

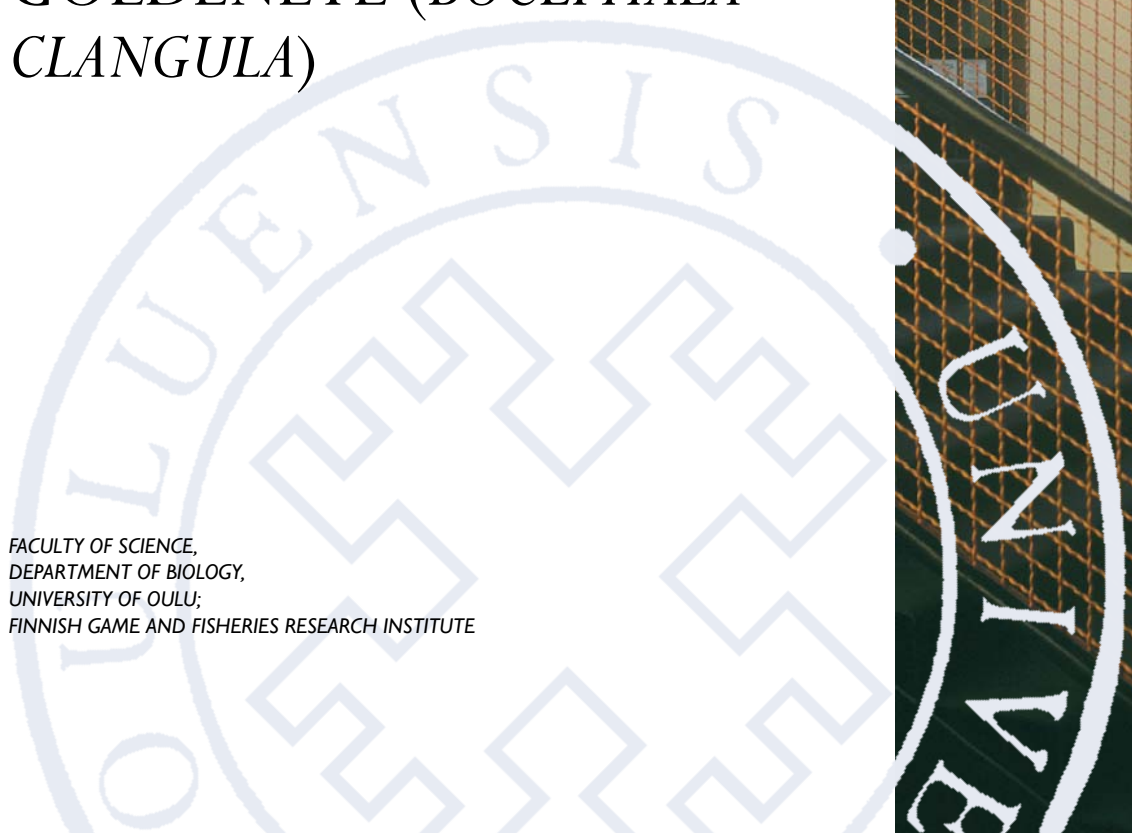
*Antti Paasivaara*

SPACE USE, HABITAT  
SELECTION AND  
REPRODUCTIVE OUTPUT  
OF BREEDING COMMON  
GOLDENEYE (*BUCEPHALA  
CLANGULA*)

FACULTY OF SCIENCE,  
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*ANTTI PAASIVAARA*

**SPACE USE, HABITAT SELECTION  
AND REPRODUCTIVE OUTPUT OF  
BREEDING COMMON GOLDENEYE  
(*BUCEPHALA CLANGULA*)**

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**Paasivaara, Antti, Space use, habitat selection and reproductive output of breeding common goldeneye (*Bucephala clangula*)**

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***Abstract***

Habitat selection is a crucial process affecting space use and reproductive success of birds. In this thesis, I investigated spatial and behavioural aspects of nest spacing, brood stage space use, habitat selection and factors affecting reproductive success of breeding common goldeneye (*Bucephala clangula*) using two large and long-term observational data sets from individually marked females.

In the nesting stage, I found that spatial nesting pattern of goldeneye females changed from one year to the next and also between spatial scales. However, increasing aggregation of nesting females decreased nesting success due to increasing rate of nest desertion and nest predation especially at small spatial scale. These results provide evidence of a density-dependent population process in the common goldeneye in terms of association between annual spatial dispersion of nesting females and annual nesting success.

In the brood stage, the most important factor affecting habitat selection was the amount of food. However, safe nest sites and food requirements of ducklings were not usually met in the same patch and females with broods adjusted their space-use tactics according to these critical breeding resources. Spatial divergence of these two obligatory resources induced brood movements at various distances shortly after hatching. During movements, broods used different landscape elements such as patches, corridors and matrix in a flexible way without clear fitness consequences in terms of duckling survival.

Goldeneye broods suffered heavy losses especially during the early brood stage. Increasing predation risk by northern pike (*Esox lucius*) decreased survival of young ducklings, but frequent total brood losses suggest that also other factors affected duckling survival. Environmental factors such as temperature or rain were not related to the survival of ducklings.

*Keywords:* duckling survival, habitat selection of broods, space use



*To my loving family*





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Oulu January 2008

Antti Paasivaara

## List of original papers

This thesis is based on the following papers, which will be referred to in the text by their Roman numerals:

- I Paasivaara A, Pöysä H, Pesonen M & Runko P (2007) Dynamics of spatial nesting dispersion and its consequences to nesting success in the common goldeneye (*Bucephala clangula*). Manuscript.
- II Paasivaara A & Pöysä H (2004) Mortality of common goldeneye (*Bucephala clangula*) in relation to predation risk by northern pike (*Esox lucius*). *Annales Zoologici Fennici* 41: 513-523.
- III Pöysä H & Paasivaara A (2006) Movements and mortality of common goldeneye *Bucephala clangula* broods in a patchy environment. *Oikos* 115: 33-42.
- IV Paasivaara A & Pöysä H (2007) Habitat patch occupancy in the common goldeneye (*Bucephala clangula*) at different stages of the breeding cycle: implications to ecological processes in a patchy environment. Manuscript.
- V Paasivaara A & Pöysä H (2006) Survival of common goldeneye (*Bucephala clangula*) ducklings in relation to weather, timing of breeding, brood size, and female condition. *Journal of Avian Biology* 38: 144-152.



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# 1 Introduction

## 1.1 Individuals and populations in a patchy environment

Basically, all biological processes, organisms and interactions are spread out in space, occurring in specific locations and temporal sequence. Therefore, spatial processes are also associated with population dynamics and species abundance and diversity. The spatial approach is particularly well embedded and conceptualised in landscape ecology (see e.g. Forman & Godron 1986, Turner 1989), coupled with metapopulation theory (e.g. Hanski & Gilpin 1997, Hanski 1999), integrating a relatively new and large branch into the rather broad field of ‘spatial ecology’ (Tillman & Kareiva 1997). Also other areas of ecological theory, such as classic optimal foraging theory (e.g. Charnov 1967) and behavioural ecology in general (e.g. Kacelnic & Cuthill 1987, Krebs & Houston 1989), but particularly the theory of habitat selection (e.g. Morris 1995, Sutherland 1996) have taken environmental complexity into account (see also Lima & Zollner 1996), although not always in a spatially explicit way (Rhodes *et al.* 2005). Indeed, it is important to expand this ‘spatial approach in ecology and population biology’ to unify behavioural and population context in ecological research (Hanski 1999).

The central premise of ‘spatial ecology’ has been the idea that all structures of the environment as well as populations of different species exhibit spatial variation in addition to temporal variation. Spatial ecology takes into account that most species of animals live in a heterogeneous or patchy environment consisting of a mosaic of habitats (e.g. Addicot *et al.* 1987, Wiens 1976, 1995, Kotliar & Wiens 1990). More simply, the environment can be thought of as a network of habitable and uninhabitable patches in which conditions are suitable or unsuitable for individuals or populations of a particular species (Dunning *et al.* 1992). Current definitions of habitat are mostly allied to the concept of patch and matrix (Forman & Godron 1986, but see Wiens 1995). Wiens (1976) defined patches as “*a surface area differing from its surroundings in nature and appearance*”. Patches come in various shapes and sizes differing in their biotic and abiotic characteristics, but also in their origin (Kotliar & Wiens 1990). In this system, configuration, i.e. spatial arrangement of patches, varies in space and time.

However, one should identify the spatiotemporal scales of different ecological processes in a patchy environment. Patches and patchiness should be

defined relative to the processes that are in the focus of interest. In recent ecological research, an enormous amount of literature has focused on large-scale, i.e. landscape- and regional-level processes such as dispersal between sub-populations (i.e. metapopulation level; Johnson & Gaines 1990, Hanski 1999, 2001) or inter-patch movement (i.e. the concept of patchy population; *sensu* Harrison 1991, see also review in Bowne & Bowers 2004), where populations are spatially structured to more or less discrete subpopulations. Moreover, recent theoretical studies have focused on these ‘metapopulation-level’ consequences when habitat patches vary in size and spatial location (see review by Hanski 1997), or consequences of spatial variation in the quality of habitat patches occupied by local populations (Pulliam 1988, 1996).

Patchiness of habitats may also have important population-level consequences by affecting the performance of individuals at smaller spatial and temporal scales than those traditionally associated with large-scale spatial processes described above (e.g. Wiens 1995, Andeassen *et al.* 1998). For example, different essential resources of individuals such as food, roosting sites and nest sites may situate in different locations in relation to another. Therefore, individuals of the species may face a patchy and dynamic pattern of different resources (e.g. Johst *et al.* 2001), and the persistence of species depends primarily on the ability of individuals to acquire space, i.e. to track, move, select and exploit their key life-cycle related needs in relation to distribution of resources and habitats of different qualities and quantities (Turner & Gardner 1991, Fahrig *et al.* 1995, Rhodes *et al.* 1996, With *et al.* 1997). Consequently, the space use pattern of individuals and the abundance and dynamics of species reflect primarily the spatial and temporal distribution of essential habitats and resources (Wiens 1976, Turner & Gardner 1991, Silver *et al.* 2000).

At the scale of the individual, interactions between individuals may inherently affect the spacing of animals, often in a scale-dependent manner (Levin 1992). Behavioural interactions such as competition, conspecific or heterospecific attraction, shared foraging activities or shared habitat selection decisions may create a non-random spatial pattern of distribution of individuals (e.g. Hansson *et al.* 1995, Begon *et al.* 2003). In conclusion, various distributional patterns of organisms are the outcome of interactions between resources, complex behavioural and demographical processes and various intra- and interspecific interactions. The acquisition of individual-level empirical information on spatial interactions among individuals and their environment is particularly challenging in highly mobile animals such as birds. Indeed, to understand essential



population-level phenomena of a particular species we must know how individuals use and explore space, and most importantly, how individuals survive and reproduce in the environment where essential resources and habitats are patchily distributed (Sutherland 1996).

## **1.2 Habitat selection in a patchy environment**

While tracking habitats and resources, individuals have to make numerous decisions regarding food acquisition, roosting, predator avoidance and reproduction-related activities such as mates and nest sites in various environmental circumstances (see e.g. Sutherland 1996). Therefore, the prominent concept when studying interactions between a complex environment and the behaviour of individuals is the study of habitat selection.

Habitat selection is a behavioural process whereby individuals preferentially use a non-random set of available habitats (e.g. Morris 1992b, 2003). Habitat can be defined many ways (see above), but the basic approach should match the species, population and state of interest (Morris 2003). The concept of habitat selection is particularly important in ecological science because it unifies the environment, space use patterns of individuals, population-level processes and evolution, and has a profound influence on the distribution, abundance, survival, reproductive output and population dynamics of many animal species (e.g. Rosenzweig 1987a, 1987b, 1991, Sutherland 1996).

Basically, habitat selection is a hierarchical decision-making process of choices differing in terms of habitat quality (Johnson 1980, Morris 1987a, Pulliam 1996). Habitat quality can be characterised by conditions appropriate for survival and reproduction, but also via costs and benefits of acquiring space (Fretwell & Lucas 1969, Jones 2001, Stamps 2001, Morris 2003). Indeed, the economic framework of optimality in the evolutionary process of behaviour should always be kept in mind (Krebs & Davis 1997), because all life history traits of an organism, including behaviour such as habitat selection, involve the idea of balance (trade-off) between costs and benefits, currencies and constraints (see also Stearns 1992). The evolutionary context of habitat selection behaviour is particularly important because it is the primary way in which mobile animals adapt to changing conditions. Therefore, studies of habitat selection should take into account the fitness costs and consequences of different habitat selection decisions (Jones 2001), which are often difficult to study in natural settings.

Individual organisms encounter their spatially complex environment at various spatial scales (e.g. Ims 1995, Wiens 1976, 1989a). In the context of patchily distributed resources, individuals may not respond to patchiness of the environment at a small spatial scale (fine-grained environment), but at larger spatial scales animals may show preference towards certain type of patches (coarse-grained environment) (MacArthur & Pianka 1966, Wiens 1976). Because the distribution of habitat patches (e.g. resources) varies in space and time, the habitat selection process operates at different spatial and temporal scales (Johnson 1980, Morris 1987a, 1987b, 1992b, Orians & Wittenberger 1991). Morris (1992b) defined two spatial scales that are likely to influence patterns of individuals' habitat selection in heterogeneous landscapes. Within animals' home range, habitat selection is determined, for example, by the differential use of resources, but at larger spatial scales, habitat selection is an integral part of dispersal and the ability to relocate the home range (Morris 1992b, Stamps 2001). Resource-exploitation-related (e.g. foraging) decisions influencing patch choice within an animal's home range can be viewed as habitat selection at one end of the scaling spectrum (Orians 1991).

In the habitat selection process individuals are thought to gather information prior to making a choice in order to assess the environment. In this process, individuals use indirect or direct cues as the basis of selection (Hildén 1965, Cody 1985). These cues should correlate with habitat quality and fitness parameters, i.e. survival and reproduction (Williams & Nichols 1984). However, in certain circumstances these cues may not always predict correctly the expected survival or reproductive output, and animals may make a poor choice as a result of some mismatch between the cues they use in selecting habitats (e.g. Battin 2004). This phenomenon may occur especially if the environment changes suddenly, as in the case of anthropogenic habitat change (Schlaepfer *et al.* 2004). It may also be that poor choices are the result of constraints (e.g. Mysterud & Ims 1998 and references therein)

The classic ideal free distribution theory assumes that individuals are free to select habitats without explicitly considering involved costs (Fretwell & Lucas 1970). However, this assumption lacks realism because there are always costs and constraints (e.g. functional or environmental constraints) associated with selecting a habitat, due, for example, to movement from one location to another (Morris 1987a). In addition, several vital factors that are not necessarily associated with habitat *per se* may also affect the habitat selection process, including predation (e.g. Lima & Dill 1990, Brown 1992, Moody *et. al.* 1996), intra- or inter-specific

competition (Rosenzweig 1981), conspecific (e.g. Stamps 1988, 2001,) or heterospecific attraction (Forsman *et al.* 1998, Mönkkönen *et al.* 1999, Thompson *et al.* 2003) and food limitation (Martin 1993, McColling 1998, Sjöberg *et al.* 2000, Gunnarsson *et al.* 2004). In addition, free choice of habitats may be limited by behavioural traits such as imprinting, natal philopatry and site fidelity. In conclusion, individuals may experience numerous trade-off situations and constraints, potentially affecting the habitat selection decision (see e.g. Mysterud & Ims 1998 and references therein).

Extensive empirical effort has been devoted to understanding the habitat distribution, abundance and population dynamics of breeding migratory birds, which are extremely mobile and must deal with a wide range of different types of habitats (e.g. Cody 1985). However, these population-level phenomena are the result of habitat-selection decisions and the reproductive success of individuals (Sutherland 1996). To understand population-level processes, one must know how individuals behave, survive and reproduce. The habitat selection process is particularly complex in the breeding season when the selection process is compounded by multiple requirements such as nests sites and food for the young. Arriving individuals must often make habitat-selection decisions very quickly and on the basis of incomplete information. Because critical resources vary in space and time, a suitable breeding environment must contain a mixture of habitat patches or resources that provide opportunities for all of the activities required for successful reproduction. Therefore, I concentrated on basic spatial, ecological and behavioural processes such as space use, movement, habitat selection during breeding season and the consequences of movement and habitat selection decisions, as well as other important characteristics of the reproductive success of common goldeneye (*Bucephala clangula*) females, a migratory waterfowl species which typically uses and exploits patchily distributed habitats such as lakes, ponds etc.

### **1.3 Breeding grounds of ducks in boreal environments**

Scandinavia, particularly Finland, is an important breeding area for European migratory waterfowl species (family *Anatidae*). During the breeding season habitat selection is one of the most important processes affecting production, population size and dynamics of animals and of small duck species in particular. Most of the studies relating to habitat selection and reproductive success of ducks have been done in the prairies of North America where water conditions vary

considerably from year to year and within a year (e.g. Rotella & Ratti 1992). The prairies constitute an extremely variable breeding environment that differs greatly from North European breeding grounds. In Scandinavia, breeding grounds are more stable as waterfowl habitats (Nummi & Pöysä 1993), and knowledge from prairie pothole regions cannot be explicitly adapted. In general, there is an enormous amount of wetlands in Scandinavia and especially in Finland, but most of them are inferior as duck habitats due to low productivity (Sjöberg *et al.* 2000). Typically, the breeding landscape of ducks consists of patches in varying configurations surrounded by an inhospitable matrix. In addition, ditches and rivers may function as corridors between patches.

Although many important studies of breeding biology, breeding habitat selection and reproductive success of northern European duck species have been conducted in recent decades (e.g. Nummi & Pöysä 1993, 1995, Elmberg *et al.* 2004, Gunnarsson *et al.* 2006), unfortunately, we still lack detailed empirical knowledge of space use pattern, habitat selection and reproductive success of breeding ducks in naturally patchy and stable boreal environments, which is the basic information needed for management and conservation planning.

## **1.4 Study species**

The common goldeneye (*Bucephla clangula*) is one of the most abundant duck species in Scandinavia, and about 60% of the northern European population breeds in Finland (Dennis & Pöysä 1998). The species is particularly suitable for studying breeding biology and reproductive success for the following reasons. First, as a secondary hole-nesting species, it readily uses nest boxes for nesting, but in natural conditions goldeneyes breed in old nests of the black woodpecker (*Dryocopus martius*). Secondly, goldeneye is a long-lived, iteroparous and precocial duck with uniparental female care and self-feeding young, which are common life-history characteristics among ducks. Finally, goldeneye is one of the most intensively studied duck species in northern Europe (see e.g. references in Pöysä & Pöysä 2002).

### **1.4.1 Nest spacing pattern of common goldeneye females**

Like all waterfowl species, goldeneyes are highly dependent on aquatic habitats, which can be defined as clear-cut habitat patches (referred to as patches) surrounded by matrix (all terrestrial habitat surrounding the lakes, referred to as

matrix). In the breeding season, matrix is needed for nesting. Nesting requirements of goldeneye females are suitable cavities or nest boxes and patches of high food abundance to meet the energy requirements of egg production. Goldeneye pairs are not particularly choosy in the selection of nesting wetlands (e.g. Danell & Sjöberg 1978, Eriksson 1983), but females are more selective when they choose nest sites (nest site prospecting behaviour; see Eadie & Gauthier 1985). No clear environmental factor has been found to explain nest site preference of females, but successful nesting by the same or other females in the preceding year affects nest site use (Dow & Fredga 1985).

Nest predation is a primary factor affecting reproductive failure in birds (Ricklefs 1969, Martin 1995, Newton 1998), including ducks (Cowardin *et al.* 1985, Owen & Black 1990, Greenwood *et al.* 1995). Therefore, numerous anti-predation tactics have evolved in birds to reduce the risk of nest predation (Lack 1968, Wiens 1989b). The nest predation rate can be very high, such as 77% (Pöysä *et al.* 1997a), and it is the major reason for nest failures of goldeneyes (Pöysä 1999a). Obviously, nest predation shapes the life histories of goldeneyes by influencing females' dispersal patterns and nest site preferences (Dow & Fredga 1983, 1985, Ruusila *et al.* 2001), and finally, the spatial and temporal distribution of nesting females (Dow & Fredga 1985, Pöysä 1999a). However, there is no spatially explicit information on how females are distributed in a local nesting population, and less is known about how dispersion of nesting females may change from season to season and what consequences changing dispersion may have (see Semel *et al.* 1988 and Pöysä & Pöysä 2002).

#### **1.4.2 Habitat requirements and survival of common goldeneye broods**

Recent studies have found that food abundance is an important factor in space use and habitat selection of common goldeneye broods (Eriksson 1978, 1979, Eadie & Keast 1982, Nummi & Pöysä 1993, Pöysä & Virtanen 1994, Wayland & McNicol 1994), but habitat patch (lake) structure, indicating cover from predators and productivity of the patch, may also influence the space use pattern and habitat selection of broods (Nummi & Pöysä 1993, 1995). Sjöberg *et al.* (2000) showed that many boreal lakes are sub-optimal duckling habitats. Therefore, resource shortage may initiate between-lake movements if the current lake does not fulfil the food requirements of a brood (Sirén 1952, Eriksson 1978, Eadie & Keast 1982, Pöysä & Virtanen 1994, Wayland & McNicol 1994). However, the consequences

of space use pattern, habitat selection and movements on survival of broods are contradicting (e.g. Rotella & Ratti 1992 vs. Dzus & Clark 1997). In addition to habitat patch characteristics, the spatial arrangement of wetlands and existence of corridors (ditches and rivers) may also have an influence on space use pattern, habitat selection and survival of goldeneye broods. However, detailed information and fitness consequences on spatial interaction between characteristics of breeding environment are lacking.

Survival of the young has an important impact on production and may have a substantial contribution to population dynamics, but it is still one of the least understood components of avian demography. Earlier studies have found much variation in the survival of common goldeneye broods (Pöysä 1992, Pöysä & Virtanen 1994, Wayland & McNicol 1994, Pöysä *et al.* 1997b, Milonoff *et al.* 1995, 1998, Blums *et al.* 2002), but in general, any environmental, habitat, non-habitat or maternal related factors explaining brood survival in their natural environment have proved difficult to identify (but see e.g. Pietz *et al.* 2003). The high rates of duckling mortality reported in earlier studies underscore the need to identify and evaluate the sources of mortality during brood-stage habitat selection (e.g., Rotella & Ratti 1992, Pöysä & Virtanen 1994, Dzus & Clark 1997).

## **1.5 The outline of this thesis**

The aim of this thesis was to provide empirical information on patterns and processes of space use, habitat selection, spatial interactions and movement related to the reproductive output of the breeding common goldeneye. Both nesting stage and brooding stage were included and combined. Individual-based explorative research in spatial ecology of European duck species has rarely been conducted. Therefore, I concentrated on spatial and behavioural aspects in nest spacing, brood stage space use, habitat selection and factors affecting reproductive success of breeding common goldeneye females using two large and long-term observational data sets from individually marked females. Habitat selection can be described at different spatial scales (Morris 1987b, Orians & Wittenberger 1991). I focused on local spatial scales, that is, space use pattern, nest site selection and habitat patch selection within home ranges of breeding goldeneyes.

First, I paid attention to spatial distributions of females, i.e. the pattern of spatial distribution of nesting females and between-year changes in it, which are manifested due to dispersal and other spacing behaviours of nesting females. In

this study, I also investigated between-year variation of spatial nesting dispersion in relation to hatching success. The consequences of the spatial pattern of nests may give an important insight into interactions of nesting individuals as well as to population-level processes in cavity-nesting birds. After that, I concentrated on space use, habitat selection and movements of females with their broods in relation to spatial characteristics of the environment at two important spatial scales. Both patch and landscape characteristics are included. Furthermore, to determine if the observed habitat use tactics of females were adaptive, I studied fitness consequences of females' decisions in terms of survival of ducklings, especially at early brood stage. Thirdly, I studied the association between spatial distributions of resources and individuals at different stages of the breeding season providing an attempt to combine space use, habitat selection, movements and distribution of individuals at different stages of the life cycle of a given species among patches at the level of landscape (Lima & Zollner 1996). Finally, I explored associations between central environmental and maternal components and reproductive success in terms of survival of young ducklings.

Specifically, in the nesting stage, I studied spatial dispersion of nesting attempts and between-year dynamics of nesting dispersion in the breeding population of common goldeneyes and the consequences of the observed spatial pattern to nesting success using extensive and long-term ringing-recapture data (Paper I). Compared to many ground-nesting species, only few empirical studies on the spatial pattern of nests have been conducted in cavity-nesting species (e.g. Järvinen 1992, Wilkin *et al.* 2006). The main objective of this thesis was to produce information to nest-box provisioning programmes, which have been used widely in conservation and management of endangered hole-nesting species or game species like the wood duck *Aix sponsa* (Semel & Sherman 1993, Roy Nielsen *et al.* 2006). The principal study questions in the nesting phase were:

1. How were nesting females dispersed among available nest sites, i.e. were they aggregated, randomly or evenly spaced? A wide range of spatial scales, were included in the analyses (Paper I).
2. How did the distribution of nesting females change in space and time, i.e. how did the spatial arrangement of nesting individuals in a local breeding population change over the years (Paper I)?

3. Was the dispersion of nesting females related to overall population density or different components of nesting success including the rate of nest desertion and nest predation (Paper I)?

In the second stage I studied habitat selection, space use, movements and survival of the radio-tagged, females with broods in patchy boreal environments (Papers II, III, IV and V). The main objective was to produce information for management and conservation purposes. The central questions in the brood rearing phase were:

1. How did the females and their brood use patches and move within their environment, i.e. what was the prevailing habitat use and movement pattern of the goldeneye at brood stage in a naturally patchy environment (II, III and V)?
2. What were the habitat-related factors affecting the habitat selection decisions of the females with their brood? Here, I included the characteristics of patches (vegetation structure and food abundance) (Paper II), configuration and connectivity of habitat patches (patch density, patch isolation and usability of corridors, Paper III).
3. What were the survival consequences of habitat selection pattern and movements of broods (II, III)? Here, I included the predation risk of the patch, specifically, the predation risk by the northern pike (*Esox lucius*) (II), patch configuration and corridors (Paper III).
4. How were the different life-history-related resources (nesting and brood rearing patches) distributed in the landscape, and were these resources correlated at the patch level? And consequently, what kind of landscape level processes may affect breeding populations of goldeneyes in a naturally patchy environment (IV)?
5. What environmental factors (other than habitat-related factors) and maternal attributes were related to the survival of ducklings? Here, I included weather (rain and temperature), condition of the female, brood size and hatching date in the analysis (V).



## 2 Material and Methods

### 2.1 Dynamics of nesting dispersion and its consequences to nesting success (I)

#### 2.1.1 Study area and breeding population

The dynamics of spatial nesting dispersion and its consequences to nesting success of females were studied using long-term and spatially extensive ringing-recapture data from Maaninka, Central Finland, during 1984 – 2006. The study area is located in the northern part of the Finnish lake district (63°N, 27°E). Collection of data began in 1984, and by 1989, the study area had reached its current size, about 280 km<sup>2</sup>. The study area consisted of 23 lakes and four bays of larger lakes, surrounded mainly by cultivated fields or a narrow forest line by the shore, especially in the central part of the study area. In the peripheral part of the study area lakes and bays are partly surrounded by deciduous, mixed or coniferous forests. The shoreline types vary from eutrophic, well-vegetated shores to oligotrophic ones with rocky, forested shores. In the oligo- and mesotrophic lake types the dominant emergent plant is the reed *Phragmites australis*, but especially in eutrophic wetlands, the shoreline is dominated by a lush stand of horsetail, *Equisetum fluviatile*, bulrush, *Schoenoblectus lacustris*, cattail, *Typha latifolia* and sedges, *Carex* spp.

A complete enumeration of all nest boxes and potential natural nest cavities was conducted every year. The first nest box survey was done at the end of April or the beginning of May, and the boxes that did not have a nesting attempt ( $\geq 1$  egg) in the first survey were checked for the second time about two weeks later. A huge amount of fieldwork was devoted every breeding season to finding systematically all potential nest sites and nesting attempts. The number of available nest sites (mainly nest boxes) increased from 63 to 465 between 1984 and 2006. During the breeding seasons 1984-2006 there has been at least 617 different nest-sites available for goldeneye females in the study area (seven natural cavities included). The average life span of the nest sites was 10.1 years (SD = 6.26, max = 23, min = 1, n = 617 nest sites).

All nesting attempts were recorded and hatching times determined. Before hatching, every female was caught and controlled or banded. All nest boxes, natural cavities and nesting attempts were recorded in a GPS-based database (Microsoft Access). ArcView 3.2 and ArcGis 9.0 programs were used to modify

the data to a more appropriate form. The GPS-based database provided versatile data such as the location (exact coordinates) of all nest sites and nesting attempts, components of nesting success (desertion and predation), reasons for nesting failure, clutch size, characteristics of the nesting female, characteristics of nesting site and surrounding habitat, and a great deal of other biometric data (for more information. see e.g. Ruusila *et al.* 2000, 2001 and Milonoff *et al.* 2002, 2004). This extensive database, including data for 1,672 goldeneye nesting attempts, 311 banded females which were captured and recaptured 1,334 times during breeding seasons in 1984-2006, provided a unique opportunity to study the long-term and landscape-level spatial processes of the nesting population in goldeneyes.

### **2.1.2 Spatial point process statistics (I)**

Potential nest-sites can be referred to as resource points whose location, temporal existence and occupation rate may vary between years. Because the null model for cases where spatial randomness is constrained by some fixed locations in space, i.e. dispersion of potential nest sites, the Nearest Neighbour Spatial Analysis (NNSA) method was used to test for spatial variation in nesting intensity of the breeding population of goldeneyes (see Davis *et al.* 2000). NNSA is an extension of Manly's (1997) nearest neighbour method, which describes the spatial pattern of a subset of points (i.e. occupied nest sites in a given year and area) from a larger finite set of sampling points (i.e. potential nests sites in a given year and area). In addition, NNSA resolves the occurrence of both aggregation and regularity at multiple spatial scales, and the spatial pattern of potential nests sites was controlled.

In Paper I, the procedure of Davis *et al.* (2000) was followed in detail. NNSA uses a Monte Carlo randomisation approach to test the non-randomness of the mean of the  $(n - 1)$ th nearest distances to reveal spatial information at various scales. Monte Carlo simulation generates the random sample distribution for each  $(n - 1)$ th distance for each subset from a larger set of points where the test statistics are mean and 95% confidence interval (i.e. 2.5% and 97.5% percentiles) for each distance. The significance level of each observed distance was the proportion of randomised mean distance values that were equal to or more extreme than the observed mean distance (Manly 1997, Davis *et al.* 2000).

## **2.2 Habitat selection, movements and survival of broods (II, III, IV, V)**

### **2.2.1 Study area and breeding population**

The brood-phase data were collected in a barren forested watershed area surrounding the Evo Game Research Station in Lammi and Padasjoki, southern Finland (ca. 100 km<sup>2</sup>), specifically, the Evo core area (75 km<sup>2</sup>) and Siperia (25 km<sup>2</sup>) (61°13'N, 26°06'E). The area is dominated by Scotch pine, *Pinus sylvestris*, or mixed forests (Scotch pine, birch, *Betula* spp., and Norway spruce, *Picea abies*), inter-dispersed with a dense network of small lakes and ponds (size range 0.014 to 49.5 ha) that comprise about 7% of the total area. Shore types of the lakes vary from oligotrophic bog and forest without emergent plants to more eutrophic shores with lush stands of *Equisetum* and *Typha* (Rask & Metsälä 1991). The lakes and ponds were referred to as patches, and these words (lake or pond and patch) are used interchangeably in this thesis.

During the breeding seasons of 1989-2001, there were 172 artificial nest boxes available for the goldeneye. Because the study area has been under intensive forest management, only few natural nest holes may be available, and therefore, the majority of goldeneye females may breed in nest boxes. Most of the nest boxes (120) were already erected before this study begun, and an additional 52 nest boxes were erected during the study (see Pöysä *et al.* 1997a).

### **2.2.2 Marking of females and data collection (II, III, IV, V)**

Goldeneye females were equipped with a radio transmitter and wing tags during the breeding seasons of 1989-2001. Females were captured during the hatching of ducklings. Nesting success, hatching date and brood size at nest exodus (initial brood size) were recorded. Also wing length, body mass, angle length and bill length of the females were measured. After the brood left the nest box, the females were located and brood size determined at least once per day for one week. The movements of marked females and their broods and duckling survival were determined until fledging (approximately 60 days of age) or until the ducklings had died.

To study patch selection by broods, broods were relocated systematically and all patches used by each brood were identified including hatching patch, patches used only temporarily (less than one day) and rearing patches (note that, hereafter,

patch or habitat selection by broods refers to selection by the female attending a given brood). With this method (i.e. used patches versus used but rejected within one day patches) most methodological pitfalls common in habitat-related studies could be eliminated (see Jones 2001). All information to track the actual route used by each brood during the movements was used to measure the distances covered by the broods through the matrix (dry land areas) and corridors (permanent ditches and rivers). If actual route of the brood was not known, shortest distance between two patches were used. All distances were measured from digital maps with ArcView GIS 3.2 software combined with spatial database from the area. On the basis of previous information, the number of nesting attempts, nesting success and brood frequency per patch was calculated.

### **2.2.3 Survival of ducklings (II, III, V)**

Two different types of survival estimates were used in this thesis. First, survival estimations of goldeneye ducklings according to Ringelman & Longcore (1982; see also Gauthier 1987, a method applied from Mayfield 1961, 1975) (II, III, V) were used to calculate brood-specific (II, III), patch-specific (II) and age-specific survival estimates (Paper V). Secondly, program MARK (White & Burnham 1999) and known fate model were used to calculate maximum likelihood estimates for survival of ducklings (Paper V). Overdispersion was controlled for by using a variance inflation factor (see Pelayo & Clark 2003 and references therein). The survival of ducklings was age-dependent, being lowest in their first week after hatching (see Paper V), a pattern consistent with earlier findings on goldeneyes (Gauthier 1987, Savard *et al.* 1991, Wayland & McNicol 1994, Pöysä & Virtanen 1994, Milonoff *et al.* 1995, Pöysä *et al.* 1997c). Therefore, first-week survival of ducklings was used in further analyses.

### **2.2.4 Environmental variables**

#### *Vegetation structure and food resources (II)*

Vegetation and morphometry of the lakes and ponds in the Evo study area were first mapped in great detail in late July 1988-1990. The vegetation structure of the patch was described with 18 variables (II), which were combined with principal component analysis (PCA) (for details, see Nummi & Pöysä 1993). The first component of PC1 arranged the patches on the gradient of oligotrophic, barren

forested patches to eutrophic, well-vegetated patches. The component scores of the patches on the gradient were used as an index of lake vegetation structure (Paper II).

Another type of variable was also used to index the vegetation structure of patches. Vegetation luxuriance of patches was indexed according to a simple habitat type classification based on vegetation structure and abundance in mid-summer (July) (Paper IV). The correlation between vegetation luxuriance and the component scores used to index vegetation structure in Paper (II) was high ( $r_s = 0.89$ ,  $n = 44$ ,  $p \ll 0.001$ ).

Food resources of the patches, i.e. the abundance of invertebrates, were sampled under water surface with activity traps (II, Murkin *et al.* 1983) in mid-summer 1990-1995. All individuals from the traps were measured and classified to length categories according to Nudds & Bowlby (1984). The index of food abundance is the total number of individuals per one trap and one trapping day weighted by the size classes of invertebrates and the proportion of the two shoreline types (II, Pöysä & Virtanen 1994, Nummi & Pöysä 1993).

### *Patch-specific predation risk by pike (II)*

Patch-specific predation risk by pike, i.e. relative threat of attack, was sampled with bite-hooks in the first half of July 2000-2001 (II). Four bite hooks per rearing patch were placed in mid-water and parallel to and about one metre from shoreline. The total number of pike attacks per lake was recorded. The same sampling procedure was repeated in two consecutive years to find out if the predation risk was constant between years. The mean number of attacks per year was used as an index of predation risk by pike for each rearing patch.

### *Landscape metrics (III)*

The effects on habitat configuration of space use, habitat selection, movements, and mortality of individuals were studied in Paper III. The habitat patch configuration was measured from digital maps with ArcView GIS 3.2 software combined with spatial database from the area. The number of patches and mean distance to the patches within a radius of one kilometre from the hatching patch were used as measures of habitat configuration around each hatching patch. In addition, the occurrence of permanent or semi-permanent ditches as corridors with inlets and outlets at the hatching patch was measured, and a quantitative

index indicating presence or absence and structure of corridors was used in the analyses (III).

*Non-spatial environmental and maternal attributes (V)*

The first-week survival of goldeneye ducklings in relation to weather, timing of breeding, brood size, and female condition was studied in Paper V. During marking of females hatching date and initial brood size were determined. Hatching date was recorded as a continuous variable starting from 1 May. In addition, females were weighed to the nearest 10 g with a Pesola spring scale and wing length was recorded to the nearest 1 mm. The residuals from the regression of body mass on wing length were used as a condition index.

Weather data were obtained from the permanent weather station at the Evo Game Research Station. The air temperature was monitored continuously by a temperature recorder during the first week after hatching for each brood. Total cumulative precipitation was also measured for the first week of each brood.

## 3 Results and discussion

### 3.1 Dynamics of spatial nesting pattern and its consequences to nesting success (I)

Nearest neighbour spatial analyses revealed substantial spatial randomness, but over several years, the indices of dispersion at all spatial scales showed an aggregative spatial pattern of nesting attempts, and the intensity of aggregation fluctuated considerably between the years, showing no clear tendency or trend (Paper I; Fig. 3). The results imply that the spatial nesting pattern in the common goldeneye is dynamic, changing from one year to the next and also from scale to scale. Therefore, the actual density of individuals is a complex function of the number of and distances between individuals at different spatial scales (see also Begon *et al.* 2003). In addition, the low rate of nest-site occupancy suggests no shortage of available nest sites, implying that the spatial nesting pattern was truly generated by nest-spacing behaviour of females.

Potential mechanisms generating aggregative spatial pattern of nesting attempts at different spatial scales are probably diverse. At a large scale, spatial variation of nest density may reflect habitat heterogeneity (Boyce & McDonald 1999, Cornulier & Bretagnolle 2006), but the results in Paper I did not provide support for this assumption. Many recent studies suggest that the most important factor affecting nest spacing pattern of goldeneye females is the dynamic balance between costs and benefits in predation risk-mediated nest site selection (e.g. Pöysä 1999a, 2003, 2006, Ruusila *et al.* 2001). Females may benefit by finding nest sites with low predation risk through natal philopatry (Ruusila *et al.* 2000, 2001) or by cueing to experienced resident conspecifics (see review in Danchin *et al.* 2001, Ahlering & Faaborg 2006, Pöysä 2006). However, aggregative nest spacing may also involve costs: increasing aggregation seemed to increase nest desertion during laying and nest predation (I). At the small scale, there were some evidence that increasing aggregation decreased overall nesting success, suggesting that these demographic components were at least to some degree density-dependent. In line with this finding, Pöysä & Pöysä (2002) found that increasing nest site availability increased the local breeding population of goldeneyes, but the number of broods showed negative density dependence of reproductive output. They suggested that density-dependent nest predation or

disturbance caused by conspecific nest parasitism may have decreased hatching success with increased population density (Pöysä & Pöysä 2002).

Increasing aggregation of nests probably intensified negative interactions among females, and therefore, decreased overall nesting success (see also Eadie *et al.* 1998). The effect was restricted to the beginning of the nesting phase since aggregation was not related to desertion during incubation, supporting the assumption of the negative effects of conspecific nest parasitism (see Pöysä 1999a). Importantly, I did not find any association between aggregation and nest desertion at large spatial scales, implying that social interactions do indeed operate at spatial scales of the close neighbourhood of active nests.

The nest predation rate also increased with aggregation, suggesting density-dependent nest predation also found by Fredga & Dow (1984). However, the results in other duck species have been contradicted (see Ackerman *et al.* 2004; Table 4) indicating complex interactions between location and the number of nests and the spatial scale corresponding to how predators respond to nests at different densities (Schmidt *et al.* 2001). The overall nest depredation rate was low, suggesting that the mechanism behind the density-dependent nest predation is a functional response of generalist predators such as the American mink (e.g. Krebs 2001). Because density of the mink population was low during the study, a numerical response of predators is not likely. In conclusion, the results in Paper I suggest the existence of density-dependent population processes in the common goldeneye in terms of association between annual spatial dispersion of females and annual nest desertion and nest predation rate. However, to evaluate the validity and generality of the present findings, further work should be conducted in other populations, and particularly in other species.

### **3.2 Space use, habitat selection, movements and survival of broods in a patchy boreal environment (II, III and IV)**

In the context of patchy environments, I studied the basic aspects of space use and the effects of patch characteristics (II) and the structure of the landscape (III) on habitat selection, movements and survival of common goldeneye broods in a naturally patchy boreal breeding environment where the landscape can be unambiguously divided into suitable patches (lakes, ponds etc.) and unsuitable matrix (all terrestrial habitats).



### **3.2.1 Patterns of space use and movements of individual broods**

Individuals should use appropriate space-use strategies depending on spatial interaction and temporal dynamics of resources, and trade-off between costs and benefits of acquiring these resources (e.g. Morris 2003). In heterogeneous landscapes, individuals may depend on a mixture of resources (e.g. safe nests sites and food), which may locate in spatially segregated habitat patches varying in size, configuration and quality (Wiens 1976). For all requirements to be fulfilled, individuals' space-use tactics should change accordingly (e.g. Wegge & Rolstad 1986, Redpath 1995). This means, for example, that individuals should expand or change their home range and resource tracking tactics. In this thesis, goldeneye females and their offspring usually deserted the hatching patch shortly after hatching (II, III), which may indicate that the current patch did not fulfil the requirements of ducklings. Still, a small proportion of females attempted to nest and rear their young in the same patch. These findings indicate the existence of different space-use tactics in females during reproduction.

If the hatching patch was deserted, the movement of the brood between the hatching patch and rearing patches was unidirectional, which differs for example from the small-scale foraging-related movement tactics usually found in birds (e.g. Robinson & Holmes 1982), but has more similarities with certain large-scale inter-patch movement patterns reviewed by Turchin (1998; category of inter-patch movement within home range with previous experience; see also McIntyre & Wiens 1999). The first rearing patch was usually reached within a couple of days, often within a few hours after hatching-patch desertion. The actual mechanism by which females perceive their environment during inter-patch movement is unclear, but unidirectional movement between hatching patch and rearing patches suggests that highly mobile females with good cognitive ability and spatial memory may gather information about routes and the quality of patches within their breeding home range before and during breeding and use that information in patch selection (Badyaev *et al.* 1996, Cartar 2004, but see Zollner & Lima 1999). In addition, during fieldwork I observed several times a female flying along a route that was shortly afterwards used for inter-patch movement by a brood. Broods usually travelled a couple of kilometres in their first week after nest exodus (III), which is not an easy task for small ducklings, involving costs in terms of time and energy and potentially, costs in terms of survival of the ducklings (but see Paper III).

During inter-patch movement broods used ditches as corridors and neighbouring wetlands as ‘stepping-stones’ if they were available. Thus, ditches can facilitate the movement of individuals and enhance the connectivity of landscape. Clustered patch configuration and corridors potentially reduced the energetic costs of travelling (III). However, broods frequently moved through the matrix, implying that their movement ability during overland travel is very good, and, indeed, broods seemed not to discriminate the matrix during inter-patch movement (III). If ditches or other type of corridors were not available, overland travel was the only option, but even if corridors were available, some broods used dry land, probably minimise the actual length of travelling, thus potentially saving travelling costs.

In conclusion, females with broods adjusted their space-use tactics according to critical breeding resources, i.e. successful nest site and food, which were not usually find in the same patch. Spatial divergence of these two obligatory resources induced brood movements at various distances shortly after hatching. During movements, broods used different landscape elements such as patches, corridors and matrix in a very flexible way. Previous observations indicated that species like the goldeneye living in naturally patchy environments have evolved good skills to successfully utilise patchily distributed resources even in the most critical period of reproduction.

### ***3.2.2 Factors affecting space use, movements and habitat selection of broods in a patchy environment (II, III, IV)***

The results of this thesis agreed with several previous studies and indicated that the main motivation of hatching-patch desertion and patch selection in general was the amount of food (i.e. the abundance of nektonic invertebrates), because food abundance was significantly higher in rearing patches than in rejected patches (IV) (see also Eriksson 1978, 1979, Eadie & Keast 1982, Pöysä & Virtanen 1994, Wayland & McNicol 1994). Therefore, food plays a major role in habitat selection of broods. The results also imply that spatial interaction between food abundance and successful nesting in current season affected the space use pattern and movements of broods (II, III, IV). These spatially separated requirements force females to move and find appropriate patches to fulfil high-energy food demands for growth and development of small ducklings. As pointed out by Sjöberg *et al.* (2000), most lakes are suboptimal for ducklings with respect to food levels, and food limitation is a common phenomenon in boreal breeding

environments of ducks (see also Gunnarsson *et al.* 2004). However, other factors may also influence patch preference of the broods, because some broods rejected their food-rich rearing patches soon after arrival and food abundance did not affect the probability of hatching-patch departure (III).

Interestingly, different broods used several different types of patches for food acquisition in the early brood phase. For example, based on data in Paper III, which considered movement and habitat selection of broods during the first week after nest exodus, over one third of all females (25/67) reared their ducklings in one or two vegetation-rich wetlands, several (17/67) females preferred made by beaver (*Castor canadensis*), some females (5/67) reared their ducklings sequentially in small ephemeral or semipermanet patches, a minor proportion of broods (8/67) used relatively small acidic ponds in the early brood phase, and finally, some broods (9/67) used oligotrophic lakes with considerably barren vegetation zones along the shoreline (Paasivaara & Pöysä unpublished data). Considering the whole brood period, broods frequently changed the rearing patch during the rearing period (II), and habitat use of a given brood was not restricted to a certain patch type. In this data set, some single females used different types of patches during the entire brood period, such as beaver pond, corridors and permanent vegetation-rich patches sequentially for rearing their young (Paasivaara & Pöysä unpublished data). Changes in foraging habits of growing ducklings may provide an explanation for rearing-patch change during the brood period (Nummi & Pöysä 1995b). Indeed, I found considerable variation in patch-use tactics between broods with respect to habitat type. In the Evo study area, beaver ponds provide high-quality food patches where the abundance of nektonic invertebrates is particularly high (II, see also Nummi 1992). The high frequency of broods in luxuriant patches may be explained simply by their long-term availability and other than permanent vegetation-rich patches may be more costly to access due to the spatially and temporally dynamic nature of these patches in comparison with permanent vegetation-rich patches. However, beaver ponds involve a high reward with respect to food (II), whereas invertebrate abundance may be less predictable in beaver ponds.

At first glance, the role of vegetation structure in habitat preference of broods seemed to contradict in the results of this thesis. The results with respect to rejection or acceptance of a certain patch on the basis of behaviour of individual broods revealed that vegetation structure of the patch was not an important factor affecting the patch-selection decision of goldeneye hen (II), which is easy to understand on the basis of the diversity of habitat-use tactics as was described

above. In contrast, based on somewhat different data in Paper IV, which was based on a long-term pattern of distribution of radiomarked broods among permanent patches in the same study area, the frequency of broods increased with increasing vegetation luxuriance of the patch (IV). Indeed, few vegetation rich lakes were highly preferred by the broods in a long-term perspective. However, study questions, hypotheses, analyses and databases differed between these papers, and it is likely that these differences may induce contradicting inferences. In addition, Paper IV considered brood frequency at the beginning of the brood phase (first week), while Paper II considered data from the entire brood period. Young broods did not necessarily change the habitat type from poor to luxuriant patches during hatching-patch desertion because of differences in food acquisition tactics with respect to habitat type (see previous paragraph). However, the inclusion of the degree of acidification and the effect of beavers in the analyses in Paper IV would clarify the role of different type of patches. Still, habitat luxuriance alone explained a considerably large amount of variance of brood frequency among patches (IV). In line with this observation was that food abundance and vegetation structure of the patch were not correlated (II) and consequently, the existence and dynamics of high-density invertebrate populations in different patches are at least to some extent independent with respect to the vegetation structure of patch.

Despite contradictory results in this thesis (Papers II, IV), vegetation-rich patches may be important in maintaining local duck populations because of their high productivity and, probably, high predictability in terms of the amount of food within and between seasons, and hence, the higher average food accessibility and energy intake over a longer time scale in both females and ducklings. In theory, individuals should maximise their fitness in terms of energy intake and survival of offspring in a long-term perspective (e.g. Krebs & Davies 1997). Indeed, by using more predictable rearing environments females may minimise the costs of reproduction (time budget costs; Milonoff *et al.* 2004, see also Ruusila *et al.* 1998), e.g. weight loss during breeding season, and minimise the costs of their own future survival and reproduction in a life-time perspective (Bell & Koufopanou 1986, Stearns 1989, Lessels 1991). Hence, permanent and productive patches offer relatively easy-access patches to goldeneye hens to recover from reproductive activities and to rear their offspring even though, while using vegetation-rich patches, females may expose their young ducklings to increasing risk of predation (II). I will discuss fitness payoffs of habitat-use tactics and the quality of patches in the next chapter.

The results in Paper III imply that the structure of the surrounding landscape in terms of the number of patches (patch density) affected the rearing patch selection, in that it influenced the initial decision of whether to leave or stay in the hatching patch. I cannot say what the actual mechanism of the process is, but previous findings indicate that the females did indeed perceive and respond to the surrounding landscape in their patch-selection decision. Consequently, the structure of the landscape affected the inter-patch connectivity and enhanced the accessibility of other patches (III, see also Andreassen *et al.* 1998, Bjornstad *et al.* 1998, Maurizen *et al.* 1999, Selonen *et al.* 2001)

Several factors not related to habitat *per se*, such as individual characteristics, previous experience and quality of females may affect the habitat patch selection of goldeneye broods. In addition, movement between patches may be associated with population-related factors such as the number and/or response of territorial conspecific females (i.e. density-dependent habitat selection; Morris 1995). Therefore, individuals may respond directly to resource depletion of the patch, or alternatively, subordinate females are forced to move to another patch (Sutherland 1996). In addition, conspecific or heterospecific attraction may affect the patch choice of goldeneye broods (Stamps 1988, Forsman *et al.* 1998), as has been found in adult mallards and teals during breeding-patch selection (Elmberg *et al.* 1997, Pöysä *et al.* 1998).

The occurrence and density of predators may also affect habitat selection of broods, but the results of Paper II indicated that females had poor skills in predation risk assessment, at least with respect to predatory fishes. However, the observed mortality rate of ducklings indicated only a relative risk of predation, not an actual behavioural pattern and mechanism of how females may respond to predation risk in a given patch. In general, animals with varying threat of being preyed on may trade off between food acquisition and other life-history-related factors such as predator avoidance, and individuals should modify their foraging behaviour accordingly (see review in Lima & Dill 1990). Consequently, goldeneye females should prefer patches where the predation risk is low. However, in circumstances of boreal breeding environments of ducks, food limitation of young ducklings is likely to modify the optimal patch choice of females (see Sjöberg *et al.* 2000). Therefore, females may be forced to use food-rich patches at the expense of predator avoidance. On the other hand, it is still an open question whether or not any antipredator behaviour component exists against predation risk by pike during the patch selection process (but see Ruusila & Pöysä 1998).

### **3.2.3 Spatial distribution of individuals at different stages of the breeding cycle: consequences of behavioural and demographic processes in a boreal landscape (IV)**

The spatial and temporal pattern of population distribution and abundance reflects the space use of individuals (Wiens *et al.* 1993). Similarly, the space-use pattern of individuals is related to the spatial and temporal pattern of resources as well as intra- and inter-specific interactions, which can affect individual fitness and, ultimately, population dynamics (Andreassen & Ims 1998).

In Paper IV, I concentrated on spatial interaction of the nesting and rearing requirements of breeding common goldeneye females. Critical resources of successful nesting, i.e. a safe nest site and rearing resources of ducklings, were not positively correlated at the patch level, indicating that critical requirements of nesting and brooding were not usually met in the same patch, which is probably a general pattern in the boreal breeding environment of ducks. In this situation, the main option for successful reproduction is the movement pattern observed above (see II, III) where individuals complemented for a lack of critical resources in a hatching patch by using alternative patches (Dunning *et al.* 1990), and the distribution of individuals changed accordingly. Importantly, patch-specific nesting success did not have a direct effect on the distribution of individuals during the brood stage. In addition, the increasing nest predation rate prevented efficiently nesting attempts of females in high-risk areas where many preferred rearing patches were located. Obviously, low-risk nesting patches and food-rich patches did not covary spatially.

In conclusion, successful reproduction is possible only in those areas where these critical resources are situated at accessible distances (see II, III) and individuals are redistributed according to these resources. The pattern of spatial redistribution gave rather a dynamic population and landscape level perspective to the space-use pattern of breeding ducks and clearly showed that spatial interaction between resources affected the overall space-use and movement pattern during the patch-selection process of breeding females (see also Nummi & Pöysä 1993).

### **3.2.4 Fitness consequences of habitat selection and movements in a patchy environment (II, III)**

In theory, females should prefer habitat patches where survival of offspring will be high (high-quality patches in terms of survival) (e.g. Fretwell & Lucas 1970,

Orians & Wittenberger 1991). In this thesis, the quality of patches varied with respect to their fitness prospects in terms of duckling survival. Clearly, the survival of young (aged 0-23 days) goldeneye ducklings was associated with the predation risk by northern pike, implying that pikes frequently catch small ducklings, affecting patch quality (II). In contrast, survival of old (over 23 days) ducklings was not related to patch-specific predation risk and in general, survival of old ducklings was high and differences among broods were small (see Paper V; Fig. 2). Still, these results provided new information on the interactions between species and importantly, a new aspect in the assessment of patch quality versus habitat preferences of ducks breeding in stable boreal environments. However, it is impossible to assess the actual patch choice of females on the basis of this data, and therefore, I can provide only speculative explanations for the processes behind the patterns.

The previous results indicate a contradiction between prevailing habitat-patch preference and survival prospects of ducklings, which suggest that females do not select the rearing habitat on the basis of predation pressure by the pike. However, almost all permanent lakes, especially vegetation-rich patches, hold an abundant fish population including pikes (Rask & Metsälä 1991). Indeed, all vegetation-rich rearing patches in Paper II had a considerably high risk of pike predation during the early brood phase. In addition, data on the relationship between survival and lake preference of broods revealed clear evidence that the lakes used most frequently in the early brood stage were not the safest ones (Paper II) and that brood occurrence in some vegetation-rich patches overlapped with high predation risk by pike, implying that vegetation-rich patches were not always optimal with respect to survival prospects of downy ducklings (II, IV). Clearly, the prevailing habitat-use pattern involved fitness costs to females due to increasing predation risk, and consequently, decreased the overall quality of the breeding environment in the early brood phase. As discussed earlier, habitat-patch choice of females may be modified by food limitation in the early brood phase (see Sjöberg *et al.* 2000) or age, experience or condition of the female (V, see also nest paragraph). However, the interaction between goldeneyes and pikes has apparently been over a long evolutionary time scale and therefore, one may assume that some appropriate antipredator tactics or strategy against predation risk by pike should have evolved (see Ruusila & Pöysä 1998). Put there is no evidence for the existence of such an assessment mechanism (see also Pöysä 1992).

Some females avoided predation by pike by using ephemeral or acidic and fishless patches for brood rearing with a considerably higher survival probability of small ducklings (II). In addition, earlier studies have found that subtle acidification increases the abundance of invertebrates, but simultaneously, decreases the abundance of fish, including pike, and consequently decreases predation risk in the acidic patches (see e.g. Pöysä *et al.* 1994). Thus, acidification decreases both food competition between goldeneye ducklings and certain fish species (e.g. perch, *Perca fluviatilis*) and predation risk; therefore, the relative effect of these two factors in the patch-selection process of females is difficult to assess. However, exploring the environment and gathering information on alternative rearing sites such as fishless floodings and other more or less ephemeral and semipermanent patches may be more costly to access than permanent vegetation-rich patches: females must spend time and energy on exploring habitat over the breeding area especially during the actual breeding season.

Alternatively, the fitness costs of using vegetation-rich patches in the early brood phase may be compensated for in other phases, for example by increased energy intake or survival of older unfledged ducklings, juvenile individuals or higher energy intake of breeding females. Females may also avoid extra travelling costs in later brood stage, because permanent vegetation-rich patches may satisfy the food requirements of ducklings of all ages (e.g. Nummi & Pöysä 1995b). In permanent vegetation-rich patches, broods may also avoid food or water depletion of more ephemeral patches at later stages of the season. In conclusion, the benefit gained through high average energy intake of ducklings and females is likely to outweigh the costs due to predation by pike. Although future survival of the brood is predicted by survival in the early brood phase (Pöysä *et al.* 1997c), I did not assess the habitat selection of juveniles and the fledging success of ducklings in a given patch. Therefore, the assessment of the role of luxuriant patches in terms of survival of older ducklings and juveniles is incomplete, should be addressed in future work.

On the basis of previous studies on goldeneyes (Wayland & McNicol 1994) and other duck species (e.g. Rotella & Ratti 1992) one may assume that inter-patch movement of broods may involve costs in terms of duckling survival. However, one of the most striking findings in this thesis was that the distance moved through a definitely inhospitable matrix (terrestrial habitats), the total distance moved or the distance moved through different landscape elements (ditches and rivers) did not decrease brood survival (III), and I found no evidence



of fitness costs of movement *per se* in terms of duckling survival. On the contrary, using a smaller dataset Pöysä & Virtanen (1994) found a positive relationship between the total distance moved and survival of ducklings. Indeed, these results imply that there were no apparent costs to living in a patchy environment and that goldeneye ducks are adapted to a patchy environment also at the most critical phase of reproduction. This finding brought new information to the discussion on the effects of matrix type on inter-patch movement and population processes in a patchy environment in general (III and references therein). However, the usability of ditches and rivers increased duckling survival, implying that ditches and rivers have an important role in the space use of broods. Broods may use these as alternative rearing sites or as predation-free refuges where the predation risk by pike may be low (see II).

### **3.3 The impact of environmental and maternal factors on survival of ducklings (V)**

In Paper V, observational data on individually marked broods revealed a clear age-dependent survival pattern of broods and ducklings, implying that the first week is the most critical period in early stages of life. A high mortality rate of young ducklings and the rapid decrease of the number of broods and ducklings during the first week clearly indicate that they are very vulnerable to single or multiple factors. In Paper II, increasing predation by pike decreased survival of young ducklings (II), but it is unlikely to cause total brood loss. Obviously, the pike is not the only predator that influences the survival of ducklings. The American mink is a common generalist predator in the study area, and footprints and faeces of the American mink as well as remains and carcasses of goldeneye ducklings on lake shoreline have been observed simultaneously with duckling reduction of given broods (personal observation). Minks have also caught and eaten a couple of radiomarked females (personal observation). Obviously, minks kill several or all ducklings depending on the degree of surprise and escape routes, but predation by mink may explain the sudden destruction of many young broods, which are more cohesive than older broods. After two or three weeks, ducklings of a single brood often spread out over wetland, potentially decreasing total brood loss. Therefore, I suggest that a great deal of the variation of survival of young broods and ducklings can be explained by mink predation (see also Pietz *et al.* 2003). Unfortunately, no valid or appropriate monitoring method at the scale of single wetland has been developed for mink abundance or activity, and therefore,

the effect on predation by mink is unclear. In addition to pike and mink, also other predators, such as large gull species (e.g. *Larus argentatus*), marsh harrier (*Circus aeruginosus*), common buzzard (*Buteo Buteo*), goshawk (*Accipiter gentilis*) and raccoon dog (*Nyctereutes procyonoides*), were observed hunting, killing or damaging goldeneye ducklings, but these were only isolated cases.

Weather with respect to temperature and rain had no effect on duckling survival, implying that weather *per se* during the early summer may not normally cause unpredictable crashes or ‘environmental noise’ in duckling production of goldeneyes, at least on the temporal scale used in this study (but see e.g. Gunnarsson *et al.* 2006). In population ecology, weather has been considered as a factor limiting populations in a density-independent fashion (e.g. Newton 1998). Even though the results in this thesis did not reveal important weather effects, one should note that the impact of weather is context and year-dependent because for example the breeding population of goldeneyes has decreased after harsh weather events in wintering areas in the Baltic Sea (Kauppinen & Väänänen 1999). Alternatively, the possible effect of weather may be masked by the overwhelming effect of predation.

The role of hatching date on survival of newly hatched ducklings was contradictory. The findings of Milonoff *et al.* (2002) agreed with the general assumption that early broods produced more recruits than late ones (see e.g. Blums *et al.* 2002 and references therein), but the results in Paper V were not in line with this general pattern. The mechanism of favouring early hatching young is well documented in altricial species (see e.g. Perrins 1970, Daan 1988), but in precocial species, especially considering nidifugous ducks, it is difficult to find general agreement in explaining the relationship between timing of breeding and high recruitment (see references in paper V). Blums *et al.* (2002) suggested that early-hatching individuals may exhibit higher social dominance deriving higher accessibility to good-quality food, and therefore, greater first-year survival, implying that advantages at early breeding promote the after-duckling stage. However, the actual mechanism of the goldeneye recruitment pattern is unclear. Again, it is possible that some overwhelming factor such as predation at early brood stage may mask the effect of hatching date in the present data.

Interestingly, increasing condition of the female was related to increasing duckling survival (V), but I could not control for the effects of female age and experience, which may correlate with condition (Blums *et al.* 2002). This is an unfortunate shortcoming, because older individuals have been observed to perform better in reproduction than young ones (see review in Newton 1989). In

addition, Milonoff *et al.* (2002) found that females in good condition lived longer than poor-condition females and consequently, condition may indicate the overall quality of the female. Any movements across the breeding area of females may incur costs with respect to time and energy and may need *a priori* information before the actual habitat-selection decision. Therefore, I suggest that high-quality females may not invest more in reproduction than poor-quality females (see Milonoff *et al.* 2002), but high-quality females may be able to allocate more resources to habitat exploration before and during current breeding season to increase their prior experience targeting optimal patch selection for young ducklings, i.e. food-rich patches with low predation risk (Badyaev *et al.* 1996, but see Pöysä *et al.* 1997c). Indeed, the effect of female quality and condition on space use, duckling survival and parental care decisions should be studied further. Further work is also needed on the effects of different factors such as predation on the survival of goldeneye ducklings and other duck species in general.



## 4 Main conclusions and management implications

In this thesis, I studied spatial interactions between the resources and individuals in relation to different components of reproductive success in breeding common goldeneye females during nesting and brood rearing phases. During the nesting phase, I found that the spacing pattern of females were dynamic, changing from one year to the next and also from scale to scale. Moreover, there was some evidence that annually changing spatial pattern of nests was related to important components of nesting success, in particular, nest desertion and nest predation, suggesting a negative density-dependent effect on the nesting success of goldeneye females. This aspect of population dynamics has been largely ignored. However, the exact mechanism behind this dynamic space-related pattern remains open for further studies.

The results in Paper I have important practical implications for management and conservation of breeding population of cavity-nesting species. Together with the findings of Pöysä & Pöysä (2002), the results in Paper I revealed that nest box provisioning programmes aiming to increase breeding numbers and duckling production may be negated due to density-dependent nest desertion and nest predation (see also Eadie *et al.* 1998). The mechanism of density-dependent nesting success is related to negative behavioural interactions between nesting females potentially due to conspecific nest parasitism, but also nest predation increases with increasing local nest density. Similarly, considering results at a small spatial scale suggests that nest boxes should not be erected too close to each other, because dense clusters of nest boxes may increase negative effects of conspecific nest parasitism (see also Semel *et al.* 1988, Semel & Sherman 1995). Indeed, the number and location of nest boxes should be carefully considered in nest-box provisioning programmes aimed to increase breeding numbers and production of common goldeneye and other hole-nesting ducks. However, before extensive nest-box provisioning programmes, it should be ensured that there are also key resources available for ducklings, which means habitat patches (lakes) of low predation risk and high food abundance (II, III, IV).

Results of Papers II, III and IV indicate that breeding goldeneye females and their ducklings are adapted to a patchy environment. Females used space in a very flexible way to meet the food requirements of ducklings and without any clear fitness costs with respect to rate of movements in relation to survival of ducklings. Indeed, my thesis clarified some crucial aspects of spatial ecology of the breeding

goldeneye duck and provided empirical information for better understanding of population dynamics of the species, which is an important game species over the northern hemisphere. In conclusion, I suggest that goldeneye can be referred to as a reference species in studies of species in a patchy environment. However, broods of goldeneye suffered heavy losses especially during the early brood stage. Although my thesis clarified some important factors affecting the survival of ducklings (II, III, V), final conclusions on the crucial demographic factors of the common goldeneye remain a challenge for the future. For example, the influence of alien predators such as the American mink remains unsolved.

The most important implication of this thesis is that management and conservation actions aimed to guarantee population persistence or to increase population density of ducks or waterbirds in general (see also Pöysä & Pöysä 2002) need to be based on landscape-level planning extending beyond a single wetland. Indeed, waterfowl have special population dynamics and frequent between-patch movements, even within critical periods of reproduction, which necessitates a large-scale approach to waterfowl management and conservation (see Haig *et al.* 1998).

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## Original papers

- I Paasivaara A, Pöysä H, Pesonen M & Runko P (2007) Dynamics of spatial nesting dispersion and its consequences to nesting success in the common goldeneye (*Bucephala clangula*). Manuscript.
- II Paasivaara A & Pöysä H (2004) Mortality of common goldeneye (*Bucephala clangula*) in relation to predation risk by northern pike (*Esox lucius*). *Annales Zoologici Fennici* 41: 513-523.
- III Pöysä H & Paasivaara A (2006) Movements and mortality of common goldeneye *Bucephala clangula* broods in a patchy environment. *Oikos* 115: 33-42.
- IV Paasivaara A & Pöysä H (2007) Habitat patch occupancy in the common goldeneye (*Bucephala clangula*) at different stages of the breeding cycle: implications to ecological processes in a patchy environment. Manuscript.
- V Paasivaara A & Pöysä H (2006) Survival of common goldeneye (*Bucephala clangula*) ducklings in relation to weather, timing of breeding, brood size, and female condition. *Journal of Avian Biology* 38: 144-152.

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