Influence of spatial scale, sex and parental presence on rates of natal philopatry in non-migratory Canada Geese *Branta canadensis*

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Abstract

Birds often nest in the same area where they were raised (natal philopatry). The level of natal philopatry among non-migratory Canada Geese *Branta canadensis* in New Haven County, Connecticut, USA, was studied by banding 731 fledglings, then following them over their lives. The proportion of fledglings that returned to New Haven County to nest as adults (*i.e.* natal return rates) was 0.22 overall: 0.31 for females and 0.12 for males. These rates increased to 0.60 for females and 0.29 for males after correcting for mortality prior to first breeding (*i.e.* natal homing rates). For 29 fledglings (2 males and 27 females) that hatched in the Maltby Lakes and returned as adults to breed in New Haven County, I knew the location of their natal site, first nesting site, final nesting site, and the identity of their parents and mate. These 29 birds are referred to as "subjects". During their first nesting year, 28 of 29 subjects (96%) raised their young at their natal brood-rearing site: 17 (59%) nested on their natal lake, 6 (21%) nested on their natal area (often an island within the lake), and 2 (7%) on their natal territory. These percentages were higher than expected if geese were selecting nest sites at random for brood-rearing sites and natal lakes, but not for natal areas or natal territories. Natal philopatry rates were similar during the subjects' first and last nesting year, and there was also no difference between subjects raised in crèche broods and those raised in two-parent families. Natal philopatry could be mistaken for parental philopatry (*i.e.* offspring nesting close to their parents). To test this, the location of nesting territories was examined for those subjects that had parents nesting concurrently on a new nesting territory rather than at the subject's natal territory. Results showed that both natal and parental philopatry occurred; distances to the natal territory and parents' current territory were similar. Geese that exhibit natal philopatry will complicate efforts to manage geese at large scales, such as states or flyways.

Key words: natal homing rates, natal philopatry, non-migratory geese, parental philopatry, site fidelity.

Natal philopatry is the propensity for an individual to stay in or return to the area of its youth. Potential benefits of natal philopatry include optimisation of foraging skills or other behaviours learned as a juvenile that are better adapted to conditions in the natal area than in other habitats (Slagsvold & Wiebe 2018). Birds in a natal area also may be more accepting of a familiar individual that grew up locally than of a stranger, because the latter are more likely to disrupt established territory boundaries and social hierarchies (Ydenberg *et al.* 1988). There can be costs associated with natal philopatry, such as intense competition for local resources or potential mates (Greenwood 1980; Dobson 1982; Wang *et al.* 2012), a reduction of fecundity or survival if the natal area has deteriorated through overuse or habitat change (Rockwell *et al.* 1993; Person *et al.* 1998, 2003; Coulson 2016), and the risk of inbreeding (Pusey 1987; Blyton *et al.* 2015). The balance between the benefits and costs of natal philopatry could differ among individuals, sexes, populations and species.

Some birds may seek to nest close to their parents (parental philopatry), which could be confused for natal philopatry if parents are nesting at their offspring's natal site whilst their offspring are also nesting. The relative importance of natal *versus* parental philopatry has rarely been tested because the natal nest site and the parents' current nest site are often the same (Morandini & Ferrer 2017).

It is difficult to compare estimates of natal philopatry between studies because the results may vary with the size of the study area. For example, Lokemoen *et al.* (1990) considered a duck to have exhibited natal philopatry if it returned to their study area, which were two 23-km^2 rectangles located in North Dakota, while Williams (1979) regarded a duck as having natal philopatry if it nested anywhere on the 100-km^2 study site where it hatched. Others considered that a bird exhibited natal philopatry if it nested on its natal waterbody (Savard & Eadie 1989) or natal nesting colony (Cooke *et al.* 1995). While it is intuitive that natal philopatry rates will increase as the size of the natal area increases, few studies have documented this. One exception is Pöysä *et al.* (1997), who showed that rates of natal philopatry in Common Goldeneye *Bucephala clangula* increased as researchers expanded their search area. Birds can exhibit natal philopatry during any year that its nests, but many scientists use only birds nesting for the first time to determine rates of natal philopatry to avoid the problem of how to count birds that exhibit natal philopatry in some years but not others.

This study examines the relative importance of natal *versus* parental philopatry by testing whether a bird exhibits natal philopatry or parental philopatry when its parents are nesting somewhere other than the bird's natal site. The study also evaluates whether sex, age, prior nesting experience, parental presence and family type (*i.e.* whether broods are raised in a crèche or by two-parent families) had an effect on natal philopatry. Rates of natal philopatry are reported simultaneously at multiple scales to determine not only if birds exhibited natal philopatry, but the precision of their philopatry. I also hypothesised that geese exhibiting natal philopatry during their first nesting attempt would be older than those that did not, and that a subject's last nest during its life would be closer to its natal nest site than its first nest because geese may have to take whatever territory is available on nesting for the first time. Additionally, I hypothesised that goslings raised by its parents would be more likely to exhibit natal fidelity than those raised in a crèche brood.

Methods

Study area

Natal philopatry by Canada Geese *Branta canadensis* was studied in New Haven County, Connecticut, USA (41.31°N, 72.93°W), which has a land area of 1,570 km^2 and a population of more than 800,000 people (Fig. 1). The terrain is mostly flat near the coast of Long Island Sound, which is on the southern border of the county, but rises to low hills (up to 320 m above sea level) in the north. There are numerous reservoirs, lakes and ponds throughout the county.

Canada Geese (hereafter geese or goose) started nesting in New Haven County during the 1970s (Conover & Chasko 1985). These geese are non-migratory; of the geese that I banded in New Haven County, most band recoveries (85%) reported by the U.S. Bird Banding Laboratory came from Connecticut, and 76% came from New Haven County (Conover 2011). Once geese started nesting in the county, they were never observed nesting elsewhere. Band returns showed the same pattern; band returns for all geese that nested in New Haven County came from Connecticut, with the exception of one recruited female that

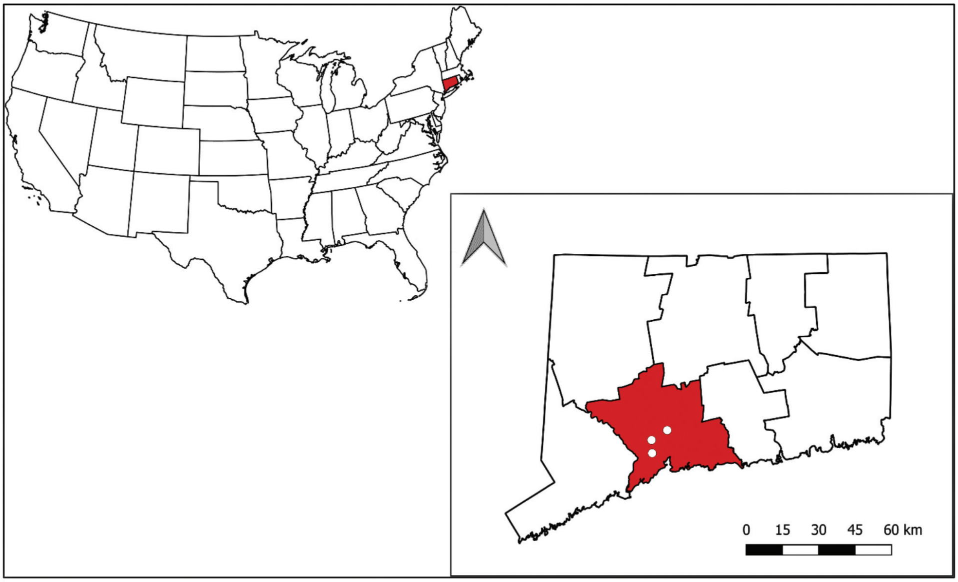

Figure 1. Map showing the location of Connecticut (in red) in the U.S., the location of New Haven County (in red) in Connecticut, and the location of the three brood-rearing sites (white dots) within New Haven County.

was found dead in New York state (Conover 2011).

Data collection

I started banding geese and monitoring their movements, survival, and reproductive success in 1984. To be included in the analyses presented here, a fledgling had to be banded for the first time prior to 2002. To locate goose nests, all waterbodies appearing on U.S. Geological Survey (USGS) maps of New Haven County were searched either from a boat or from shore. Additional goose nests were located during flights by the Connecticut Department of Environmental Protection and by reports from members of the public. All known nesting sites in New Haven County were checked during the nesting season to locate nests and to identify which geese were paired together or defended territories. Nests were found by systematically searching the shore and islands for nests. They were also located by watching for single males, which usually meant that an active nest was nearby. A female was considered to have reproduced in any year in which it was seen incubating on a nest or attending a brood. A male was considered to have reproduced during any year that it was observed defending a territory that contained a nest with an incubating female or attending a brood (Craighead & Stockstad 1964).

After hatching, most parents brought their broods to one of three brood-rearing sites, sometimes travelling several kilometres to reach them (Fig. 1). Each brood-rearing site was located on a reservoir complex of 2–4 lakes. The three complexes were in the River West watershed, River Mill watershed (Whitney Lakes) and River Cove watershed (Maltby Lakes). Adjacent to these lakes were golf courses, shopping centres and apartment buildings. The broods foraged on the lawns associated with these areas.

Goslings and adults were captured by herding them into funnel traps during the last week in June and the first two weeks of July, immediately before the goslings could fly (*i.e.* they were fledglings) and while the adults were flightless during their annual moult (Smith *et al.* 1999). The sex of each individual was determined by cloacal examination, and the birds were then banded with a USGS aluminium tarsus band and either a large tarsus plastic band or a neck collar (Spinner Plastics, Springfield, Illinois, USA). Each plastic tarsus band and neck collar had a unique combination of letters and numbers large enough to be identifiable from a distance in the field. Collars were identical to those used extensively on geese throughout the Atlantic Flyway (Hestbeck *et al.* 1991). Goslings were assigned to parents by observing their associations post-banding. Individual goslings were not marked at hatching; however, broods were sometimes individually dyed or marked with ink at hatching when multiple broods of the same age occurred at the same place, so that the broods subsequently could be differentiated.

My observations of where the geese nested ceased in 2008 (when the youngest birds were 7 years old), and my last observations, made to determine whether the birds were still alive, were during 2010. Band recoveries from the U.S. Bird Banding Laboratory up to 2015 were included in the analyses: 31 years after the first goslings and 14 years after the last goslings were banded. Given the length of this study, most geese were followed throughout their lives (*i.e.* they were known to have died before the end of the study). A goose was considered to be dead on receiving a report of its death from the U.S. Bird Banding Laboratory, on finding its carcass, on a hunter informing me that a banded goose had been shot, or when I and other people no longer saw it alive.

Data analysis

Data from all fledglings banded in New Haven County were used to calculate the natal return rate and natal homing rate to the county. Natal return rate was calculated as the proportion of birds that returned as first-time breeders to New Haven County; natal homing rate was calculated as natal return rate adjusted for mortality that occurred during the period preceding the first nesting attempt (Anderson *et al.* 1992). The natal homing rate was determined by dividing the natal return rate by the survival rate for the period from fledgling to recruitment. Annual survival rates (S) were 0.88 for juvenile females, 0.77 for adult females, 0.84 for juvenile males, and 0.71 for adult males in New Haven County (Conover *et al.* 2015). In New Haven County, most geese had nested by the beginning of their fourth year of life (Conover 2012); the delay was due to a scarcity of suitable nesting sites (Gosser & Conover 1999). By then, 52% of females and 42% of males banded as fledglings were still alive.

For the finer-grain analyses of natal site fidelity, I limited my study to fledglings that hatched at the Malty Lakes complex. To be included as a study bird ("subject") for this part of the study, I had to be able to identify both of its parents, know where the subject hatched and was raised as a gosling, and locate where the subject nested during its first and last nesting attempt and where it raised its offspring. I also had to be able to identify its mate(s). This information was known for 29 fledglings (2 males and 27 females), and they became the subjects for this part of the study. Henceforth, "subject" refers only to these 29 fledglings. These analyses were limited to fledglings that hatched on the Maltby Lakes because the lakes were unique: there were only 19 nesting areas which geese could use, they were occupied by geese every year, and geese did not nest elsewhere on the Maltby Lakes. The 19 nesting areas included 12 islands (all < 40 m in length), two peninsulas, three dams, and two mainland shorelines. The Maltby Lakes were also unique because they contained only 39 nesting territories within the 19 nesting areas used by geese. In the Maltby Lakes, nesting territories on islands contained 4–10 m of shoreline while mainland territories contained 30–60 m of shoreline. The 39 goose nesting territories were occupied almost every year; any open territory was quickly occupied by new geese. Apart from the dams, the shoreline was wooded with a thick understory. Geese rarely nested in these wooded areas because an abundance of Red Foxes *Vulpes vulpes* made nesting in these locations dangerous. Hence, nesting sites in the Maltby Lakes were limited and competition for them was high (Gosser & Conover 1999).

Natal philopatry was assessed at five different spatial scales. From largest to smallest, the scales were: (1) New Haven County *versus* anywhere else in North America, (2) the Maltby Lake brood-rearing site *versus* the other two brood-rearing sites in the county, (3) its natal lake *versus* any of the other two lakes in the Maltby Lakes Complex, (4) its natal nesting area *versus* any other natal nesting area (often an island) within the Maltby Lakes, and (5) its natal nesting territory *versus* any of the nesting territories in the Maltby Lakes. For each scale, I tested whether the proportion of subjects that exhibited natal philopatry was higher than the proportion expected by calculating the latter based on the subjects' distribution if they selected nesting areas at random. For example, subjects should raise their brood at the Maltby Lakes brood-rearing site 33% of the time if distributed randomly, given that there are two other brood-rearing sites in the county. If selecting lakes at random, the geese should nest on their natal lake 25% of the time. The Maltby Lakes consist of three lakes, and I added an additional lake for geese nesting anywhere else in New Haven County. This approach is conservative given that I located geese nesting in 18 other lakes, ponds and rivers in the county where geese nested at least occasionally. If selecting natal areas randomly, given 18 natal areas in the Maltby Lakes and an additional one added to the statistical analysis for all other nesting areas in New Haven County, subjects theoretically would be expected to nest in their natal area 5.3% of the time. Hence, I assumed that natal philopatry occurred at the spatial scale of nesting area if > 5.3% of the goslings included in the study returned to nest in their natal area. If selecting natal nesting territories at random, subjects should nest 2.5% of the time on their natal nesting territory, given the 39 nesting territories in the Maltby Lakes and an additional one for geese nesting in any other nesting territory in New Haven County. A Fisher exact probability test was used to compare actual *versus* expected values, because the observed or expected values for at least one cell were < 5 in some comparisons (Siegel 1956).

One-way Mann-Whitney *U*-tests corrected for ties (Siegel 1956) were used to test the hypothesis that fledglings that exhibited natal philopatry would be older than fledglings that did not. A separate test was conducted at each scale. For this and all of the subsequent tests, my study was limited to the 29 subjects used for the finer-grain analyses of natal site fidelity. A subject's age on first nesting was determined by counting the years from hatching to nesting.

In New Haven County, goslings were raised in two different types of families; some parents raised the offspring by themselves (two-parent family), while others joined with other parents to raise their offspring together in a group (described alternately as a gang brood or crèche brood), resulting in a cohesive group of goslings from two or more broods accompanied by four or more parents (Conover 2009). However, to be included in this test, goslings had to be raised in a crèche brood attended by only four parents; more parents than that made it too difficult to assess a fledgling's natal site. Fisher exact probability tests were used to compare natal philopatry rates between (1) subjects raised in two-parent families *versus* crèche broods, (2) subjects nesting for the first time during their lives *versus* the last time, and (3) subjects that were nesting when a parent was alive *versus* subjects that had no living parent, and (4) subjects that were nesting when a parent(s) was also nesting in the county *versus* subjects that were nesting when none of their parent(s) were nesting in the county.

To distinguish between natal site philopatry from parental philopatry, I identified those subjects that had parents nesting concurrently with them but at a site different from the subject's natal territory (where the parents had nested when the subject hatched). I assumed that if a subject was exhibiting natal site philopatry, its nest would be closer to its natal site than to the current nest of its parent(s). Subjects exhibiting parental philopatry would do the opposite. Topographical maps were used to measure the linear distance from each subject's nesting territory to: (1) the current location of its parents' nesting territory, and (2) its natal territory. These distances were compared using a Student's *t*-test for paired data because these distance data were normally distributed (Siegel 1956). All comparisons were considered significant if $P < 0.05$.

Some birds were paired with a new mate that had nested with a different mate the previous year. This meant that the subject's mate already had an established breeding territory somewhere else. Topographical maps were examined to determine whether the subject's new nesting site was closer to its natal territory or to its new mate's prior nesting territory.

Results

A total of 391 female and 340 male fledglings were banded in New Haven County between 1984 and 2001, of which 161 returned as adults to nest in the county (natal return rate = 0.22, $n = 731$ fledglings). The natal return rate for females (0.31) and males (0.12) differed significantly ($\chi^2_1 = 36.76$, $P < 0.001$). Natal homing rate to the county was 0.60 for females and 0.29 for males, and also differed significantly.

Twenty-nine fledglings known to have hatched at the Maltby Lakes went on to nest as adults in New Haven County and met the other criteria to become one of my subjects. Twenty eight of the 29 subjects (96%) were seen raising their first brood on the Maltby Lakes brood-rearing site; the one exception raised its first brood at Lake Whitney in New Haven County, but then raised next year's brood on the Maltby Lakes. None were reported or observed raising a brood outside the county. The proportion that returned to raise their brood at their natal brood-rearing site was much higher than the expected rate of 33% (Fisher exact test: $P = 0.004$).

Seventeen of 29 subjects (59%) first nested at their natal lake; 6 of the 29 subjects (21%) first nested in their natal area (*e.g.* on a particular island within the lake), and 2 of 29 subjects (7%) first nested on their natal territory. The expected percentages for nesting based on subjects selecting sites at random were 25% for natal lakes, 5.5% for natal areas, and 2.5% for natal territories. The percentage of subjects that returned to their natal lake were higher than expected based these expected values

($P = 0.02$) but not for natal area ($P = 0.18$, n.s.) or natal territory ($P = 0.76$, n.s.). The proportion of subjects that nested on their natal lake, natal area, and natal nesting territory during their first nesting year and their last year were similar ($\chi^2_1 = 0.00$, 0.74, 0.00, respectively, $P = 1.00$, 0.39, 1.00, n.s. in each case).

The mean (± s.e.) age on first nesting was 4.2 years (± 0.5, $n = 17$ geese) for subjects that first nested on their natal lake and 3.1 years (± 0.4, $n = 12$) for those that first nested on a non-natal lake; these differences were not significant ($z = 1.58$, $P = 0.06$, n.s.). Those that nested on their natal area were 4.2 years (± 0.9, $n = 6$) while the geese that nested on a non-natal area were aged 3.6 years (± 0.4, $n = 23$); these differences also were not significant ($z = 0.74$, $P = 0.23$, n.s.). The two geese that nested at their natal territory were an average of 5.0 years old ± 1.0 while the 27 geese that nested on a non-natal nesting territory were an average of 3.6 ± 0.4 years old.

Fifteen subjects were raised in crèche brood, and 14 raised by their parents (two-parent families); 67% of those raised in crèche broods returned to the natal lake, 27% to their natal area, and 7% to their natal territory. In contrast, 50% of the subjects raised by their parents returned to their natal lake, 14% to their natal area, and 7% to their natal territory. None of these differences were significant ($P = 0.30$, $P = 0.36$ and $P = 0.78$, respectively, n.s. in each case).

Having a parent alive ($n = 17$) or dead ($n = 12$) when a subject was nesting for the first time made no difference to a subject's natal philopatry. Natal lakes were used by 59% of the subjects with a surviving parent present, *versus* 56% without a living parent; natal areas by 20% with a surviving parent *versus* 22% without a surviving parent, and natal territories by 5% with a surviving parent *versus* 11% without a surviving parent. Fisher exact P-values ranged from 0.48–0.91 (n.s.) for all of these comparisons.

There were 17 occasions when the location of their parents' current territory differed from the subject's natal territory; two subjects were sampled twice because both the subjects and their parents had moved since the subject's first nesting year. The subjects' nesting territory were located on average 341 ± 79 m ($\bar{x}$ ± s.e.) from their natal territory, and 403 ± 79 m from their parents' more recent territory. This difference was not significant ($t_{16} = 0.62$, $P = 0.55$, n.s.).

Four subjects (all females) paired with a bird that occupied a nesting territory with another mate during the previous year. Two subjects nested in their mate's former territory, one nested in its natal territory, and one nested in the lake where its mate had a territory but on a different island.

Discussion

Most studies of natal philopatry seek information on return rates and rely upon the recapture or re-sightings of banded individuals, or the movements of birds fitted with a transmitter that signals the bird's location. These studies provide a minimum estimate of actual natal return rates because many of the marked individuals may have returned to their natal area but were not detected. Detectability itself is a product of the ease of detection and the intensity of the search effort; my study is no different. The data presented here are based on observations of geese with large plastic tarsus bands or neck collars that could be read at a distance, which (noting that the geese could also be identified by their more durable USGS metal bands on recapture) were replaced as they wore out. Hence, I would lose track of a bird only if it lost its collar and tarsus band in the same year it lost its USGS band (most subjects were captured annually), but I do not think that this happened frequently because I rarely found a goose with a collar or plastic band that did not also have its USGS band. Whilst waterbodies in New Haven County were searched for banded geese multiple times during each incubation and brood-rearing periods, some nesting geese were missed, especially when their nests were quickly depredated or abandoned. This would not affect natal return rates, however, except for a goose which nested only in that one year and did not return to its natal area to breed in subsequent years. Missing such birds would decrease estimates of natal return and natal homing rates to below the actual rates, so the natal return and homing rates reported here are conservative.

The natal return rates for Canada Geese to New Haven County were higher for females (0.31) than for males (0.12). Other studies of philopatry in waterfowl likewise found that females have higher natal return rates than males (Williams 1979; Greenwood 1980; Anderson *et al.* 1992; Mabry *et al.* 2013). Among geese, Cooke *et al.* (1995) reported return rates of 0.3 of male and 0.8 for female Snow Geese *Anser caerulescens* banded as fledglings at La Pérouse Bay, Manitoba, that were later detected nesting as adults in the colony. Natal return rates of Canada Geese in the Northwest Territories were 0.06 for males and 0.10 for females (MacInnes & Lieff 1968 as cited by Anderson *et al.* 1992).

Subjects occupied the Maltby Lake brood-rearing site and their natal lake more frequently than expected based on chance but not their natal area or natal nesting territory. Lack of fidelity to natal territories was expected because many parents were still nesting there during the same year that their fledgling nested. Female Common Goldeneyes also rarely nested in their natal nest box for the same reason (Ruusila *et al.* 2001). Among Snow Geese, females return to their natal colony to nest (Cooke *et al.* 1995), but once there, nests were randomly distributed in the colony rather than being close to their natal nest (Cooke & Abraham 1980). Coleman & Minton (1979) found, on analysing natal philopatry for Mute Swans *Cygnus olor* in a 1,440 km^2 study area, that 19 (37%) of 52 females that returned to nest were < 1.6 km from their natal site and 15 more nested 1.6–8.0 km from their natal site. Males were less likely to return: seven nested < 1.6 km of their natal nest, and 13 nested 1.6–8.0 km away from it.

Most research on the precision of natal philopatry in waterfowl has focussed on *Bucephala*; these ducks nest in tree cavities and nest boxes, making it easier to locate their nests and track their movements over years. Pöysä *et al.* (1997) reported that 22 of 30 female Common Goldeneyes that exhibited natal philopatry nested within 1.0 km of their natal nest box, 16 nested within 0.5 km of it, and three nested in the same nest box where they hatched. Dow

& Fredga (1983) reported that Common Goldeneyes that exhibited natal philopatry nested an average of 1.05 ± 0.24 km from their natal nest (range: 0.0–6.0 km). Savard and Eadie (1989) located five female Barrow's Goldeneyes *Bucephala islandica* and Common Goldeneyes that returned to their natal lake to nest; three of them nested within 100 m of the natal nest. Among female Buffleheads *Bucephala albeola* that exhibited natal philopatry, distances between their own nest and their natal nest ranged from 0.0–4.5 km with a mean of 1.0 km (Gauthier 1990). In Finland, female Common Goldeneyes nested an average of 1.4 km from their natal nest box (Ruusila *et al.* 2001). At the Savanna River Plant in South Carolina, 5% of Wood Ducks *Aix sponsa* fledglings returned to the Savanna River Plant to nest. Of these locally recruited ducks, 40% nested in their natal wetland and an additional 35% nested in the nearest wetland to it that contained nest boxes.

I hypothesised that the precision of natal philopatry would be higher during a subjects' last nesting year before dying than during its first because a young goose may not be able to compete successfully for a nesting territory in its natal area (Luna *et al.* 2021) but may be more successful in later years. In my study, however, there were no differences in natal philopatry between a subject's first nesting year and its last. This was supported by the finding that geese exhibiting natal fidelity were similar age to those that did not. In contrast to my results, natal philopatry increased with age in Black Brant (Lindberg *et al.* 1998).

Natal philopatry rates were similar between geese nesting for the first time and those nesting for the last times in their lives. At all spatial scales, the age of philopatric geese were slightly older than non-philopatric geese but the difference was not statistically significant. Neither age nor nesting experience, therefore, seemed to be a factor influencing natal philopatry in my study area. Natal return rates were also similar between: (1) subjects raised in crèche broods compared with those raised in two-parent families, and (2) subjects that had a parent nesting compared to those that did not. A parent's presence made no difference in the probability of a fledgling returning to its natal area, natal lake, natal area or natal territory to nest. The presence or absence of a parent likewise made no difference in the precision of natal philopatry among Common Goldeneyes (Pöysä *et al.* 1997) or Northern Flickers *Colaptes auratus* (Wiebe 2020).

A conflict may arise between a newly paired male and female about selecting their first nest site together, especially if one mate has already established a breeding territory from the prior year but with a different mate and wants to nest there again, whereas its mate wants to return to its natal area. The sample size is very small (n = 4 birds) but results to date for Canada Geese in New Haven County indicate that neither sex dominates in this choice of nest site. Half of the females nested on their new mates' former territory, one returned to its natal territory, and one pair established a new territory. In contrast, female Snow Geese dominate this conflict with the males transferring to their mate's natal colony (Lieff 1973; Cooke *et al.* 1975, 1981); likewise, male Wood Ducks follow females to their natal area (Hepp *et al.* 1989).

Some of my subjects nested closer to their natal territory than their parents' concurrent nesting territory while others nested closer to their parents' current nesting territory. Similar results were found for Common Goldeneyes (Pöysä *et al.* 1997; Ruusila *et al.* 2001).

Most non-migratory Canada Geese nesting in New Haven County returned to nest not only in the same watershed where they were raised, but also on the same lake. This complicates the task of managing goose populations because agencies manage them at large scales (*i.e.* states or flyways). Management on this large scale does not work as well when most geese that hatch in a watershed exhibit strong natal philopatry to that same watershed. The problem is that geese in one watershed may be overharvested and declining in number due to a high level of hunter access in that area, whereas those elsewhere are increasing due to a lack of places where hunting is allowed. Geese might be expected to move from an area with abundant conspecifics to an area with few, but this is less likely to happen when geese exhibit strong natal philopatry. In Connecticut, non-migratory geese are considered a nuisance, and the state wildlife agency is often tasked with trying to reduce their numbers. This task becomes harder when goose populations in different watersheds are variably impacted by any effort to reduce their populations and are highly philopatric. This many explain, in part, why residents in some parts of the state complain that there are too many geese while residents elsewhere complain that there are too few.

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References

Anderson, M.G., Rhymer, J.M. & Rohwer, F.C. 1992. Philopatry, dispersal and genetic structure of waterfowl populations. *In* B.D.J. Batt, A.D. Afton, M.G. Anderson, C.D. Ankney, D.H. Johnson, J.A. Kadlec & G.L. Krapu (eds.), *Ecology and Management of Breeding Waterfowl*, pp. 365–395, University of Minnesota Press, Minneapolis, USA.

Baldassarre, G.A. 2014. *Ducks, Geese and Swans of North America*. Johns Hopkins University Press, Baltimore, Maryland, USA.

Blyton, M.D., Banks, J.S.C. & Peakall, R. 2015. The effect of sex biased dispersal on opposite sexed spatial genetic structure and inbreeding risk. *Molecular Ecology* 24: 1681–1695.

Coleman, A.E. & Minton, C.T.D. 1979. Pairing and breeding of Mute Swans in relation to natal area. *Wildfowl* 30: 217–230.

Conover, M.R. 2009. Gang brooding in Canada Geese: role of parental condition and experience. *Condor* 111: 276–282.

Conover, M.R. 2011. Population growth and movements of Canada Geese in New Haven, Connecticut during a 25-year period. *Waterbirds* 34: 412–421.

Conover, M.R. 2012. Delayed nesting by female Canada Geese (*Branta canadensis*): benefits and costs. *Auk* 129: 140–146.

Conover, M.R. & Chasko, G.C. 1985. Nuisance goose problems in the eastern United States. *Wildlife Society Bulletin* 13: 228–233.

Conover, M.R., Dinkins, J.B. & Ruzicka, R.E. 2015. Consequences of hunter harvest, winter weather, and increasing population size on survival of non-migratory Canada Geese in Connecticut. *Journal of Wildlife Management* 79: 1239–1245.

Cooke, F. & Abraham, K.F. 1980. Habitat and locality selection in Lesser Snow Geese: the role of previous experience. *Proceedings of the International Ornithological Congress* 17: 998–1004.

Cooke, F., MacInnes, C.D. & Prevett, J.P. 1975. Gene flow between breeding populations of Lesser Snow Geese. *Auk* 92: 493–510.

Cooke, F., Bousfield, M.A. & Sadura, A. 1981. Mate change and reproductive success in the Lesser Snow Goose. *Condor* 83: 322–327.

Cooke, F., Rockwell, R.F. & Lank, D.E. 1995. *The Snow Geese of La Pérouse Bay: Natural Selection in the Wild*. Oxford University Press, Oxford, UK.

Coulson, J.C. 2016. A review of philopatry in seabirds and comparisons with other waterbird species. *Waterbirds* 39: 229–326.

Craighead, L.L. & Stockstad, D.S. 1964. Breeding age of Canada Geese. *Journal of Wildlife Management* 28: 57–64.

Dobson, F.S. 1982. Competition for mates and predominant juvenile male dispersal in mammals. *Animal Behaviour* 30: 1183–1192.

Dow, H. & Fredga, S. 1983. Breeding and natal dispersal of the goldeneye, *Bucephala clangula*. *Journal of Animal Ecology* 52: 681–695.

Gauthier, G. 1990. Philopatry, nest-site fidelity, and reproductive performance in Bufflehead. *Auk* 107: 126–132.

Gosser, A.L. & Conover, M.R. 1999. Will the availability of insular nesting sites limit reproduction in urban Canada Goose populations? *Journal of Wildlife Management* 63: 369–373.

Greenwood, P. 1980. Mating systems, philopatry and dispersal in birds and mammals. *Animal Behaviour* 28: 1140–1162.

Hepp, G.R., Kennamer, R.A. & Harvey, W.F. 1989. Recruitment and natal philopatry of Wood Ducks. *Ecology* 70: 897–903.

Hestbeck, J.B., Nichols, J.D. & Malecki, R.A. 1991. Estimates of movement and site fidelity using mark-recapture data of wintering Canada Geese. *Ecology* 72: 523–533.

Lieff, B.C. 1973. The summer feeding ecology of Blue and Canada Geese at the McConnell River Northwest Territories. Ph.D. thesis, University of Western Ontario, London, Canada.

Lindberg, M.S., Sedinger, J.S., Derksen, D.V. & Rockwell, R.F. 1998. Natal and breeding philopatry in a Black Brant, *Branta bernicla nigricans*, metapopulation. *Ecology* 79: 1893–1904.

Lokemoen, J.T., Duebbert, H.F. & Sharp, D.E. 1990. Homing and reproductive habits of Mallards, Gadwalls, and Blue-winged Teal. *Wildlife Monographs* 106: 3–28.

Luna, Á., Lois, N.A., Rodríguez-Martinez, S., Palma, A., Sanz-Aguilar, A., Tella, J.L. & Carrete, M. 2021. Urban life promotes delayed dispersal and family living in a non-social bird species. *Scientific Reports* 11: 107. https://doi.org/10.1038/s41598-020-80344-8.

Mabry, K.E., Shelley, E.L., Davis, K.E., Blumstein, D.T. & van Vuren, D.H. 2013.

Social mating system and sex-biased dispersal in mammals and birds: a phylogenetic analysis. *PLoS ONE* 8: e57980.

MacInnes, C.D. & Lieff, B.C. 1968. Individual behavior and composition of a local population of Canada Geese. *In* R.L. Hine & C. Schoenfeld (eds.), *Canada Goose Management,* pp. 93–101. Dembar Educational Research Services, Madison, Wisconsin, USA.

Morandini, V. & Ferrer, M. 2017. Natal philopatry: local experience or social attraction? An experiment with Spanish Imperial Eagles. *Animal Behaviour* 130: 153–157.

Person, B.T., Babcock, C.A. & Ruess, R.W. 1998. Forage variation in brood-rearing areas used by Pacific Black Brant Geese on the Yukon-Kuskokwim Delta, Alaska. *Journal of Ecology* 86: 243–259.

Person, B.T., Herzog, M.P., Ruess R.W., Sedinger, J.S., Anthony, R.M. & Babcock, C.A. 2003. Feedback dynamics of grazing lawns: coupling vegetation change with animal growth. *Oecology* 135: 583–592.

Pöysä, H., Runko, P. & Ruusila, V. 1997. Natal philopatry and the local resource competition hypothesis: data from the Common Goldeneye. *Journal of Avian Biology* 28: 63–67.

Pusey, A.E. 1987. Sex-biased dispersal and inbreeding avoidance in birds and mammals. *Trends in Evolutionary Ecology* 2: 295–299.

Rockwell, R.F., Cooch, E.G., Thompson, C.B. & Cooke, F. 1993. Age and reproductive success in female Lesser Snow Geese: experience, senescence and the cost of philopatry. *Journal of Animal Ecology* 62: 323–333.

Ruusila, V., Pöysä, H. & Runko, P. 2001. Costs and benefits of female-biased natal philopatry in the Common Goldeneye. *Behavioral Ecology* 12: 686–690.

Savard, J.-P.L. & Eadie, J.M. 1989. Survival and breeding philopatry in Barrow's and Common goldeneyes. *Condor* 91: 198–203.

Siegel, S. 1956. *Nonparametric Statistics for the Behavioral Sciences.* McGraw Hill, New York, USA.

Slagsvold, T. & Wiebe, K.L. 2018. Immigrants and locally recruited birds differ in prey delivered to their offspring in Blue Tits and Great Tits. *Animal Behaviour* 139: 127–135.

Smith, A.E., Craven S.R. & Curtis, P.D. 1999. *Managing Canada Geese in Urban Environments.* Jack Berryman Institute Publication No. 16, Utah State University, Logan, Utah, USA.

Ydenberg, R.C., Giraldeau, L.A. & Falls, J.B. 1988. Neighbours, strangers, and the asymmetric war of attrition. *Animal Behaviour* 36: 343–347.

Wang, Y., Lane, A. & Ding, P. 2012. Sex-biased dispersal of a frog (*Odorrana schmackeri*) is affected by patch isolation and resource limitation in a fragmented landscape. *PloS ONE* 7(10): p.e47683.

Wiebe, K.L. 2020. Local recruitment in Northern Flickers is related to environmental factors at multiple scales and provides reproductive benefits to yearling breeders settling close to home. *Auk* 137(2): 1–10.

Williams, M. 1979. The social structure, breeding and population dynamics of Paradise Shelduck in the Gisborne-East Coast District. *Notornis* 26: 213–272.