added to the resulting attribute table. This new shapefile was edited, by carefully tracing and cutting out each polygon present on the digitalized developmental stage map.

Each polygon was then assigned the correct developmental stage from the original paper map (developmental stage 1 - 5). On Flenvoll, two areas which were known to be recent clear-cuts, logged in the winter of 2010/2011 (Arild Berget pers. comm.), were changed from developmental stage 5 to developmental stage 1. In the event that a polygon had no developmental stage (unmapped forest, or other habitat type), it was assigned a developmental stage of 0. An exception was the Bryn Nord area, where according to the developmental stage maps there was no productive forest for logging purposes. However, all forest in this area was known to be old mature forest (Håkon Sætre pers. comm.), and was accordingly assigned to developmental stage 5. The area of each developmental stage polygon was then calculated using the “Recalculate Area Geometry” option in the “Area” field. Although the overall 100% MCP for each locality was employed as a perimeter, the developmental stage polygons created extended past this boundary, to later allow for developmental stage information to be extracted for different home range estimators.

Combining the maps

The resulting developmental stage maps were then combined with the AR5 habitat map, in ArcGIS, to create a new joint habitat and developmental stage layer per locality. This allowed habitat areas previously characterized as land type forest to be split into developmental stage 1 - 5, or left as forest of unknown (0) developmental stage. The amount of total forest within the overall 100% MCP ranged from 50.8 to 96.5 ($\bar{x} = 71.3 \pm 6.8$) %, per locality (Appendix 4). Of the total forest, unknown developmental stage ranged from 0.0 to 19.9 ($\bar{x} = 9.6 \pm 2.6$) %, per locality (Appendix 5), with Bryn Nord having the least, and Tøråsen the most. I checked for potential discrepancies between the AR5 habitat map and the joint habitat and developmental stage map, by comparing the total habitat areas of each, per locality. As the highest percentage difference between the two was 0.5% (on Storfallet), I was satisfied that the joint habitat and developmental stage map was an accurate representation, and could be employed in future analyses.

Habitat and developmental stage proportions

Proportions of each habitat and developmental stage type were derived per locality, using ArcGIS, for the overall 100% and 95% MCPs, the overall 95% kernel, and the foraging 50% kernel. As mountainous habitat was only present at Flenvoll, it was not used in further analyses. Likewise, as agricultural habitat was only present on two of the six overall 100% MCPs (Tøråsen and Flenvoll) it was not used further as an explanatory variable when looking at home range size, or core foraging area use.

2.7. Core foraging area use

Core areas, represented by a 50% kernel, can be used to look at resource utilization patterns. More specifically, by comparing proportions of habitat found within the 50% kernel to proportions of habitat found within the 100% MCP, preference for (or avoidance of) certain types of habitat can be distinguished. This represents Johnson's third-order selection, where selection of a resource within a home range is measured against its availability (Johnson 1980). A Wilcoxon signed-rank test was run to compare proportions of habitat and developmental stage available (within the overall 100% MCP) to the proportions that were utilized intensively (within the 50% foraging kernel).

In order to look more closely at the core foraging areas, all locations used to derive the foraging kernel were classified as either belonging to the core area (within the 50% isopleth) or belonging to the overall home range (outside of the 50% isopleth, but within the overall 100% MCP). Euclidean distances from each location to each habitat type and each developmental stage type were calculated. A Generalized Linear Mixed Model was run in R, using the packages MuMIn (Bartoń 2013) and lme4 (Bates et al. 2012). The model type was a logistic regression, where the binomial response variable was the probability of being inside (1) or outside (0) the core area. Global models were run on both a coarse and fine scale. The coarse scale considered the distances to the various habitat types of bog, bog with forest, forest, water, and road. The finer scale included the same habitat types, but split forest into the further categories of pooled developmental stage 1 and 2, developmental stage 3, and pooled developmental stage 4 and 5. Distance to the nest was included in the models as a covariate. Individual ID was fitted as a random variable, because repeated measurements were made on the same individuals, and therefore individual variation needed to be taken into account.

The global models were checked for intercorrelation of fixed effects. Intercorrelation was determined when the correlation value was ≥ 0.5 , or ≤ -0.5 . When intercorrelation between a fixed effect and the covariate (distance to nest) occurred, the fixed effect was removed from consideration. For both the coarse and fine scales, the best-fit model was selected from the candidate models, by AIC selection. Competing candidate models were considered where $\Delta AIC < 2.0$ (Burnham and Anderson 2002). In accordance with the principles of parsimony, the best-fit model was the one with the lowest AIC value, and the least amount of explanatory variables (Burnham and Anderson 2002). The resulting variables that best explained increased likelihood of being in a core foraging area were examined, on both the coarse and fine scale. Sigmaplot 12.0 (Systat Software 2011) was used to depict the relationship between probability of being in the core foraging area and the explanatory variables of the best-fit habitat model.

2.8. Nest centrality and distances

Village (1990) found that kestrels do not necessarily center their home range on the nest. I therefore tested for nest centrality by measuring the distance from the arithmetic mean of the

overall 100% MCP to the nest (A), and the distance from the arithmetic mean through the nest to the perimeter (B). A ratio of A/B indicated how centrally located the nest was. In the case of complete centrality ($A = 0$), the ratio would be 0. On the other extreme, where the nest was located on the perimeter ($A = B$), the ratio would be 1.0. When the nest was located between the arithmetic mean and the perimeter, the ratio would return a value between 0 and 1.0 (Fig. 4).

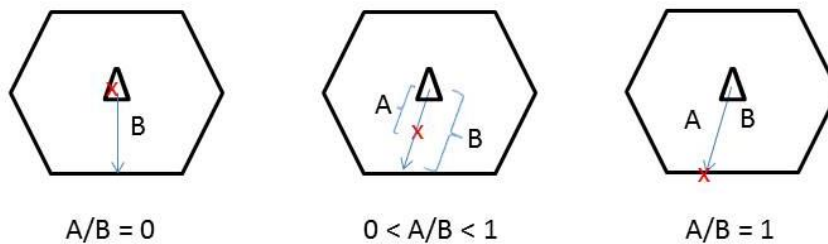


Figure 4. Possible relationships between distance from arithmetic mean to nest, and distance from arithmetic mean to perimeter. Δ = the location of the arithmetic mean, and x = the location of the nest.

3. RESULTS

3.1. Tracking effort

A total of 589 locations were taken before fledging, with each kestrel female located between 49 and 141 times ($\bar{x} = 98 \pm 13$). The number of absolute locations, used in the overall kernel analysis, ranged from 40 to 120 ($\bar{x} = 73 \pm 13$). The number of foraging locations, used in the foraging MCP analysis, ranged from 40 to 110 ($\bar{x} = 75 \pm 11$). The number of foraging kernel locations, used in the foraging kernel analysis, ranged from 30 to 71 ($\bar{x} = 50 \pm 7$). The number of days each kestrel was tracked ranged from 2 to 6 ($\bar{x} = 5 \pm 1$), and the number of hours tracked ranged from 14.5 to 30.0 ($\bar{x} = 26.3 \pm 2.4$). Due to the study design, the kestrel that was tracked the least before molting occurred was at Storfallet. However, in spite of the smaller amount of locations at this locality, an adequate number was reached to calculate home range sizes (Table 1, Fig. 7).

Table 1. Overview of number of days and hours tracked, and number of locations for each female kestrel.

Locality	Total number of locations	Number of absolute locations	Number of foraging locations *	Number of foraging kernel locations **	Number of days tracked	Number of hours tracked
Bryn Nord	125	120	72	67	5	30.0
Storflendammen	87	67	63	43	5	28.0
Storfallet	49	40	40	31	2	14.5
Husfliden	141	100	110	71	6	28.5
Tøråsen	102	56	101	55	6	28.0
Flenvoll	85	52	63	30	6	29.0
Total	589	435	449	297	30	158.0

* Locations that were taken more than 100 m away from the nest.

** Absolute locations that were taken more than 100 m away from the nest.

The Schoener's ratios computed indicated that the total dataset was autocorrelated, per locality (Table 2). The time to independence between relocations varied between kestrels, and ranged from 2.50 to 11.00 (median = 3.51, $\bar{x} = 4.40 \pm 1.33$) minutes. Storflendammen had the smallest TTI, whereas Flenvoll had the largest.

Table 2. Overview of Schoener's ratio, and time to independence, for all localities.

Locality	Schoener's ratio	Time to independence (minutes)
Bryn Nord	1.02	2.65
Storflendammen	1.15	2.50
Storfallet	1.01	3.52
Husfliden	1.48	3.14
Tøråsen	0.79	3.59
Flenvoll	1.38	11.00

Post-fledge tracking on Tøråsen and Storflendammen led to a total of 141 observations. The Storflendammen female was located 75 times over the course of 4 days, and 51 of the observations were absolute. The Tøråsen female was located 66 times over 3 days, with 42 absolute observations.

3.2. Home range sizes

3.2.1. Overall

The median overall 100% MCP was 0.94 (range 0.69 - 6.16, $\bar{x} = 1.84 \pm 0.87$) km², while the median overall 95% MCP was 0.72 (range 0.39 - 3.88, $\bar{x} = 1.22 \pm 0.54$) km². The median

overall 95% kernel was 0.98 (range 0.48 - 4.69, $\bar{x} = 1.60 \pm 0.64$) km² (Table 3, Fig. 5). Outliers had an effect, as the median overall 95% MCP was 23.9% smaller than the median overall 100% MCP (see Appendices 6a.–f. for a detailed view of each home range). There was a significant difference between the 95% MCP and the 95% kernel (median = 0.72 km² vs. median = 0.98 km², $p = 0.03$, $r = -0.62$, Wilcoxon signed-rank test), indicating that the type of estimator used to calculate home range size mattered. In this case, the 95% kernel provided a larger estimate of home range size than the 95% MCP. The Flenvoll locality had a markedly larger home range, when compared with all other localities, for each estimator type.

Table 3. Home range sizes (km²) per estimator type, for each female kestrel.

Locality	100% MCP	95% MCP	95% Kernel
Bryn Nord	0.69	0.39	0.48
Storflendammen	0.89	0.75	0.85
Storfallet	0.86	0.45	1.09
Husfliden	1.00	0.69	0.87
Tøråsen	1.45	1.18	1.64
Flenvoll	6.16	3.88	4.69

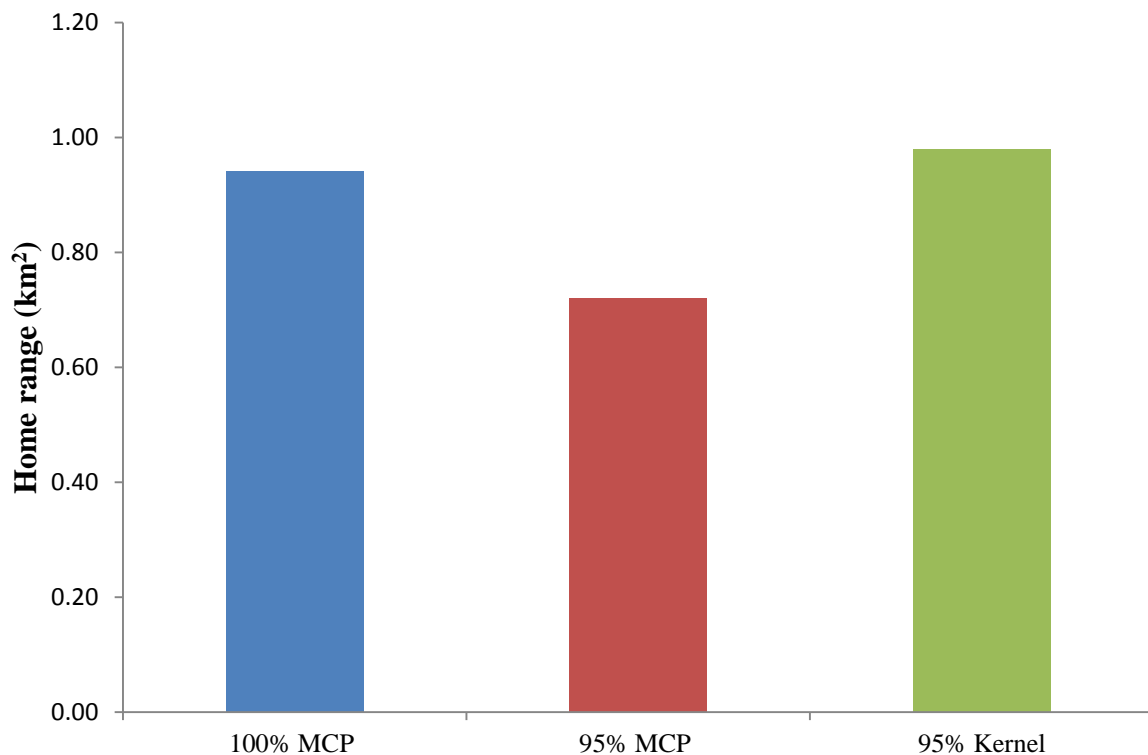


Figure 5. Median overall home range per estimator type for female kestrels (n = 6).

3.2.2. Home range overlap

None of the six home ranges overlapped with one another (Fig. 6). Although territoriality was not investigated in this study, I observed nest guarding on Flenvoll. The female engaged in an altercation with another kestrel within the 100 m buffer around the nest, at a distance of 25 m from the nest. In order to investigate the potential for home range overlap between the six focal nests and neighboring kestrels, all known kestrel nests where nestlings were successfully raised during the breeding season ($n = 23$) within the study site area were plotted (Ole Petter Blestad pers comm.). A hypothetical home range was centrally overlaid on these nests (Fig. 6).

When comparing these hypothetical home ranges to the 100% MCP of each focal nest, the potential for home range overlap did occur, for three of the six nests. Tøråsen experienced the most potential overlap, as the home ranges for three of its neighboring nests were shown to overlap with the 100% MCP. Visually, it was also the nest that experienced the densest clustering of neighboring nests, as indicated by Fig. 6. Bryn Nord was overlapped by the home range of one neighboring nest, as was Flenvoll. Using this method, the 100% MCPs of Storflendammen, Storfallet and Husfliden did not overlap with those of neighboring nests. When looking at the distances between each focal nest and its nearest neighboring nest, the range was from 0.33 to 1.44 ($\bar{x} = 0.92 \pm 0.17$) km, with Tøråsen having the closest neighbor, and Storfallet the farthest.

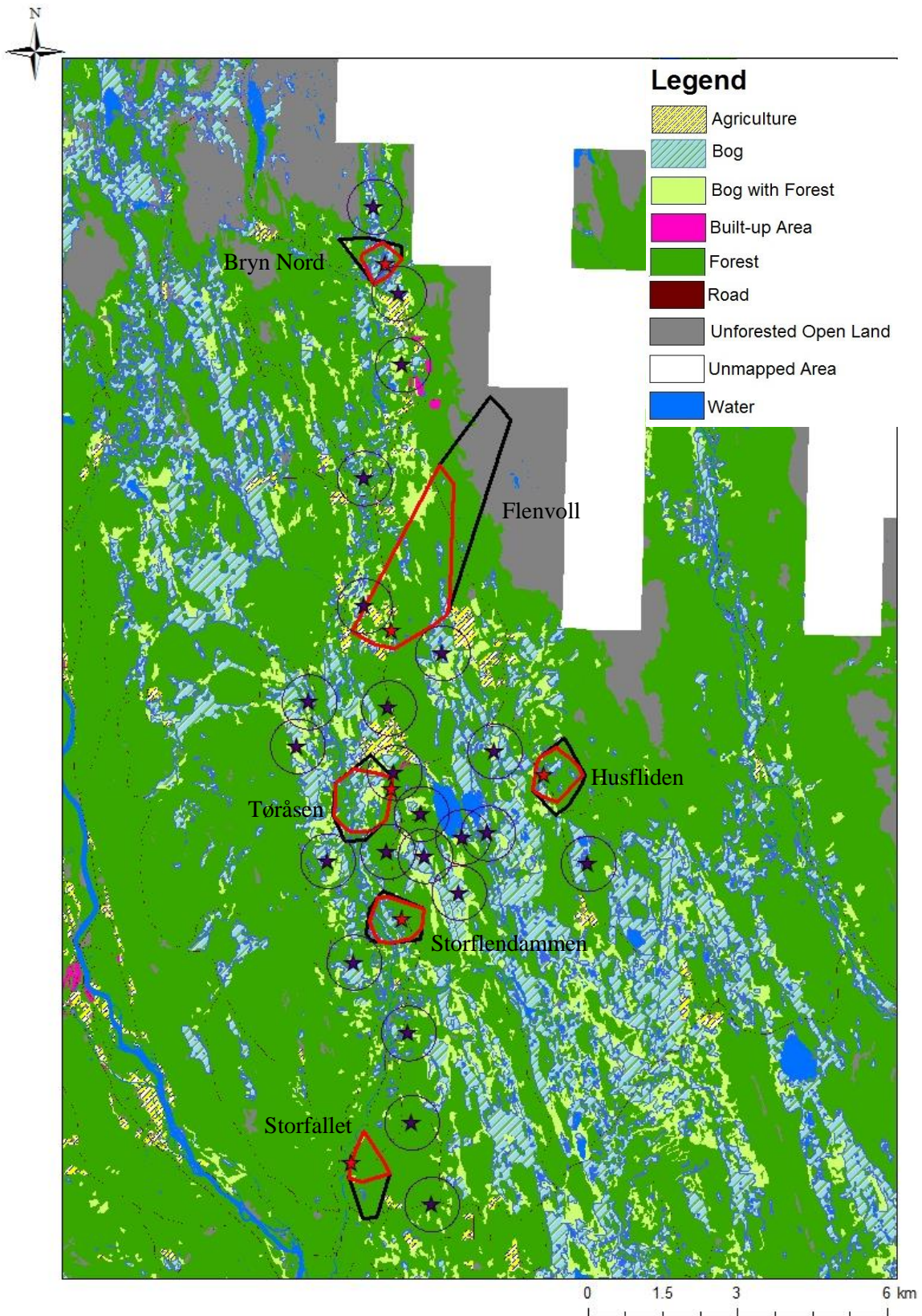


Figure 6. The 100% and 95% MCP home ranges (black and red polygons, respectively) of female kestrels, with nest locations indicated by a red star ($n = 6$). Known neighboring nests are indicated by a purple star, and hypothetical home ranges by a purple circle ($n = 23$). Hypothetical home ranges were generated by taking the median of the overall 100% MCPs of the six focal nests (0.94 km^2), and smoothing this to a circle, with radius 548 m.

3.2.3. Number of locations

The accumulated 100% MCP home range area curves showed visually that an asymptote had been reached for five of the six localities (Fig. 7). This indicates that an adequate sampling effort was achieved. In the case of Flenvoll, the last five locations taken caused a dramatic increase in the 100% MCP, as the estimated home range size increased from 4.92 to 6.16 km².

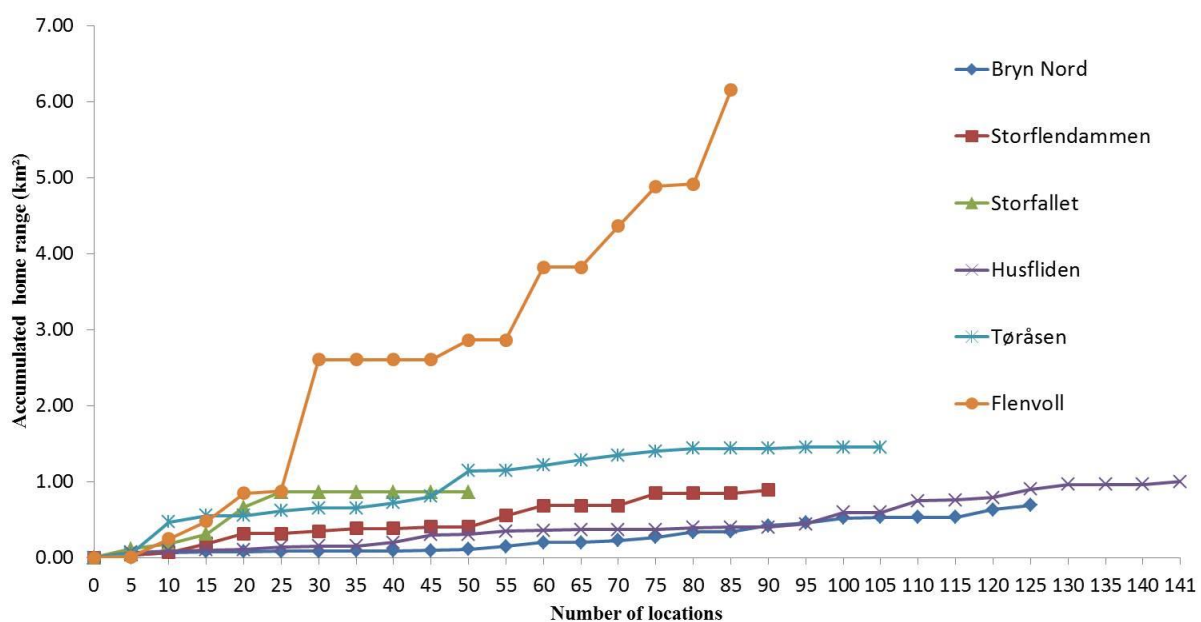


Figure 7. Accumulated home range sizes by number of locations, plotted by 5 location increments, per locality (n = 6).

3.2.4. Foraging

The median foraging 100% MCP for females was 0.94 (range 0.69 - 6.16, $\bar{x} = 1.84 \pm 0.87$) km², which was the same as that of the overall 100% MCP. The median foraging 95% MCP was 0.71 (range 0.49 - 4.84, $\bar{x} = 1.44 \pm 0.69$) km², and the median foraging 95% kernel was 1.16 (range 0.72 - 9.89, $\bar{x} = 2.61 \pm 1.46$) km² (Table 4, Fig. 8). As with the overall MCPs, outliers had a similar effect on the foraging MCPs, as the median foraging 95% MCP was 24.5% smaller than the median foraging 100% MCP. The type of estimator used to calculate foraging home range size also had an impact, as there was a significant difference between the 95% MCP and the 95% kernel (median = 0.71 km² vs. median = 1.16 km², p = 0.03, r = -0.62, Wilcoxon signed-rank test). As with the overall home ranges, the foraging 95% kernel gave a larger estimate of home range size than the foraging 95% MCP. In addition, the foraging

95% kernel gave a larger estimate of home range size than the foraging 100% MCP. When visualizing the 95% foraging kernel, dual centers of activity were found on Flenvoll and Storfallet (Fig. 16). As with overall home range, the Flenvoll locality had a markedly larger home range size, compared to all other localities, across all foraging estimator types.

Table 4. Foraging home range sizes (km²) per estimator type, for each female kestrel.

Locality	100% MCP	95% MCP	95% Kernel
Bryn Nord	0.69	0.49	0.72
Storflendammen	0.89	0.70	1.11
Storfallet	0.86	0.69	1.20
Husfliden	1.00	0.72	1.10
Tøråsen	1.45	1.19	1.62
Flenvoll	6.16	4.84	9.89

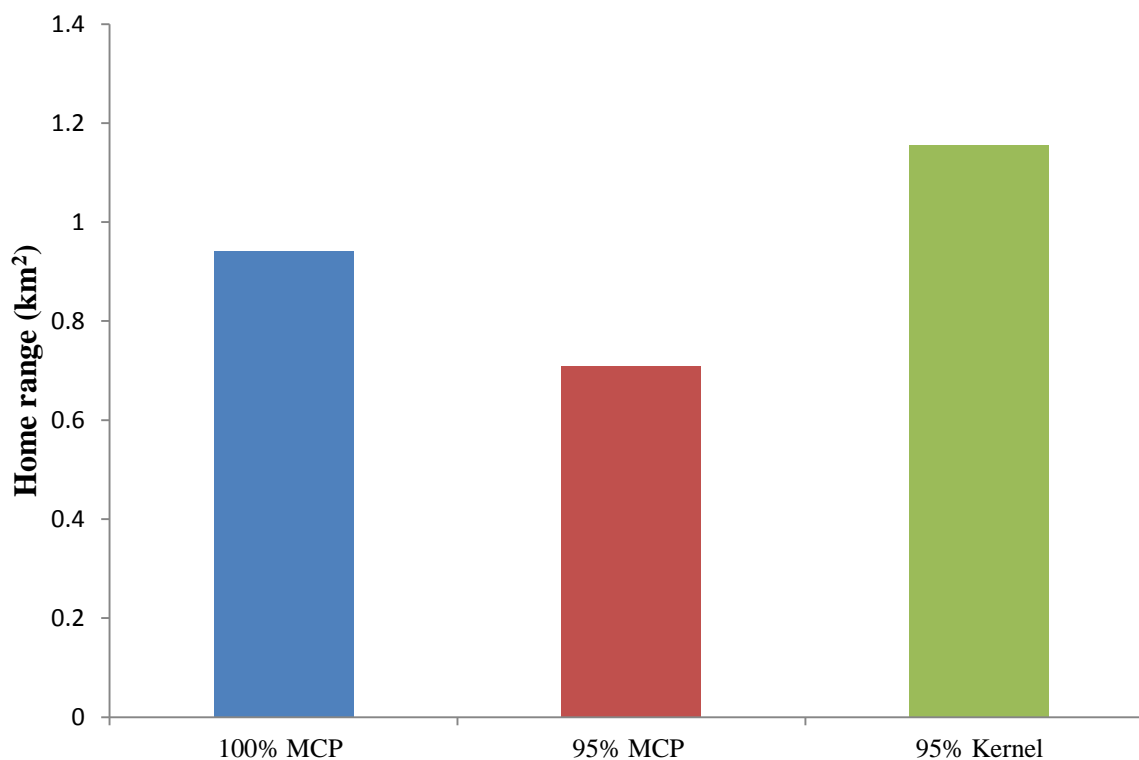


Figure 8. Median foraging home range per estimator type, for female kestrels (n = 6).

3.3. Variables that influenced home range size

A Spearman's rank correlation was run on each explanatory variable, for the three overall home range size estimator types (Table 5). The 100% MCP was significantly positively correlated with the proportion of forest developmental stage 3 (Table 5, Fig. 9). The 95% MCP was positively correlated with the proportion of bog with forest within the home range,

and negatively correlated with pooled developmental stage 4 and 5, and these results approached significance (Table 5).

Table 5. Spearman's rank order correlation of variables potentially affecting female kestrel home range size, per estimator type (n = 6).

	Home range estimator					
	100% MCP		95% MCP		95% Kernel	
	r_s	p	r_s	p	r_s	p
Number of locations	-0.09	0.87	-0.26	0.62	-0.77	0.07 ^(*)
Number of hours tracked	0.03	0.96	-0.06	0.91	-0.23	0.66
Age of female	0.29	0.57	0.29	0.57	-0.10	0.85
Wing chord length of female	-0.26	0.62	-0.09	0.87	-0.66	0.16
Average brood age	0.49	0.32	0.41	0.42	0.00	1.00
Brood size	-0.68	0.14	-0.56	0.25	-0.80	0.05 ^(*)
Proportion of bog in home range	-0.26	0.62	-0.20	0.70	-0.54	0.27
Proportion of bog with forest in home range	0.71	0.11	0.77	0.07 ^(*)	0.89	0.02*
Proportion of forest in home range	-0.26	0.62	0.03	0.96	-0.09	0.87
Proportion of pooled forest developmental stage 1 and 2 in home range	-0.09	0.87	-0.09	0.87	0.09	0.87
Proportion of forest developmental stage 3 in home range	0.83	0.04*	0.60	0.21	0.94	<0.01*
Proportion of pooled forest developmental stage 4 and 5 in home range	-0.71	0.11	-0.77	0.07 ^(*)	-0.94	<0.01*
Proportion of road in home range	0.09	0.87	0.09	0.87	-0.43	0.40
Proportion of water in home range	-0.26	0.62	-0.26	0.62	-0.54	0.27
<i>Microtus</i> vole trapping index	-0.54	0.27	-0.66	0.16	-0.77	0.07 ^(*)
Bank vole trapping index	0.09	0.87	0.31	0.54	0.09	0.87
Wood lemming trapping index	-0.49	0.33	-0.26	0.62	-0.37	0.47
Total microtine rodent trapping index	-0.37	0.47	-0.26	0.62	-0.37	0.47

* Probability is significant (p < 0.05)

(*) Probability approaches significance (p < 0.1)

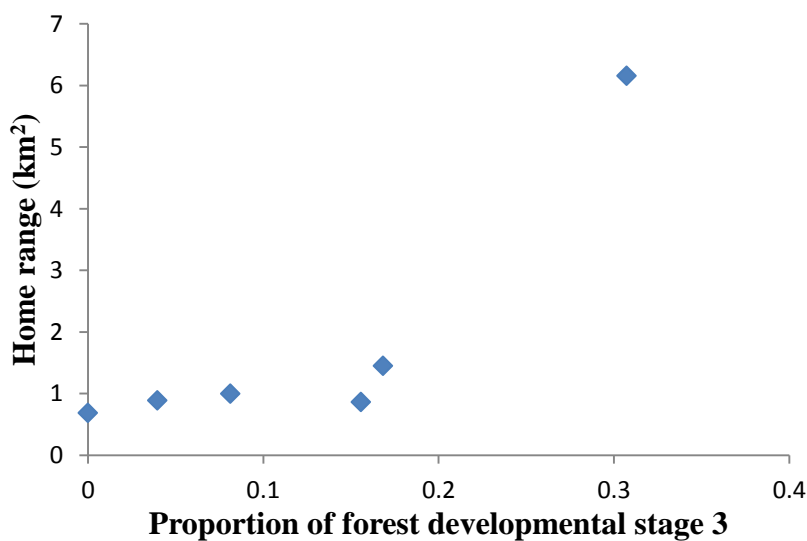


Figure 9. The relationship between female kestrel 100% MCP (km²) and the proportion of forest developmental stage 3 within the home range.

The 95% kernel was significantly positively correlated with proportion of bog with forest (Table 5, Fig. 10), and with proportion of developmental stage 3 (Table 5, Fig. 11), and significantly negatively correlated with pooled developmental stage 4 and 5 (Table 5, Fig. 12).

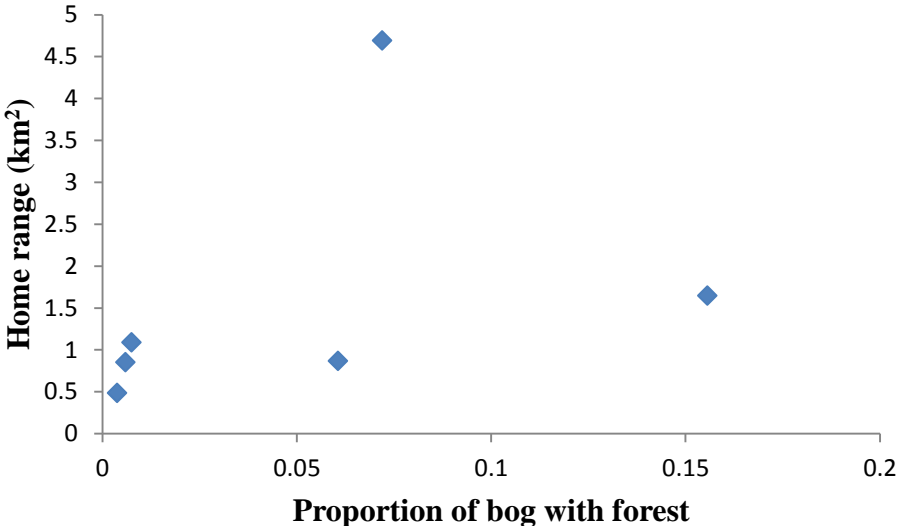


Figure 10. The relationship between female kestrel 95% kernel (km²) and the proportion of bog with forest within the home range.

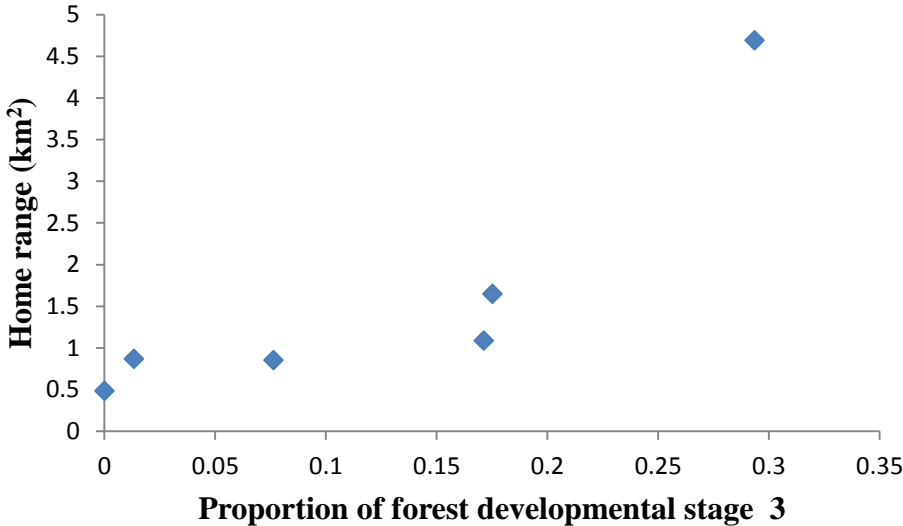


Figure 11. The relationship between female kestrel 95% kernel (km²) and the proportion of forest developmental stage 3 within the home range.

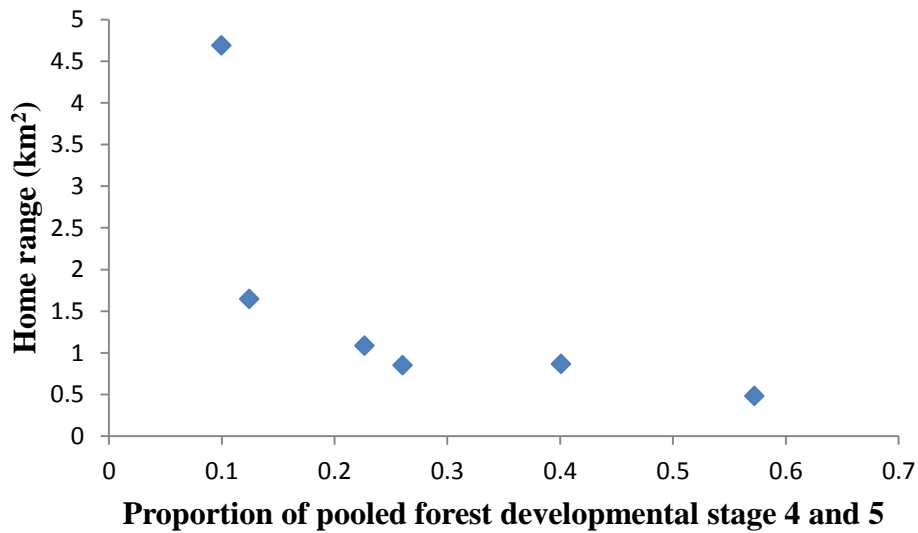


Figure 12. The relationship between female kestrel 95% kernel (km²) and the proportion of pooled forest developmental stage 4 and 5 within the home range.

In addition, results approached significance for a negative correlation with number of locations (Table 5), with proportion of bog in home range (Table 5), and with *Microtus* vole trapping index (Table 5, Fig. 13).

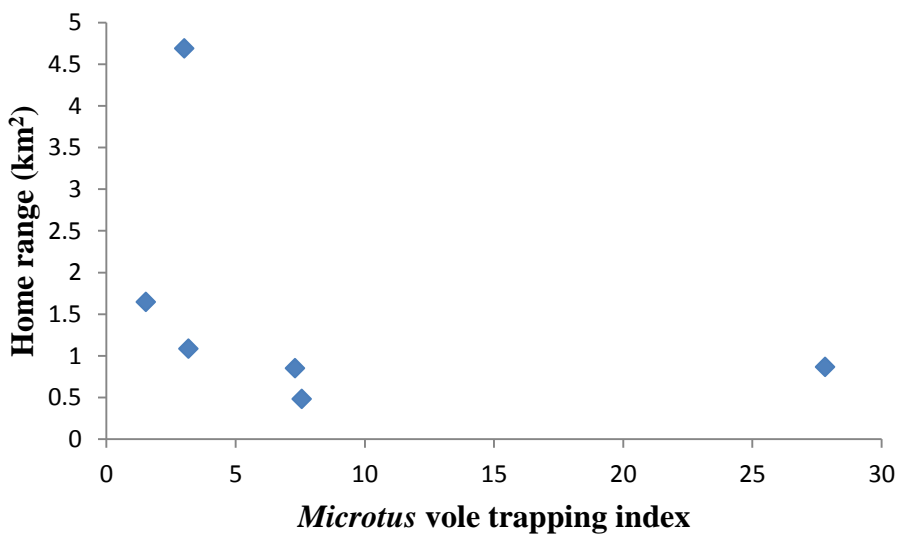


Figure 13. The relationship between female kestrel 95% kernel (km²) and the *Microtus* vole trapping index.

3.4. Core foraging area use

The median foraging 50% kernel for females was 0.27 (range 0.14 - 1.65, $\bar{x} = 0.50 \pm 0.23$) km², with Bryn Nord having the smallest core area, and Flenvoll the largest (Fig. 16, see

Appendices 6a.–f. for a detailed view of each core foraging area). There was significantly less pooled forest developmental stage 4 and 5 within the core foraging area than within the home range (Table 6). There was also significantly less water within the core foraging area than within the home range (Table 6). Both the proportion of bog and the proportion of pooled forest developmental stage 1 and 2 were shown to be greater in the core foraging area than in the home range, with the results approaching significance (Table 6).

Table 6. Wilcoxon signed-rank test for pairwise comparison of habitat proportions within the overall 100% MCP versus the foraging 50% kernel (n = 6).

	Median (100% MCP)	Median (Core area)	r **	p
Proportion of bog	0.172	0.251	-0.54	0.06 ^(*)
Proportion of bog with forest	0.037	0.012	-0.12	0.69
Proportion of forest	0.709	0.696	-0.41	0.16
Proportion of pooled forest developmental stage 1 and 2	0.183	0.300	-0.51	0.08 ^(*)
Proportion of forest developmental stage 3	0.118	0.107	-0.04	0.89
Proportion of pooled forest developmental stage 4 and 5	0.274	0.202	-0.62	0.03*
Proportion of road	0.003	0.006	-0.36	0.22
Proportion of water	0.009	< 0.001	-0.58	0.04*

* Probability is significant (p < 0.05)

(*) Probability approaches significance (p < 0.1)

** Effect size. $r = z/\sqrt{N}$, where N = the number of observations.

When looking at the binomial regression on the coarser scale of habitat, distance to water and distance to road were intercorrelated with the covariate, distance from nest. The resulting global model included the four variables of distance to bog, distance to bog with forest, distance to forest, and distance to nest, using 297 observations from all six localities. Of the four resulting top candidate models, the first three were within a Δ AIC value of 2.0 (Table 7). The best-fit model included the fixed effects of distance to bog and distance to nest.

Table 7. AIC-based model selection among candidate binomial regression models for predicting the probability of being in the core area based on distance to habitat, and distance to nest.

Model	Explanatory variables	AIC	Δ AIC
1	Distance to bog + Distance to nest	223.14	0.00
2	Distance to bog + Distance to nest + Distance to bog with forest	224.83	1.70
3	Distance to bog + Distance to nest + Distance to forest	225.13	1.99
4	Distance to bog + Distance to nest + Distance to bog with forest + Distance to forest	226.82	3.68

* Δ AIC is the difference between the AIC of the best-fit model, and the AIC of each subsequent candidate model.

When looking at the best-fit model, the probability of being in a core area decreased with distance to nest, and decreased with distance to bog. The results were highly significant (Table 8). In other words, one was more likely to be in the core foraging area of female kestrels the closer one approached the nest, and the closer one approached bog (Fig. 14). A more detailed depiction of this relationship is offered in Figure 15, on a limited scale of distances.

Table 8. Estimates of variables in the best-fit model for predicting the probability of being in the core area based on distance to habitat, and distance to nest.

	Estimate	SE	z	p
(Intercept)	6.9474	1.3097	5.305	< 0.0001
Distance to bog	-0.0075	0.0023	-3.261	0.0011
Distance to nest	-0.0120	0.0014	-8.578	< 0.0001

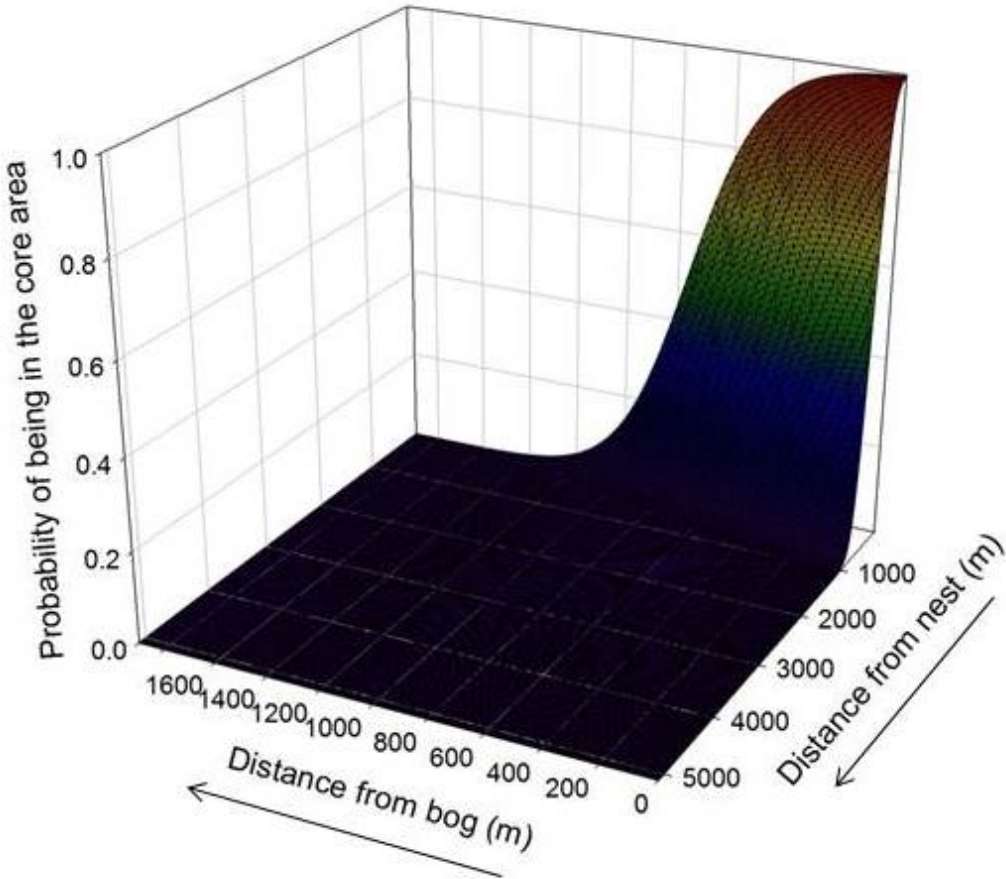


Figure 14. The relationship between the probability of being in the core foraging area, distance to bog, and distance to nest.

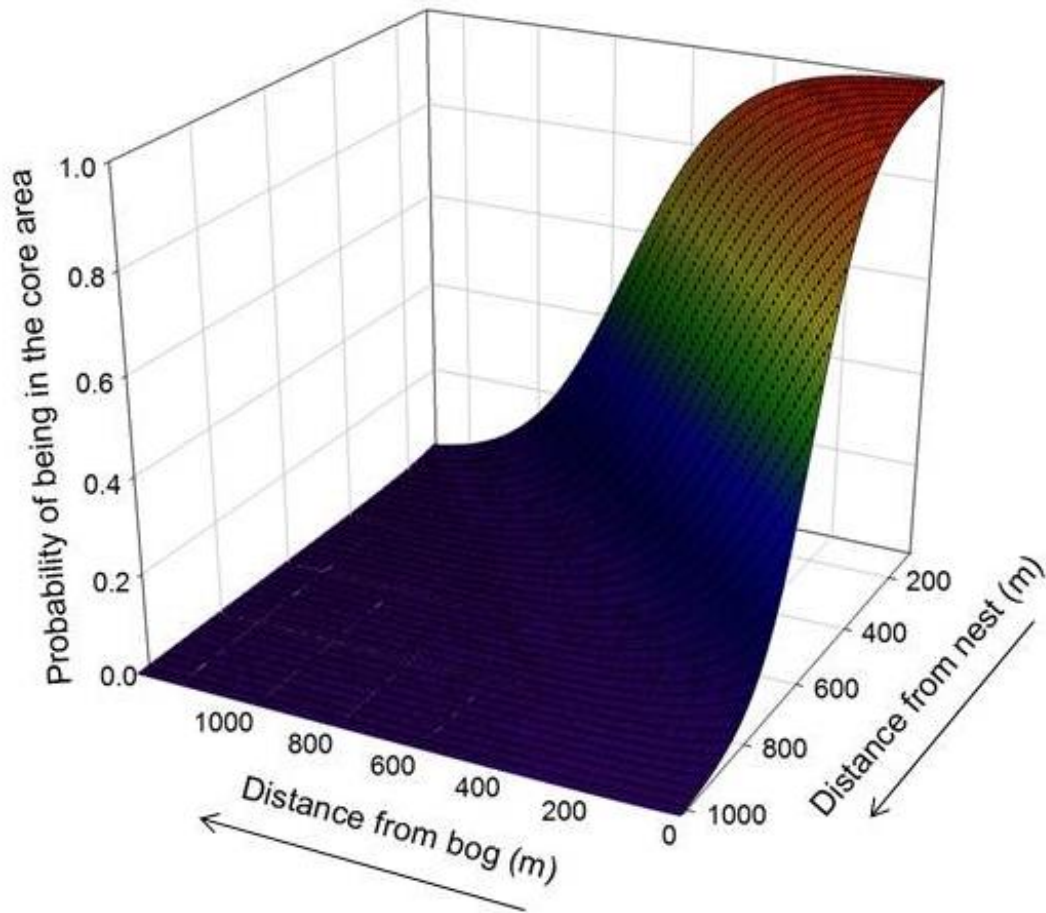


Figure 15. The relationship between the probability of being in the core foraging area, distance to bog, and distance to nest, depicted on a limited scale.

When looking at the finer scale of habitat and developmental stage, distance to water, distance to road, distance to bog with forest, and distance to pooled forest developmental stage 1 and 2, were all found to be intercorrelated with the covariate, distance to nest. This led to a global model that included the four variables of distance to bog, distance to developmental stage 3, distance to pooled developmental stage 4 and 5, and distance to nest, using 230 observations from 5 localities (Bryn Nord dropped). As with the coarse scale of habitat, the best-fit model included the fixed effects of distance to bog and distance to nest (Table 9).

Table 9. AIC-based model selection among candidate binomial regression models for predicting the probability of being in the core area based on distance to habitat and developmental stage, and distance to nest.

Model	Explanatory variables	AIC	Δ AIC*
1	Distance to bog + Distance to nest	173.37	0.00
2	Distance to bog + Distance to nest + Distance to developmental stage 3	173.70	0.32
3	Distance to bog + Distance to nest + Distance to pooled developmental stage 4 and 5	174.19	0.81
4	Distance to bog + Distance to nest + Distance to developmental stage 3 + Distance to pooled developmental stage 4 and 5	174.13	0.76
5	Distance to nest	178.34	4.97

* Δ AIC is the difference between the AIC of the best-fit model, and the AIC of each subsequent candidate model.

The probability of being in a core area decreased with distance to nest, and decreased with distance to bog. Again, the results were highly significant (Table 10). Candidate model 2 and candidate model 3 (Table 9) were looked at, as they included distance to developmental stage 3 and distance to pooled developmental stage 4 and 5 respectively. However, the results were not significant ($p = 0.20$ for distance to developmental stage 3, $p = 0.26$ for distance to pooled developmental stage 4 and 5). As the global model for habitat was run on a different subset of data than the global model for habitat and developmental stage, the results are not directly comparable. However, as the best-fit model for habitat and developmental stage included the same variables as the best-fit model for habitat alone, this indicated that the distance to nest and the distance to bog were the two most important explanatory variables for the probability of being in the core foraging area, irrespective of developmental stage.

Table 10. Estimates of variables in the best-fit model for predicting the probability of being in the core area based on distance to habitat and developmental stage, and distance to nest.

	Estimate	SE	z	p
(Intercept)	6.7815	1.2942	5.240	< 0.0001
Distance to bog	-0.0059	0.0022	-2.661	0.0078
Distance to nest	-0.0110	0.0015	-7.545	< 0.0001

As distance to nest significantly affected the probability of being in the core area, the distances from each nest to the arithmetic mean (center) of each core foraging area were measured. There was a range from 25 - 445 ($\bar{x} = 183 \pm 65$) m, from Flenvoll to Tøråsen.

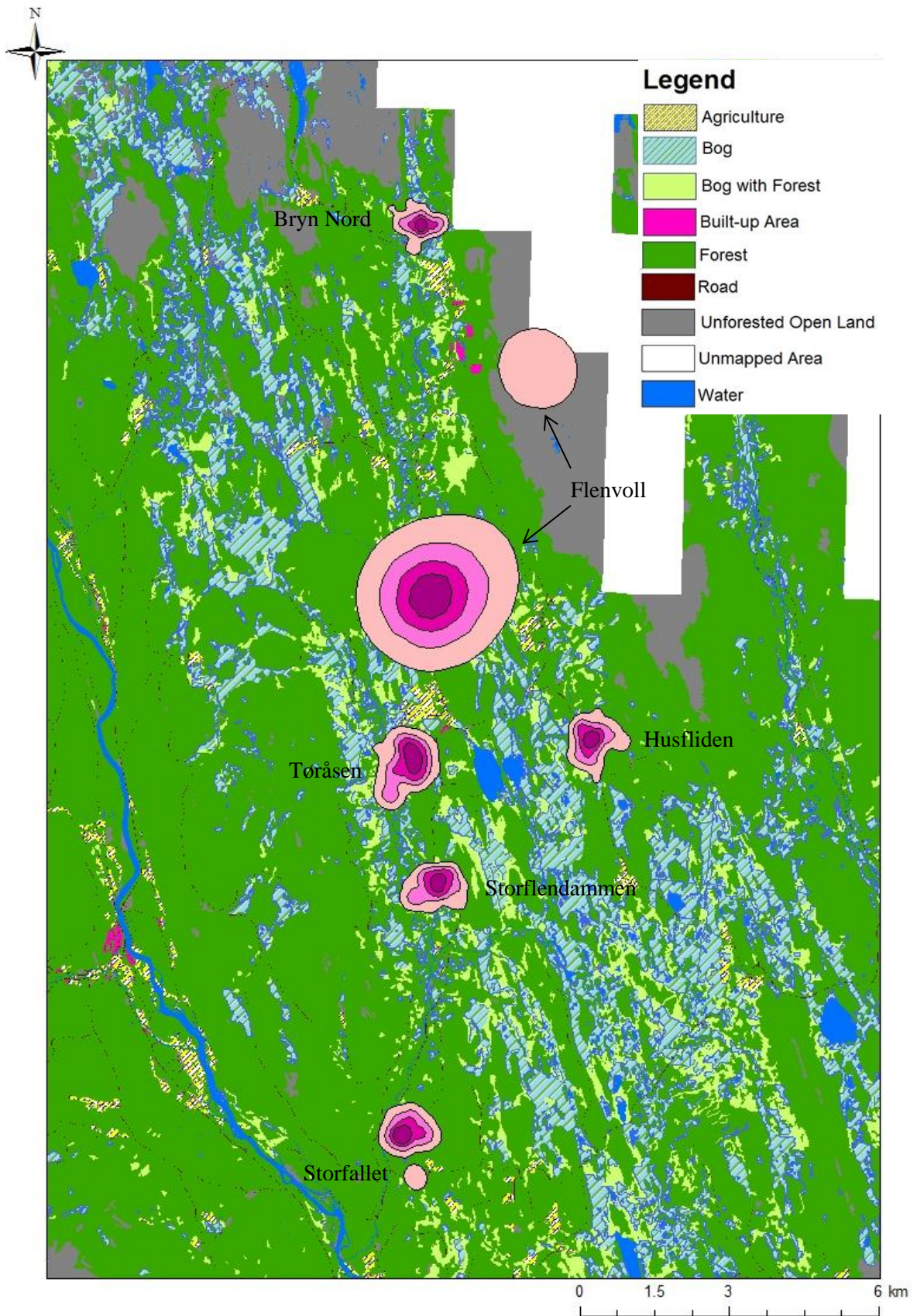


Figure 16. Foraging kernels of female kestrels ($n = 6$). The 95%, 75%, 50% and 25% isopleths are depicted, as darkening shades of pink.

3.5. Nest centricity and distances

Females differed greatly in the maximum distance they travelled from the nest, in the pre-fledging period. The range was 785 - 5083 (median = 1019, $\bar{x} = 1731 \pm 677$) m, with the shortest distance belonging to Storflendammen, and the longest distance to Flenvoll. When looking at all locations, females were located 395 ± 23 SE (range 0 - 5083, n = 589) m from the nest. The test for centricity showed a range of 0.29 - 1.00 ($\bar{x} = 0.72 \pm 0.11$) for the ratio. On Storfallet and Tøråsen, the nests were located at the edge of the respective 100% MCP perimeters. The most centric nest was on Storflendammen, which was also a nest surrounded by a cluster of neighboring nests (Table 11, Fig. 6).

Table 11. Distances and centricity ratios, for all localities (n = 6).

Locality	Distance from arithmetic mean to nest (m)	Distance from arithmetic mean to perimeter (m)	Centricity ratio*
Bryn Nord	293	474	0.62
Storflendammen	172	586	0.29
Storfallet	446	445	1.00
Husfliden	264	468	0.56
Tøråsen	626	628	1.00
Flenvoll	2052	2405	0.85

* 0 = nest located in the center of the 100% MCP, 1.00 = nest located on the range's perimeter.

When looking at the pre-fledge locations of molted tail feathers, the distances from the nest ranged from 5 - 440 ($\bar{x} = 284 \pm 103$, n = 4) m, from Storfallet to Bryn Nord respectively. The close distance on Storfallet suggested that molting occurred as the female flew out from the nest. On Bryn Nord, the molted tail feathers were located in a 12 m high spruce tree in an area of coniferous forest, the tallest in a 25 m radius. The spruce was located at the bottom of a slope overlooking a bog, to the southwest of the nest. On Flenvoll, the molt was localized to a small group of spruce trees on the edge of the clear-cut, 253 m to the west of the nest. Although the radiotransmitter was assumed to be in one of these trees, it was never retrieved. Molting occurred post-fledge in a forested area on Storflendammen, dominated by birch, and 919 m from the nest. The molt was never retrieved on Tøråsen, as the female flew over the electric bear fence prior to molting.

3.6. Post-fledge

Home range sizes were calculated, using the 100% MCP and 95% MCP estimators, on all post-fledge observations at Storflendammen (n = 75) and Tøråsen (n = 66) (Fig. 17). The Storflendammen female had a 100% MCP of 1.27 km², and a 95% MCP of 1.04 km². The Tøråsen female had a 100% MCP of 3.63 km², and a 95% MCP of 2.76 km². At both localities, the nest still formed a part of the home range. On Storflendammen, the female's post-fledge 100% MCP shifted westwards. Although the nest was still included inside this perimeter, it was not as centrally located as on the pre-fledge 100% MCP. The home range shifted in relation to the nest location, as indicated by the centricity test. The test resulted in a ratio of 0.73, as compared to the pre-fledge ratio of 0.29. On Tøråsen, the post-fledge 100% MCP also extended westwards, and was elongated. As with the pre-fledge 100% MCP, the nest remained on the perimeter of the 100% MCP. On Storflendammen, the post-fledge distances from the nest ranged from 40 - 1248 ($\bar{x} = 532 \pm 33$, n = 75) m. On Tøråsen, the distances from the nest ranged from 146 - 2515 ($\bar{x} = 1236 \pm 68$, n = 66) m.

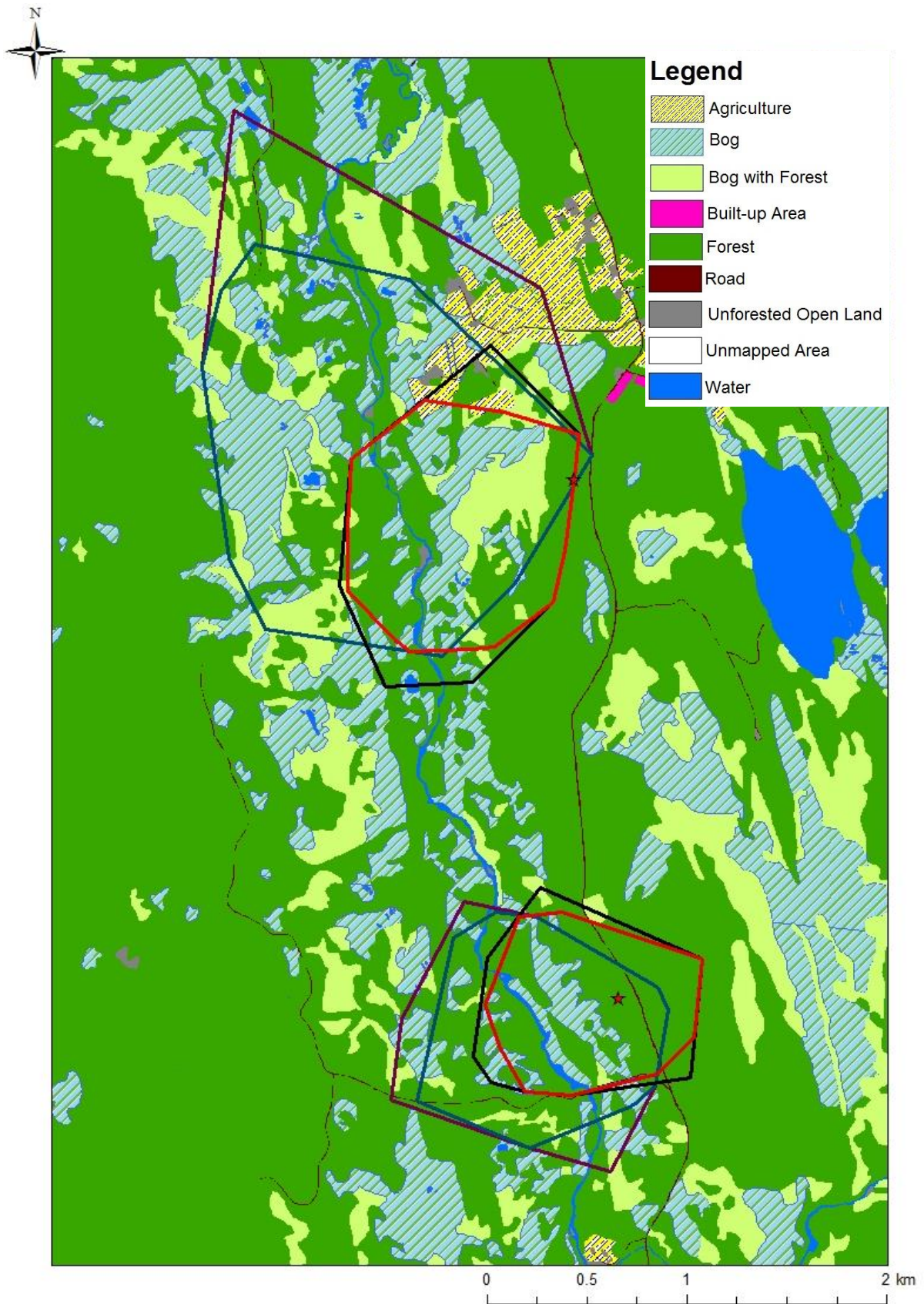


Figure 17. Post-fledge 100% (purple) and 95% (blue) MCPs for Tøråsen (top) and Storflendammen (bottom), overlaid on habitat map. The red star is the position of the nest. The 100% and 95% MCPs pre-fledge are shown for perspective, in black and red respectively.

4. DISCUSSION

4.1. Home range

4.1.1. Estimator types

No single estimator type constitutes the golden standard when it comes to answering questions of home range; rather, the estimator type chosen should reflect the questions being asked (Kenward et al. 2001). I used the 100% MCP, 95% MCP, and 95% kernel estimators to look at the overall and foraging home range sizes of the six female kestrels. My results showed a clear effect of outliers, as the overall and foraging 95% MCP median estimates (0.72 km² and 0.71 km², respectively) were respectively 23.9% and 24.5% smaller than their 100% MCP counterparts (0.94 km² in both cases). Løken (2009) conducted research on three breeding male kestrels in the same study area, and found a range of 0.81 - 3.55 km² for the overall 100% MCPs, and a range of 0.71 - 3.01 km² for the overall 95% MCPs, but did not statistically conclude that outliers had an effect. This may in part have been due to the small number of individuals he tracked. In addition, I found a statistically significant difference between the 95% MCPs, and the 95% kernels, for both the overall and foraging ranges, with kernels consistently returning the larger value at each locality.

Kernels are known to overestimate home range size (Worton 1995), and may be less useful in determining actual size than in portraying area use. When it comes to kernels, deciding which smoothing parameter to use is the single most important choice made (Worton 1995; Seaman & Powell 1996), as results may vary depending on this. In general, h_{ref} tends to oversmooth (Seaman & Powell 1996), and can lead to a larger home range size than the MCP method, and this was supported by my data. The MCP estimator may lead to a more accurate portrayal of actual home range size than the kernel, especially when sample sizes are small (Boyle et al. 2009). Although the $h_{\text{ls cv}}$ method often performs better than the h_{ref} , it has the disadvantage of potentially not working when locations are spatially close to one another (Gitzen et al. 2006), as was the case with my dataset. In addition, overestimation of home range size can still occur with $h_{\text{ls cv}}$, for example when samples are less than 50 (Seaman et al. 1999). Interestingly, when utilizing the kestrel dataset collected by Andrew Village, Börger et al. (2006a) found no difference between the performance of h_{ref} and $h_{\text{ls cv}}$, indicating that the choice of h_{ref} as a smoothing parameter may not be as problematic as once thought. Taking all of this into account, I feel that the choice of h_{ref} provided a reasonable kernel estimator

type for my dataset, and that the MCP estimator outperformed the kernel when looking at actual home range size.

4.1.2. Tracking effort and time to independence

In addition to sample size (Seaman et al. 1999; Kie et al. 2010), home range size can be affected by the time scale of a study (Börger et al. 2008), and by sampling interval (Swihart & Slade 1985a). Swihart and Slade (1985a) point to the issue of autocorrelation, which can bias estimates of home range size. However, autocorrelation may not be as large an issue as securing an adequate sample size (Swihart & Slade 1997). When I calculated the overall 100% MCPs, the number of locations used per locality ranged from 49 to 141, from Storfallet at the lowest to Husfliden at the highest. This was in keeping with the suggestion by Kenward (2001) that a minimum of 30 data points was needed. Village (1982b) found that a sample size of only 25 was adequate for calculating the 100% MCPs of kestrels in his study, and Løken (2009) was satisfied with a range of 32 to 52 locations. Odum and Kuenzler (1955) showed that accumulated 100% MCP home range area curves level off the closer the true home range size is approached. My data suggests that this occurred at five of the six localities, with the exception of Flenvoll. It is possible that the leap from 4.92 to 6.16 km² on Flenvoll represented an exploratory excursion, to locations seldom used in the home range by the female, as the overall 95% MCP was 3.88 km². However, tracking was difficult at this location, and there were times when the female flew out of range to the northeast, possibly to the mountain. It is therefore likely that, had she been located in those instances, an asymptote would have been reached much earlier on the area curve.

As regards sampling effort for the kernel estimators, I had a range of 40 (Storfallet) to 120 (Bryn Nord) locations used for overall kernel estimation, and 30 (Flenvoll) to 71 (Husfliden) observations for the foraging kernels. Seaman et al. (1999) indicated a minimum requirement of 30 observations needed per locality, and my dataset was in accordance with this. In addition, while the number of days used to track kestrels ranged from 2 to 6, Village (1990) indicated that the kestrel covers all parts of its home range in a matter of days. Therefore, although I cannot discount the possibility that home range size would have been altered, an adequate sampling procedure was followed, for the purposes of my study.

The Schoener's ratios I calculated indicated that my dataset was spatially autocorrelated at each locality, as the values ranged from 0.79 to 1.48, and deviated significantly from the optimal ratio of 2.0 (Rodgers & Kie 2011). However, research conducted by Cresswell and Smith (1992) on home range sizes derived from simulated data indicated that continuous monitoring might only be problematic with high levels of autocorrelation. Based on this, Kenward (2001) suggests using a Schoener's ratio of 1.0 as the standard for autocorrelation, rather than 2.0. By this standard, autocorrelation in my study was only a potential issue at Tøråsen. It has been suggested that autocorrelation can be removed by subsampling data (Swihart & Slade 1985b), but this creates additional problems as it removes biological significance, and often leads to inaccurate and underestimated home range sizes (Rooney et al. 1998; De Solla et al. 1999). In addition, while I calculated a TTI range from 2.50 to 11.00 (median = 3.51, \bar{x} = 4.40) minutes, this may be longer than the actual time needed for an individual to cross its home range (De Solla et al. 1999), as the TTI represents the most extreme circumstance. The kestrel has an average directional flight speed of 8.3 m/s (Videler et al. 1983), and can cross its range in a matter of minutes (Village 1990). Taking all of this into account, while I recognize the potential for autocorrelation, I believe that it was best to keep the dataset intact, and the subsequent home range estimates derived were valid.

4.1.3. Home range size

I found an almost tenfold variation with regards to the overall 100% MCPs of the six female kestrels in my study. The smallest home range size belonged to the Bryn Nord female, whereas the Flenvoll female had the largest (0.69 km² and 6.16 km², respectively). The median home range size of 0.94 km² was different from the median of 2.23 km² found for the three male kestrels in Løken's study (2009). However, there was no statistically significant difference between the two datasets (Wilcoxon's rank-sum test, $W = 11$, $p = 0.71$). Village (1982b) found home range size means of 3.11, 4.08, and 5.69 km² over three summers, for varying numbers of male kestrels (9, 20, and 19 respectively), corrected for small sample size. These means are larger than the mean I obtained on the six females (1.84 km²), and the mean Løken (2009) found for the three males (2.20 km²). Village commented that female home ranges were not looked at in his study, as limited data indicated small female ranges were entirely encompassed by the home ranges of male partners (Village 1982b). It is known that in raptors such as the European sparrowhawk (*Accipiter nisus*) females are capable of ranging

further afield than males in the nestling period (Marquiss & Newton 1982; Selås & Rafoss 1999), particularly when prey abundance is low (Marquiss & Newton 1982).

4.1.4. Home range overlap

My results indicated that none of the six female kestrel home ranges overlapped with one another, with reference to the overall 100% MCPs. However, when taking the hypothetical home ranges of neighboring nests into account, the potential for overlap occurred at the three locations of Bryn Nord, Tøråsen, and Flenvoll. The kestrel that experienced the densest clustering of neighboring nests, Tøråsen, also exhibited the most potential for home range overlap, with three of its neighbors hypothetically overlapping. This nest was likewise the one that had the closest nearest neighbor, as the closest occupied nestbox was located only 330 m away. In addition, it is interesting to note that the shapes of both the Tøråsen and Storflendammen (which also had a dense clustering of occupied neighboring nests) home ranges were fairly regular. This can be contrasted in particular with the elongated home range of Flenvoll, where the female appeared to utilize space that allowed her to avoid neighboring kestrels to a larger extent. Kestrels are known to tolerate each other's presence, when hunting, and experience range overlap in the breeding season, particularly when the abundance of *Microtus* voles is high (Village 1982b, 1983), as was the case throughout my study site.

Although territoriality was not directly measured in this study, the personal observation of the Flenvoll female attacking another kestrel within 25 m of the nest is in keeping with other studies. Female kestrel aggression towards conspecifics occurs throughout the breeding season, and intensifies during the nestling rearing stage (Cavé 1968; Wiklund & Village 1992). Nest defense has been documented at a maximum distance of 35 m from the nest in females (Cavé 1968), whereas studies on male kestrels have shown territories ranging from 250 m to 1 km from the nest (Village 1983). In addition, female aggression has been shown to be positively correlated with brood size (Wiklund & Village 1992). As the six respective brood sizes were relatively high in my study, it is reasonable to assume that female aggression and nestling protection were likewise high. Conspecifics near the nest can be viewed as predators (Newton 1979), which accounts for nest defense in the breeding season.

4.2. Variables that influenced home range size

Determining whether or not a true home range size has been captured is often not as interesting as looking at the underlying explanatory factors of home range size variation (Börger et al. 2006a). It is important to keep in mind that my sample size was only six individuals, and therefore results should be interpreted with caution. The home range estimator that scored the most significant correlations, with regards to explanatory variables, was the overall 95% kernel; it was negatively correlated with proportion of pooled developmental stage 4 and 5, and positively correlated with proportion of bog with forest, and with proportion of developmental stage 3. In addition, the overall 100% MCP was also significantly positively correlated with the proportion of forest developmental stage 3.

On a landscape scale, my results suggest that developmental stage 3 was an undesirable habitat for the female kestrels, as an increase in the proportion of this habitat was significantly correlated with an increase in home range size. In addition, my results indicate that the pooled developmental stage 4 and 5 habitat was favorable, as the proportion of this habitat was significantly negatively correlated with the overall 95% kernel. Løken (2009) found neither a preference for nor an avoidance of developmental stage 3 in male kestrels, using point analysis. Likewise, his results suggested that male kestrels showed neither a preference for nor an avoidance of developmental stage 4, but utilized developmental stage 5 less than randomly expected. Habitat distribution within home ranges can considerably affect home range size (Börger et al. 2006b). When considering the ranging behavior of kestrels, it is not just prey availability, but also vegetation structure that can have an impact (Cavé 1968; Pettifor 1983). This is because vegetation cover can alter prey detection, capture, and foraging behavior in raptors (Janes 1985). A predator like the kestrel may experience difficulties in detecting and catching prey below dense canopy, as it depends on locating its prey visually (Valkama et al. 1995). Developmental stage 3 represents dense growth, as the forest is ready for thinning at this stage (Landsskogtakseringen 2008). In addition, although the kestrel is an open-country raptor, mature boreal forest may offer suitable habitat, due to openings in the canopy (Sonerud 1991). Clear-cuts and young developmental stage 2 forest offer prime hunting grounds in the early spring for raptors, when snow melting has occurred and the ground vegetation is low (Sonerud 1986). However, as the summer progresses, the cover offered by graminoids in these areas may make prey detection and capture more

difficult than in mature forest (Sonerud 1991), as has been observed in the Tengmalm's owl (*Aegolius funereus*) (Sonerud et al. 1986). My study was conducted in summer, when ground vegetation was fairly high, which may help explain why a significant negative correlation was seen between home range size and proportion of pooled developmental stage 4 and 5, but not pooled developmental stage 1 and 2.

The significant positive correlation I found between home range size and proportion of bog with forest is somewhat surprising, when considered purely from a habitat preference perspective. Kestrels utilize open habitat such as bog with forest when foraging (Valkama et al. 1995). Løken (2009) found that male kestrels significantly utilized bog with forest, based on buffer and point analysis. Larsen (2012) did not find this result, but utilized buffer analysis to determine that the female kestrels showed a significant preference for the open habitat of bog, although a 100 m radius around the nest (to be discussed in section 4.3) was not employed in that study. When considering home range size as it relates to the proportion of bog with forest, it would be reasonable to expect a negative correlation. However, the results found might be explained by factors other than comparisons to habitat preference or avoidance, and do not necessarily disagree with the conclusions drawn by Løken (2009) or Larsen (2012), as the observational scale differs (buffer versus landscape) (Wheatley & Johnson 2009). Size, shape, patchiness of the landscape, and distance of habitat from the nest may have played a role. In particular, patch size and shape of habitat within Fennoscandian boreal forests have been shown to have implications for the distribution of raptor species (Niemi & Hanowski 1997, and references therein).

In addition, I would like to highlight the negative correlation between the overall 95% kernel home range size and the *Microtus* vole trapping index, which approached significance. My results are in keeping with previous studies on male kestrels (Village 1982b; Løken 2009), suggesting that female kestrels follow the same trend. Numerous studies have shown that *Microtus* voles form a primary part of the diet of the kestrel (Hagen 1952; Cavé 1968; Village 1982a; Korpimäki 1985). My study season was no exception, as Støvern (2012) found a functional response for *Microtus* voles, followed by wood lemmings. The link between decreasing home range size and increasing prey abundance has been shown in several studies on raptors, such as prairie falcons (*Falco mexicanus*) (Marzluff et al. 1997a) and European sparrowhawks (Marquiss & Newton 1982). That my results only approached significance

may be due in part to the small sample size. However, it is likely that other factors played a role as well.

Raptors have smaller range sizes when there is abundant prey near the nest site (Newton 1979). Therefore, while the relative abundance of *Microtus* voles differed between nest sites, even the “poorest” locality of Tøråsen (snap-trapping index 1.52) might have had a suitable abundance, whereas the exceptional locality of Husfliden (snap-trapping index 27.81) might not have been “better” than Bryn Nord (with a high snap-trapping index of 7.56), from a kestrel’s perspective. *Microtus* voles in general are found to prefer clear-cuts and young plantations (e.g. developmental stage 2) (Ims 1991; Petty et al. 2003), although vegetation cover and structure may modify this on a temporal and spatial scale (Gorini et al. 2011). However in my study year *Microtus* voles were found in abundance across all habitat types. It is possible that the female kestrels experienced a prey saturation point, past which a further increase in *Microtus* vole abundance made no further difference as to home range size, and that prey abundance therefore did not influence home range size as strongly as other factors (see e.g. Casagrande et al. 2008).

Although clear trends could be seen with regards to the correlations, it is important to note that correlations could not be ranked against one another. In addition, other factors may have been at play in determining the difference between home range sizes, such as the already noted neighboring pairs, and polygyny. Polygyny is known to occur in raptors, and has been documented in kestrels (Newton 1979). Korpimäki (1988) showed that on average 10% of breeding male kestrels formed extra-pair matings when conditions were favorable, in years of high vole abundance. As already mentioned, the abundance of *Microtus* voles was exceptional in my study year, across all localities (Geir A. Sonerud pers. comm.). Therefore, the likelihood that polygyny occurred within the general study area would have been high. The male on Flenvoll was never sighted during radio-tracking, and the male on Tøråsen was only spotted once at the nest site. Taking these observations into account, it is highly plausible that the Flenvoll and Tøråsen females were paired with polygynous males. Therefore, these two females may have assumed a larger proportion of provisioning duties, and consequently needed to utilize a larger home range. This is supported by the fact that these two females held the largest overall home ranges, across all estimator types.

4.3. Core foraging area use

Female kestrels in the breeding season are central-place foragers, and their time is split between nest guarding and foraging duties during the nestling stage (Village 1990). As with other central-place foragers, a distinction may be made as to the use of a nest site area versus a foraging area (Rosenberg & McKelvey 1999), hence necessitating a delineation between the two. Raptors in general frequently utilize the same perches in the nest site area, as evidenced by pellets, whitewash, and prey remains (Newton 1979), and female kestrels have been shown to consistently use the same perches near the nest to pluck and eat prey foraged elsewhere (Village 1982a). On Husfliden, the female was observed on a dead birch stump 78 m away from the nest, and on closer inspection of the stump I observed prey remains and whitewash, indicating that it was a preferred perch. Likewise, on Bryn Nord the female was observed on 14 occasions in two trees near the nest site (a dead pine and an alive pine), at distances of 94 m and 95 m from the nest, respectively. On closer inspection, I found 24 pellets and whitewash at the dead pine, again indicating that this was a preferred perch. Therefore, the exclusion zone that I employed of 100 m radius when looking at foraging was reasonable.

There was large individual variation in the core areas in my study, as the 50% foraging kernels ranged between 0.14 - 1.65 km². This variation was in proportion with the variation found in the 95% foraging kernels, as the location with the smallest 50% kernel (Bryn Nord) likewise had the smallest 95% kernel, and the location with the largest 50% kernel (Flenvoll) also had the largest 95% kernel.

The use of a core area should naturally differ from random use of the home range in general (Powell 2000). When looking at the proportions of habitat and developmental stage present in the core area versus the 100% overall MCP, certain trends could be distinguished. Both the proportion of pooled developmental stage 4 and 5, and the proportion of water, were significantly less in the core area than in the home range, whereas a trend approaching significance existed for a higher proportion of pooled developmental stage 1 and 2, and proportion of bog, within the core area. However, these results may not necessarily denote a general preference for or avoidance of habitat per se, as core areas may be more affected by individual variation, whereas habitat distribution may instead influence the home range to a larger extent (Börger et al. 2006b).

Pettifor (1984) found that for kestrels in an agricultural setting, the large individual variation in the proportion of time spent foraging over lode banks was not significantly correlated to the amount of this habitat present in their territory. In a study on golden eagles (*Aquila chrysaetos*), Marzluff et al. (1997b) found individual variation in how core areas were selected in the breeding season, with regards to proportion of shrub habitat included, the native habitat of the preferred prey type (black-tailed jackrabbit, *Lepus californicus*). Home ranges with a high proportion of shrubs did not have a high proportion of shrubs in the core area, but home ranges with more fragmented landscapes led to core areas with a higher proportion of shrubs. Likewise, a study done on prairie falcons (Marzluff et al. 1997a) found similar discrepancies in the placement of core areas within the home range, with regards to habitat associated with the Townsend's ground squirrel (*Spermophilus townsendii*), and suggests a connection with degree of habitat fragmentation, and availability of the preferred prey type. It is reasonable to assume therefore that, as in section 4.2, factors other than habitat preference or avoidance helped determine the selection of core areas within my study, as prey was abundant across a variety of habitat types.

When looking at factors that influenced the probability of being in the core area, the best-fit model on the coarse scale (habitat only) and the best-fit model on the fine scale (habitat and developmental stage taken into account) both included the fixed effects of distance to bog and distance to nest. On both scales the probability of being in the core foraging area increased with decreased distance to nest and decreased distance to bog, and these results were highly significant. Börger et al. (2006b) found no difference in their results when looking at habitat selection on both a fine and coarse scale. Therefore, my results indicate that, while developmental stage may play a role in home range size (section 4.2), it does not appear to do so in core area use. The importance of being near bog in the core area appears to correspond with the increased proportion of bog found within the core area, mentioned above. Kestrels are known to forage, in general, over open bog (Valkama et al. 1995). Løken (2009) found an increased use of bog by male kestrels, and Larsen (2012) likewise described a general preference for bog by the female kestrels in my study season. My results are in keeping with these findings, and highlight the importance of open habitat for female kestrels foraging specifically in the highly utilized core area.

The finding that the probability of being in the core area increased with decreased distance to nest is of importance. Mitchell and Powell (2004) suggest that the selection of habitat is not

solely dependent on habitat preference, but on the distance needed to reach suitable habitat patches from the center of the home range. Rosenberg and McKelvey (1999) noted that there is a danger for the nest site to create bias, when looking at the foraging patterns of a central-place forager. Both observations highlight the necessity of taking the nest site area into account. Research on prairie falcons has shown that they tend to forage near the nest site (Squires et al. 1993), and when prey was available close to the nest there was a decrease in the distance travelled when foraging (Marzluff et al. 1997a). Distance travelled from the nest can be linked to optimal foraging effort (Andersson 1978), and birds are likely to take prey near the nest, when prey is abundant (Andersson 1981). The mean distance in my study between the nest and the center of the core foraging area was 183 m, with a range of 25 - 445 m, from Flenvoll to Tøråsen. It is reasonable to assume that if the study had been conducted in a year with a poorer *Microtus* vole abundance, a larger distance between the nest and core foraging area would have been observed.

4.4 Nest centricity and distances

There was large individual variation between female kestrels for the maximum distance travelled from the nest in the pre-fledging period. The female on Storflendammen was located closest to the nest, at a maximum distance of 785 m, while the Flenvoll female was located the furthest away (5.08 km). The mean maximum distance was 1.73 km, which corresponded with the mean maximum distance Village (1983) found in male kestrels of 1.79 km, showing that foraging females are capable of travelling as far as males in the breeding season.

The nest centricity test indicated a difference in the extent to which females centered their 100% MCP home ranges on the nestbox, as the ratio ranged from 0.29 (more closely centered) to 1.00 (nestbox on the home range perimeter). Storfallet and Tøråsen had the nestbox located on the perimeter, whereas Storflendammen had the most centric nest. This difference could reflect the influence of occupied neighboring nests, as it would be reasonable to assume that the dense clustering of nests around Storflendammen could have led to a restriction of the female's movements in any one direction. Village (1990) found that male kestrels did not always center their breeding home ranges on the nest either, but often foraged in one particular direction, which led to the nest being located on the home range perimeter.

Interestingly, male kestrels with the closest neighbors experienced the least amount of centrality in his study. Likewise, research on female European sparrowhawks in the breeding season indicated a difference in nest centrality between individual females (Selås & Rafoss 1999), shown to have home ranges that were less centered on the nest than males.

4.5. Post-fledge

Home range sizes should only be calculated over biologically significant time intervals, and not when an animal is on the move between areas (Powell 2000). Taking this into account, it is not of interest to discuss the actual 100% MCP sizes of the post-fledge ranges for Storflendammen and Tøråsen, as it is natural that they would be larger than their pre-fledge counterparts (1.27 km² versus 0.89 km² for Storflendammen, and 3.63 km² versus 1.45 km² for Tøråsen). What is of interest is the shape and direction of the ranges, and the extent to which the nest site was included. At both localities, post-fledge tracking was terminated ten days after the last pre-fledge locations were taken, and the nest site was still included in the post-fledge ranges. In the case of Tøråsen, the centrality test revealed that the nest remained on the perimeter (pre-fledge and post-fledge ratios of 1.00), whereas the centrality test on Storflendammen indicated a shift in the range perimeter away from the nest (post-fledge ratio of 0.73, compared to the pre-fledge ratio of 0.29). Little is still known about the post-fledging movement patterns in kestrels, but females can return to the nest site in the early stages after fledging has occurred, with prey for the young fledglings (Village 1990; Bustamante 1994). I personally observed this to be the case at Tøråsen, where the female returned to the nest with a small rodent, followed by the fledglings.

It is known that certain raptor species continue to utilize the nest site for the delivery of prey in the early fledging period (Newton 1979). Prey delivery by females to the nest site has been documented in e.g. the closely related lesser kestrel (*Falco naumanni*) (Bustamante & Negro 1994) and European sparrowhawks, where prey availability influences the willingness of adults to continue provisioning (Eldegard et al. 2003). As prey was highly available in our study period, this may have led to the females choosing to continue to provision close to the nest site area in the early fledging period. In addition, it is known that in raptor species fledglings soon learn to disperse from the nest site, if the adults approach the nest consistently from the same direction (Newton 1979). In both Tøråsen and Storflendammen, the female

post-fledge ranges shifted westwards, elongating in the same direction as their pre-fledge ranges, which lends support to Newton's (1979) observation.

4.6. Limitations and thoughts for future research

Although general conclusions can be drawn from my study, it is important to recognize the limitations, and consider improvements for future studies. It can be difficult to draw general conclusions when studying a small number of individuals (Seaman et al. 1999), which is why my results should be interpreted with humility. When conducting field-intensive VHF radiotelemetry studies, a trade-off often occurs between time and resources utilized per tracked individual, versus tagging and tracking a larger number of individuals (Börger et al. 2006a). In general, efforts should be made towards the latter, as variation between individuals can be significant (Börger et al. 2006a, 2006b), and larger sample sizes lead to greater statistical power. Therefore, I would recommend a follow-up study with a larger sample size of female kestrels, coupled with the tagging and tracking of their mates.

In addition, although home range sizes appeared to level off in my study, and although a kestrel can cover its home range in a few days, I cannot completely discount the possibility that stratification of the data occurred, in particular with reference to Storfallet, which only saw two days of tracking. In a study conducted on a sandy flat in the Netherlands, individual kestrels were shown to consistently utilize the same spatial areas at the same time of day (Rijnsdorp et al. 1981), and so the possibility of time-tabling should be considered (Kenward 2001). Continuous sampling uncovers interesting temporal and spatial trends, but I would recommend future studies that utilize this method to use shorter bursts, to allow for data to be collected on more than one kestrel per day. Likewise, while several authors agree that the focus should shift away from autocorrelation, the same authors agree that a standard sampling interval should be set prior to tracking (e.g. De Solla et al. 1999). Utilizing a kernel method that accounts for both spatial and temporal autocorrelation, such as the "time kernel" (Katajisto & Moilanen 2006) would minimize this problem. However, programming adjustments need to be made to allow for its use with R software (Katajisto pers. comm.). My results indicated that five of the kestrels had a biological time to independence of under 5 minutes, and so a reasonable minimum sampling interval to employ in continuous sampling could be set at that.

With regards to nest site bias, my study took this into account when looking at foraging areas, by utilizing an exclusion zone of 100 m radius. However, it is possible that kestrels were still more easily located near nest site areas than further away from them, due to the varying terrains and locations of observers. If difficult terrain led to an undersampling of areas that were difficult to traverse, it is possible that core areas shifted, or that only one 50% isopleth was generated where multiple ones might have existed. Other foraging areas might have been more extensively utilized than analysis suggests, e.g. on Flenvoll where there was mountainous terrain and the female travelled large distances, or on Tøråsen and Storflendammen where the river impeded tracking. Future studies should take these limitations into account, when selecting nest locations, by recognizing the extent of home range that females are capable of utilizing.

It is known that the size and shape of different available forestry developmental stages is important to raptors (Niemi & Hanowski 1997, and references therein), and may have implications as far as management practices. However, the degree of fragmentation was not measured in my study, and thus could not be accounted for. In Norway, 90% of forest is privately owned and managed on a small landscape level (Gorini et al. 2011), and therefore modern day forestry management strategies may impact kestrels, in ways not yet considered. Likewise, the importance of edge habitat has been documented in kestrels (Larsen 2012), and a negative correlation between home range size and proportion of edge (border between closed and open habitat) has been found in species such as the hooded crow (*Corvus corone cornix*) in a mixed boreal forest and farmland landscape (Smedshaug et al. 2002). Therefore, some of the spatial trends seen, such as the importance of forestry developmental stage 4 and 5, may have been impacted by the degree of accompanying edge habitat. Future studies should seek to take this into account, on a landscape scale.

Very little research has been done as far as post-fledge behavior and area use in kestrels (but see e.g. Bustamante 1994), so this would be of interest to investigate in future studies. In particular, interactions between females and nestlings could be explored by continuous sampling, to more accurately determine behavior around fledging time, and in the immediate post-fledge period. Observations taken in the post-fledge period could be analyzed using first-passage time analysis (Fauchald & Tveraa 2003), to investigate the time required for females to leave an area of known radius, and hence give an indication of spatial and temporal dynamics once the nest site no longer plays a central role.

5. CONCLUSION

I found a large variation in home range size, maximum distance travelled from the nest, and nest centrality, for the six female kestrels. There was potential range overlap with neighboring breeding females, and home range shapes indicated a tendency to minimize this where possible. I found a positive correlation for home range size with the proportion of bog with forest, and the proportion of forest of developmental stage 3, and a negative correlation with the proportion of pooled developmental stage 4 and 5. Forestry fragmentation, and the size and shape of developmental stages, could have influenced home range size, but further studies should be conducted to verify this. I found a trend for a negative correlation between home range size and *Microtus* vole abundance, in keeping with other studies. Factors such as canopy density and ground vegetation height may have influenced prey availability, and hence impacted my results. The probability of being in the core foraging area increased with decreased distance to nest and decreased distance to bog, indicating the importance for the female kestrel of staying close to the nest and foraging in open habitat. I found no indication that distance to developmental stage influenced the probability of being in the core foraging area, suggesting that finer scale habitat categories may only influence home range size. Post-fledge tracking on two nests showed that the nest site is important in the early fledging period, in keeping with other studies of raptors. Future research should track a larger number of female kestrels in the breeding season, as well as their mates. Behavior and area use of both the female and fledglings should also be closely monitored, to shed more light on spatial and temporal dynamics during this critical stage.

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APPENDIX

Appendix 1. Variables measured on female kestrels and nestlings per location (n = 6).

Locality	Wing chord length of female (mm)	Age of female (years)	Brood size when tracking started	Brood age when tracking started (days)	Average brood age during tracking (days)
Bryn Nord	258	1	5	15	19.5
Storflendammen	263	2	6	16	22
Storfallet	242	1	5	12	17
Husfliden	256	2	5	13	23.5
Tøråsen	257	2	4	13	22
Flenvoll	248	1	4	14	21.5

Appendix 2a. Snap-trapping indices for small mammals, per location (n = 6).

Locality	<i>Microtus</i> vole*	Bank vole (<i>Myodes glareolus</i>)	Wood lemming (<i>Myopus schisticolor</i>)	Total microtine rodents
Bryn Nord	7.56	6.55	18.09	32.20
Storflendammen	7.30	11.46	45.18	63.94
Storfallet	3.17	5.35	39.25	47.77
Husfliden	27.81	2.63	12.71	43.15
Tøråsen	1.52	4.63	34.12	40.27
Flenvoll	3.01	16.71	9.07	28.79

*Field vole (*Microtus agrestis*), and tundra vole (*Microtus oeconomus*) pooled.

** This includes lemming (*Lemmus lemmus*), and grey-sided vole (*Myodes rufocanus*).

Appendix 2b. Average snap-trapping indices (\pm SE) for small mammals, per habitat type. The number of localities where observations were made per habitat type is indicated in parentheses.

Small mammal species	Clear-cut (5)	Forest (6)	Bog with forest (2)	Bog (4)
<i>Microtus</i> vole *	15.2 \pm 10.2	1.0 \pm 0.7	21.4 \pm 21.4	9.0 \pm 6.8
Bank vole (<i>Myodes glareolus</i>)	7.6 \pm 6.1	15.2 \pm 5.1	0.0 \pm 0.0	13.2 \pm 9.1
Wood lemming (<i>Myopus schisticolor</i>)	25.9 \pm 7.5	32.1 \pm 7.6	33.3 \pm 6.7	19.8 \pm 9.1
Total microtine rodents **	52.6 \pm 4.6	57.7 \pm 15.0	61.7 \pm 21.7	49.5 \pm 19.8

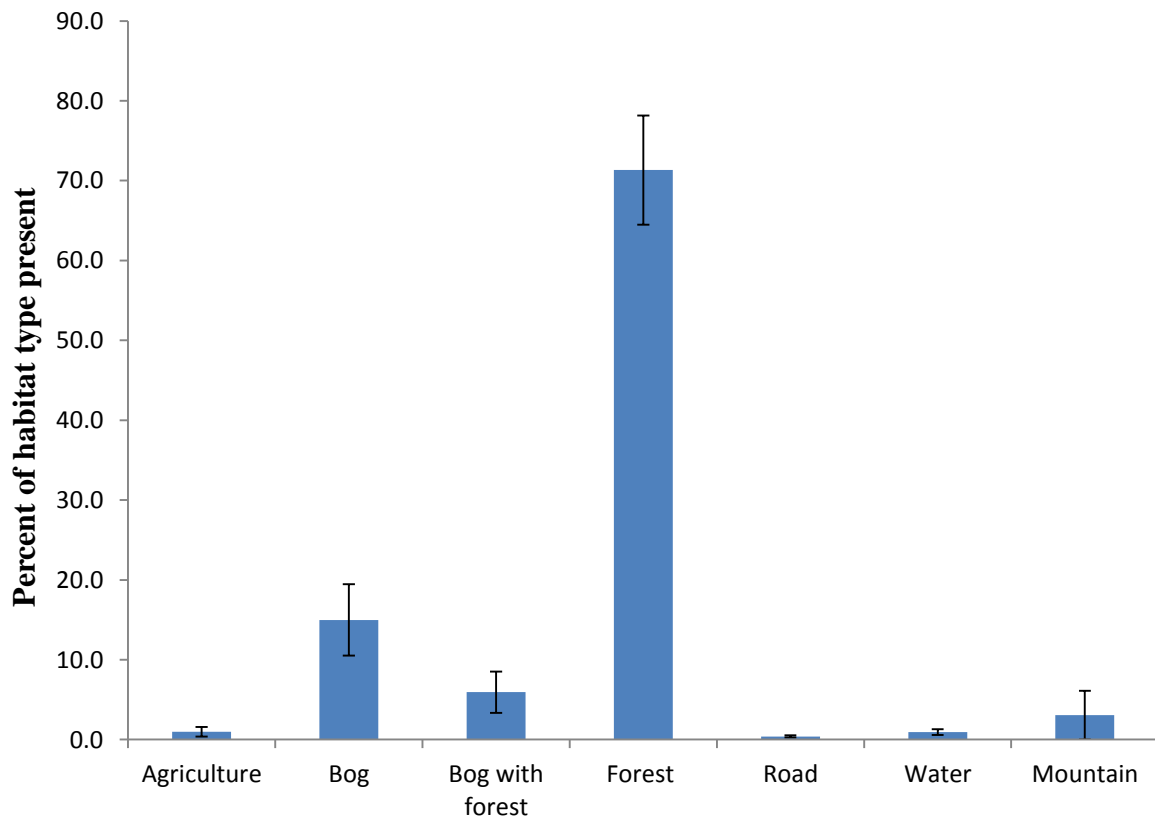
* Field vole (*Microtus agrestis*), and tundra vole (*Microtus oeconomus*) pooled.

** This includes lemming (*Lemmus lemmus*), and grey-sided vole (*Myodes rufocanus*).

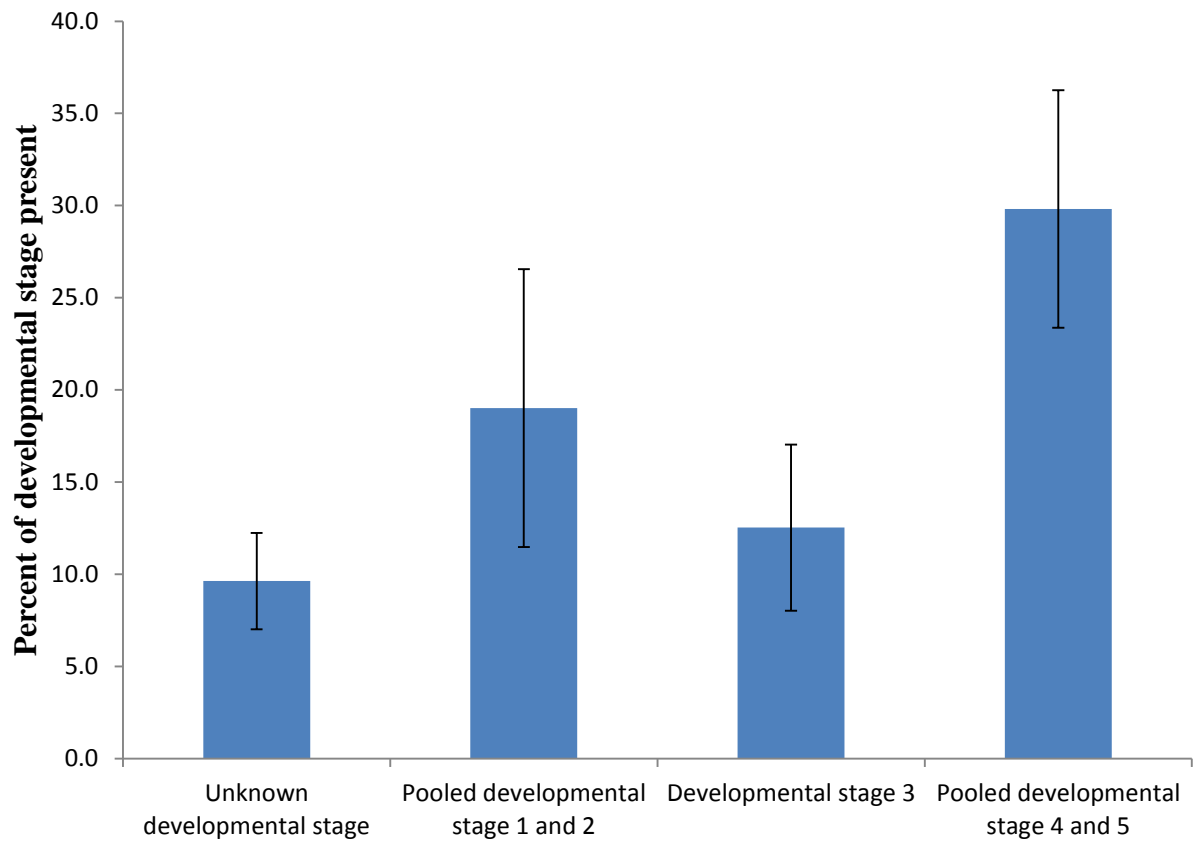
Appendix 3. Habitat types derived from the AR5 classification system.

Land type attribute	Land type code	Tree type attribute	Tree type code	Habitat type
Fully cultivated land	21	na	na	Agriculture
Surface cultivated land	22	na	na	
Pasture	23	na	na	
Peat bog	60	Unforested	39	Bog
	60	Coniferous	31	Bog with forest
	60	Deciduous	32	
	60	Mixed	33	
Forest	30	Coniferous	31	Coniferous forest
	30	Deciduous	32	Deciduous forest
	30	Mixed	33	Mixed forest
Water	80	na	na	Water
Transport network area	12	na	na	Road
Open land	50	Unforested	39	Unforested open land
Built-up area	11	na	na	Built-up area
Unmapped	99	na	na	Unmapped area

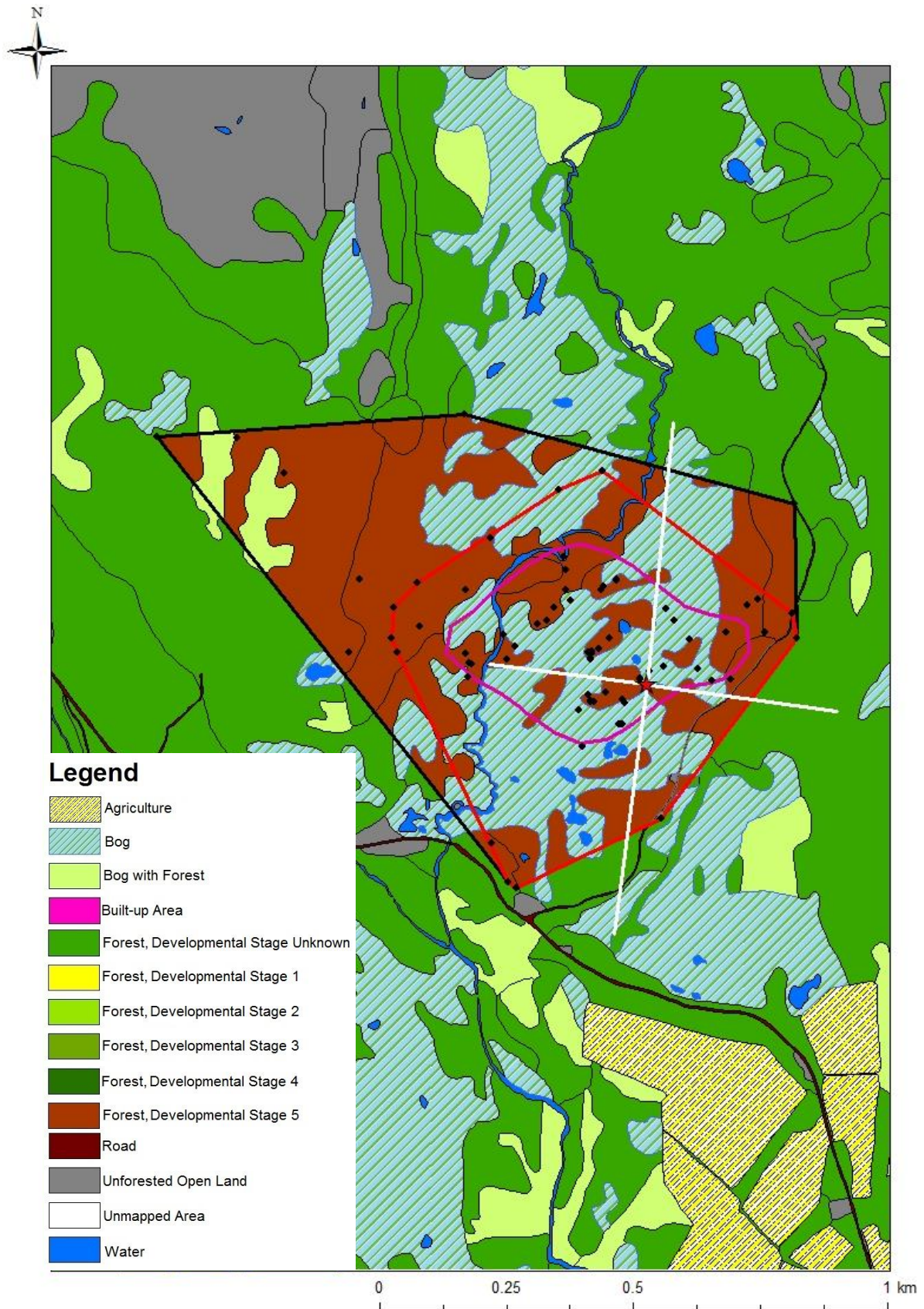
Appendix 4. Habitat type present, as mean \pm SE percent, across all localities (n = 6).



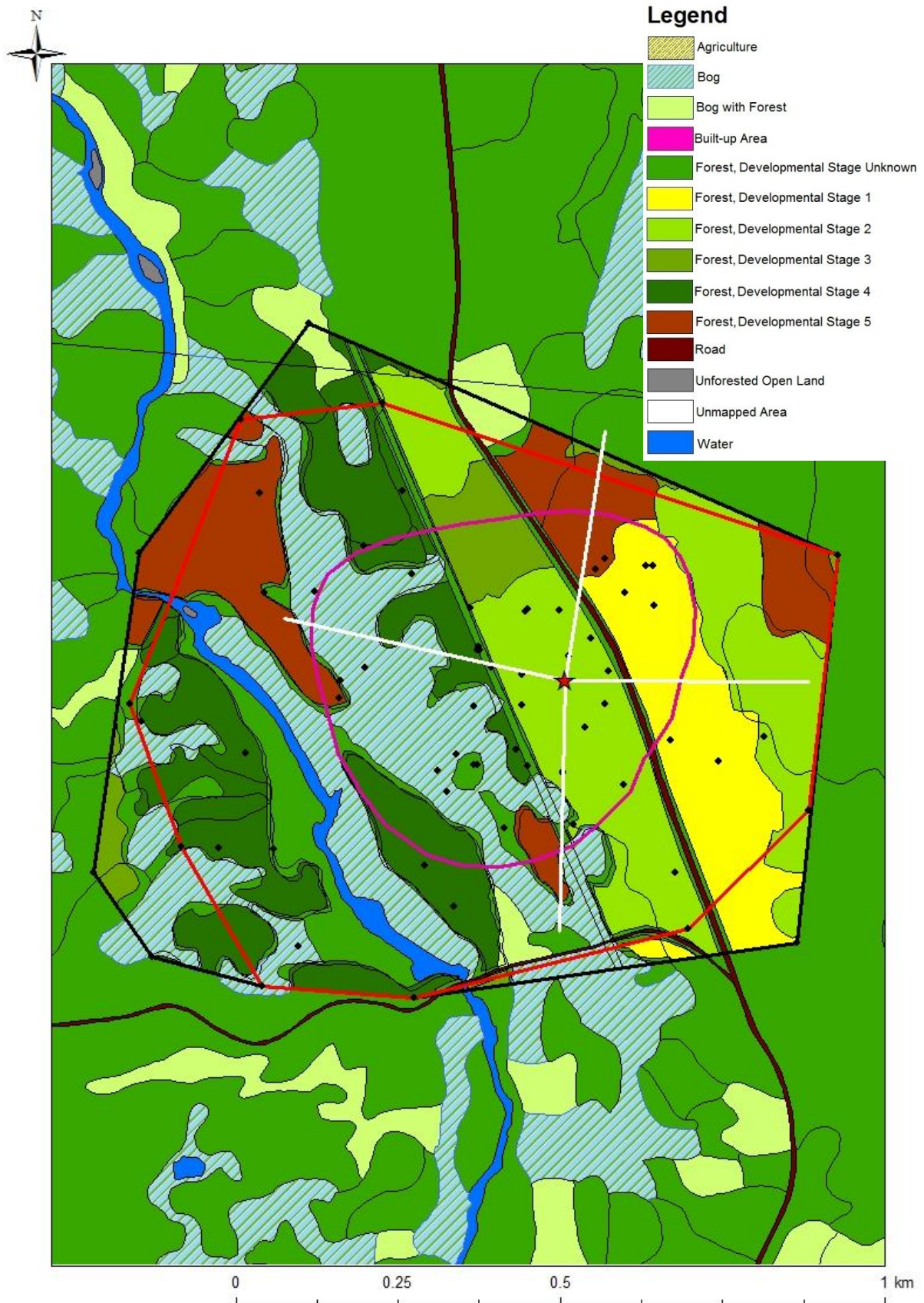
Appendix 5. Forest developmental stage present, as mean \pm SE percent, across all localities (n = 6).



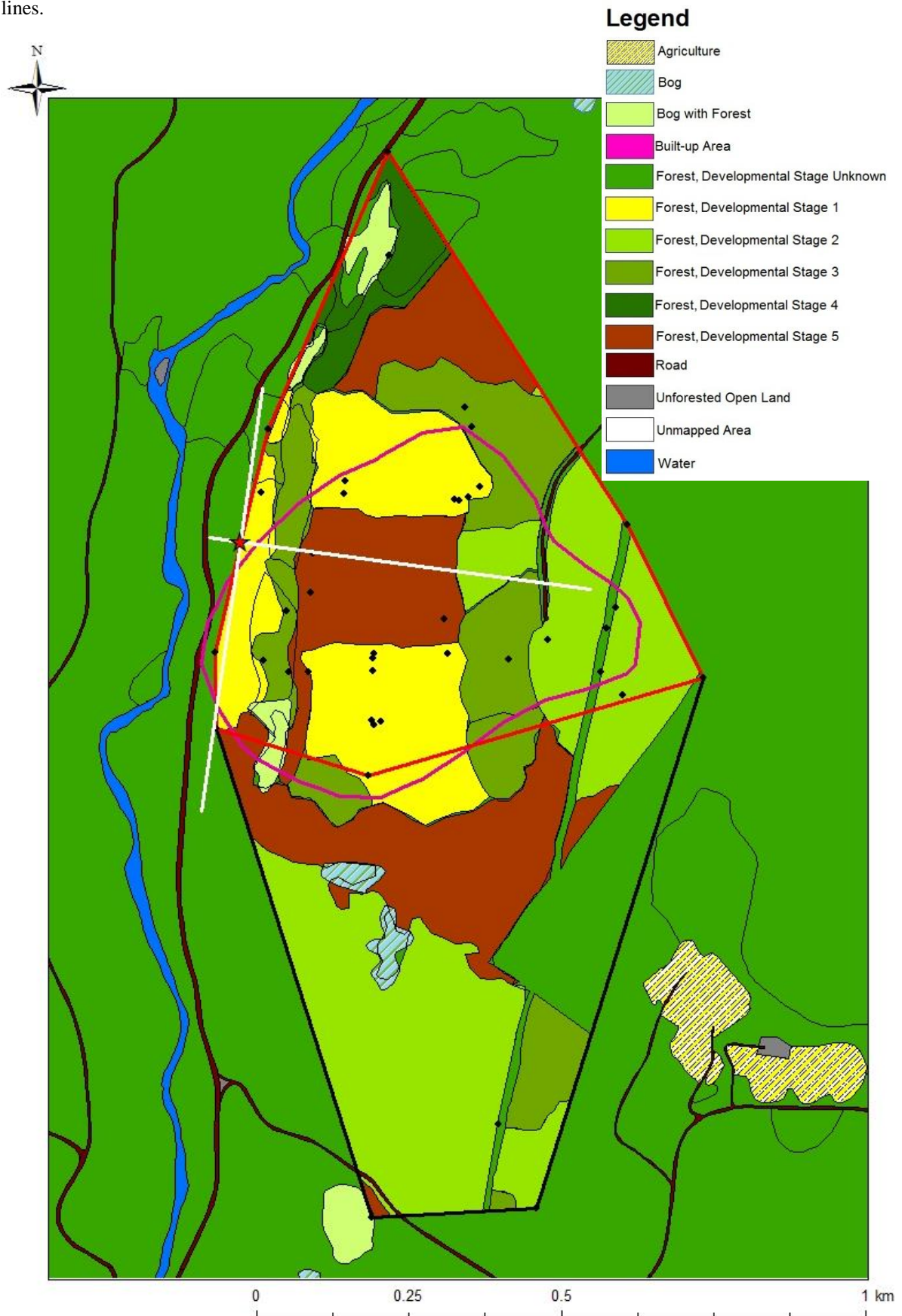
Appendix 6a. Bryn Nord 100% MCP (black outline) and 95% MCP (red outline) home ranges, overlaid on habitat and developmental stage map. The pink outline denotes the core foraging area, the 50% kernel. The red star is the position of the nest. The black dots represent the locations taken (n = 125). The white lines indicate the trap lines.



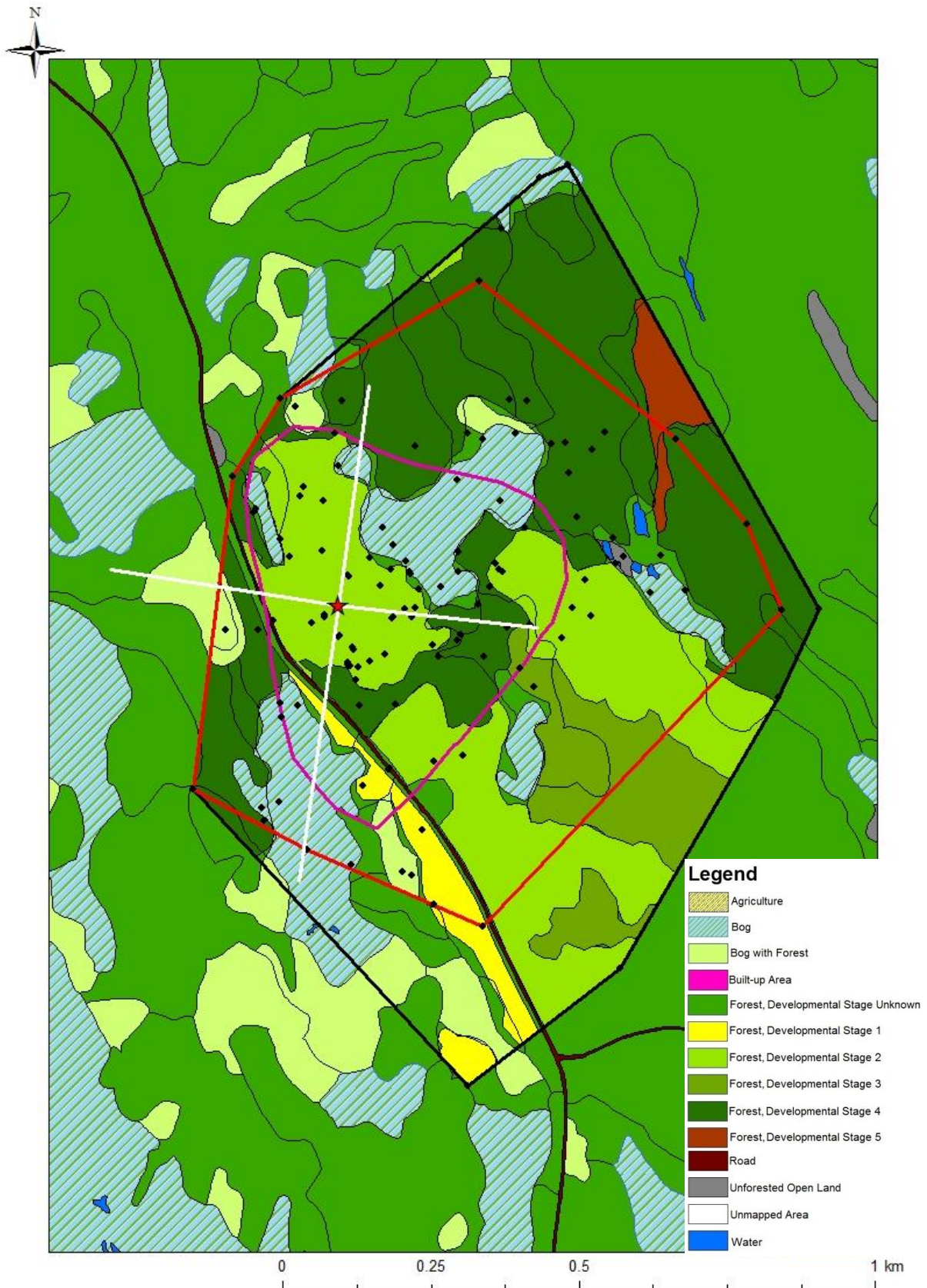
Appendix 6b. Storflendammen 100% MCP (black outline) and 95% MCP (red outline) home ranges, overlaid on habitat and developmental stage map. The pink outline denotes the core foraging area, the 50% kernel. The red star is the position of the nest. The black dots represent the locations taken ($n = 87$). The white lines indicate the trap lines.



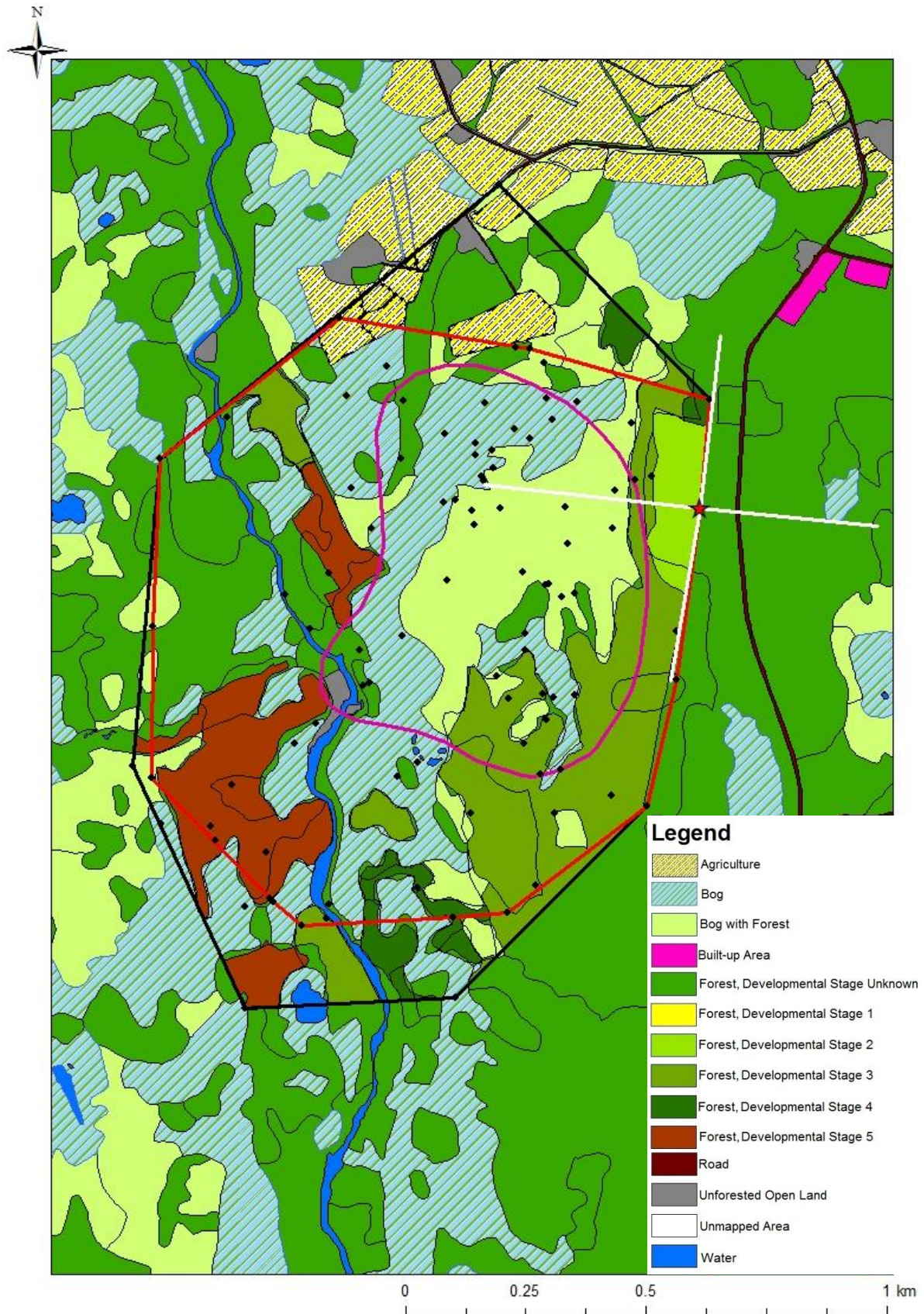
Appendix 6c. Storfallet 100% MCP (black outline) and 95% MCP (red outline) home ranges, overlaid on habitat and developmental stage map. The pink outline denotes the core foraging area, the 50% kernel. The red star is the position of the nest. The black dots represent the locations taken (n = 49). The white lines indicate the trap lines.



Appendix 6d. Husfliden 100% MCP (black outline) and 95% MCP (red outline) home ranges, overlaid on habitat and developmental stage map. The pink outline denotes the core foraging area, the 50% kernel. The red star is the position of the nest. The black dots represent the locations taken (n = 141). The white lines indicate the trap lines.



Appendix 6e. Tøråsen 100% MCP (black outline) and 95% MCP (red outline) home ranges, overlaid on habitat and developmental stage map. The pink outline denotes the core foraging area, the 50% kernel. The red star is the position of the nest. The black dots represent the locations taken (n = 102). The white lines indicate the trap lines.



Appendix 6f. Flenvoll 100% MCP (black outline) and 95% MCP (red outline) home ranges, overlaid on habitat and developmental stage map. The pink outline denotes the core foraging area, the 50% kernel. The red star is the position of the nest. The black dots represent the locations taken (n = 85). The white lines indicate the trap lines.

