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Rearing conditions of greylag geese affect habitat choice throughout life

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Anthropogenic changes to the landscape such as fertilization and mowing schemes have been correlated with goslings obtaining a higher weight gain during the first weeks of their life, which in turn increases breeding success and survival at the adult stage. As goose numbers rise, conflicts with farmers become stronger as the birds use agricultural sites for foraging. In this study, habitat choice for individually marked greylag geese from four different rearing conditions, categorized by their temporal application of fertilizer, was documented over a seventeen-year period. Weekly observations took place on a resident population of wild greylag geese within the Ooijpolder, the Netherlands. The region comprises of areas dedicated to nature restoration as well as agricultural use. In essence, we infer the habitat choice of greylag geese from the frequency of sightings of individually marked geese in different habitat patches, and model habitat choice as a function of rearing conditions, age, and seasonality. Despite a general preference for agricultural grassland, about 40% of the habitat choice was determined by the rearing condition of geese. Interestingly, geese reared in restored meadows, a less favorable rearing habitat, exhibited strong habitat fidelity and preferred to forage in meadows in the spring. Habitat choice was furthermore influenced by age of adult geese and seasonal changes in plant availability. We discuss management implications of our results on habitat choice in an agricultural landscape for increasing resident goose populations. An efficient management measure would be the limitation of goose access to improved grassland during rearing period in the spring.

Over the last four decades there has been an astonishing goose population increase in Europe as well as in North America (Ankney 1996, Fox et al. 2010). In particular, resident greylag geese *Anser anser* in the Netherlands have had an unprecedented rise after a population crash from a few geese in 1960s to approximately 439 000 at present day (Schekkerman 2012, Lensink et al. 2013). This population explosion has been attributed to a shift in habitat use from natural vegetation to agricultural grasslands improved by the application of fertilizer as well as reduction in hunting pressure (Madsen and Fox 1995, van Eerden et al. 2005). Specifically, a longer plant availability and higher crude protein content in improved grassland along with spilled harvest crops has supported the rise in goose numbers (Fox et al. 2005). This preference has an obvious benefit to the geese as population growth was observed when the rearing sites were on farmland i.e. cultivated pasture and agricultural crops (Feige et al. 2008, Madsen et al. 2014). Consequently, the mounting numbers of geese on agricultural lands has caused a substantial increase in perceived losses to agricultural grass and crops (Madsen et al. 2014). Recurrent conflict increases in landscapes with both agricultural fields and extensive wetlands or lake systems (Merkens et al. 2012).

Flexibility in habitat usage is advantageous when anthropogenic modification is common in the landscape (van Eerden et al. 2005). This is in accordance with the ideal distribution, where animals are expected to forage in profitable areas (Fretwell 1972). While barnacle geese generally show strong site fidelity, females do adjust their choice of rearing pasture within an area to take advantage of the most rewarding food resource (Lindberg and Sedinger 1998, Black et al. 2007). In addition, if a pasture becomes more desirable, it will have a higher influx of birds from other sites (Bos and Stahl 2003). After parental greylag geese travel with their young from the breeding sites to their rearing sites, they restrict their movement once settled at a profitable rearing site (Paakspuu 1963, Hudec and Rooth 1970, Dick 1991). Flexibility in the choice of rearing sites is vital in a dynamic cultivated landscape, as a change in a pasture's fertilizer level affects the rearing area's attributes.

The benefits of good rearing conditions in the first eight weeks of a gosling's life have far reaching consequences for life history parameters across goose species. Goslings have a limited gastrointestinal capacity; consequently greater snow geese goslings foraging in low nutritious rearing sites cannot compensate quality with quantity (Manseau and Gauthier 1993). Without sufficient nutrients the young will not be able to complete their growth and remain smaller than those that had access to better food resources (Mainguy et al. 2006). Goslings raised on food with experimentally higher protein content, had a steeper growth curve and survival (Richman et al. 2015). Vegetation with a higher nutritional content in snow goose rearing sites positively influences gosling weight at fledging (Aubin et al. 1993). Furthermore, adult body size is highly correlated to the access of high quality food during the first eight weeks of life; barnacle geese cannot significantly increase their body size after they mature (Loonen et al. 1997). Heavier goslings have a higher survival rate until breeding age and they have a better chance of breeding (Nilsson et al. 1997, van der Jeugd and Larsson 1998). Moreover, larger lesser snow geese females produce more and larger eggs, which in turn become larger young (Cooch et al. 1991). Lastly, large barnacle geese have a higher survival rate and an overall higher lifetime reproduction output (Black et al. 2007). As a consequence, the rearing habitat is a useful variable to include as a steering factor for the fitness of adult geese.

The same factors that increase fitness also influence site choice through competition for resources. Favorable rearing areas, such as pasture that have been enriched by fertilizer, offer goslings higher levels of crude protein and digestibility than natural grassland (van Eerden et al 1996). Therefore, geese from favorable rearing sites are expected to forage in improved grassland as adults. Due to competitive advantages, access to preferred foraging habitats rises with body mass and family members (Kortrschal et al. 1993, Poisbleau et al. 2006). However, geese with lower competitive abilities may be more prone to risk antagonistic interactions to benefit from more profitable habitat (Scales et al. 2013). With the current study we intend to bridge the gap in knowledge on the effects of rearing condition in habitat choice later in life.

In this study the rearing conditions of goslings are classified in terms of the grassland subjected to different fertilizer regimes. Fertilizer application to pastures is used as an established proxy for the attractiveness of foraging site for geese. It has been documented that pastures improved with fertilizer have an increased number of foraging geese (Bos et al. 2008). In addition, geese families in agricultural grassland produced elevated numbers of recruits (Black et al. 1991). Modern agricultural landscapes are applied with varying levels of fertilizer; therefore it is worthwhile to examine the differences between developed and natural rearing conditions on adult goose habitat choice.

We developed a statistical model to examine the effects of rearing condition on habitat choice. In doing so we took into account age of geese and seasonality. Age is an important factor in determining the position of individual geese in flock hierarchy, and therefore affects access to food resources (Weiß et al. 2011). In addition, seasonality affects the profitability of habitat through changes in plant phenology and availability (McKay et al. 2006, Black et al. 2007). The resident goose population presents the opportunity to examine the effects of these factors on habitat choice, while excluding the influence of migration as a stressor. Hence, the model simultaneously examines how habitat choices of resident greylag geese are affected by rearing condition, age and seasonality.

Currently, there is little insight to how habitat choice is affected by the state of individual rearing conditions. Modern agricultural landscapes are composed of a variety of different rearing opportunities for geese. Given the economical impacts of geese on the agricultural lands, it is vital to examine the different influences on goose habitat choice and how they interact. In this study, we examined 1) whether habitat choice is non-random with respect to habitat availability, and 2) whether habitat choice of individual geese is affected by rearing conditions.

Methods

Field site and protocol

Between 1997 and 2013, 359 greylag goose goslings were individually marked with neckbands in the Ooijpolder, the Netherlands (51°51′N, 05°55′E) and have been followed almost weekly throughout their life. The geese were generally caught for ringing during the molting period of parental birds at the rearing areas (end of May through mid July), when they form flocks close to the water as anti-predator behaviour (Kahlert 2003, Voslamber et al. 2010). Molting geese were caught in funnels (Persson 1994). In most years only adults with young were caught, but in some years we also caught a number of non-breeding birds. Weekly observations of the geese were conducted by a single observer from 1997 to 2013 when site-specific resightings were recorded via a 7 × binocular or 20–60 × telescope using a car as shelter. There was no difference in readability of the greylag goose neck rings between habitats.

Rearing conditions

In this study, rearing condition refers to the amount of fertilizer applied to the grassland where the goslings were reared. Rearing conditions were categorized between 1 and 4, with 4 referring to the annual application of fertilizer, in 3 referring to no fertilizer application in that particular breeding season, 2 referring to no fertilization within the last three years, and 1 referring to a situation when fertilizer has been applied longer than three years ago. In the text, rearing sites 1 and 2 will be referred to as less favourable, while rearing areas 3 and 4 are favourable. The management in our study area varied between years. Therefore, a particular rearing condition depends on the fertilizer regime rather than a specific location.

Habitats

From digitized maps we obtained information on six major habitat types relevant to adult geese in our study area (Table 1). The location of the habitats can change throughout the years and is representative of a dynamic landscape. Hence, habitat fidelity is examined rather than site fidelity. There was a decline in agricultural pastures and a

Table 1. Description of major habitat classes used to categorize habitat choice of greylag geese in this study, including the number of times geese were sighted in each respective habitat, and the proportion of the habitats within the Ooijpolder.

Habitats	Description of habitat	No. geese sightings	Proportion of habitat
Natural tubers	swamp, water	350	0.031
Natural vegetation	restored meadow	1763	0.189
Agricultural grass	pasture	8830	0.478
Agricultural corn	spilled corn	1282	0.128
Agricultural grain	spilled grain	1247	0.101
Agricultural tubers	potatoes, sugar beet	1206	0.070

concurrent increase in natural grassland (Supplementary material Appendix 1 Fig. A1). However, during the course of the study period the total area available to the greylag geese did not decrease.

Statistics

For the analyses we only utilized the observations of ringed young for which the rearing conditions were known. In total, 359 individuals were observed over 17 years, with individuals being observed between 1 and 311 times ($n = 359$, $\bar{x} = 46.49 \pm 56.02$). The total number of observations amounted to 14 678. The sampling of individuals from the rearing habitats was reflective of the spring consensus in the Ooijpolder (Avé, Voslamber, Hallman and Stahl unpubl.).

When the adult geese were resighted, each observation was assigned to one of the six habitat categories (listed in Table 1) resulting in a dataset that was treated as a multinomial distribution with six mutually exclusive and independent possible outcomes. We used multinomial logistic regression (package = "mlogit", Croissant 2013) in statistical software R (<www.r-project.org>) to examine the probability of whether a goose would forage on a particular habitat type based on the explanatory variables; rearing condition, age, seasonality (expressed as month of the observation), and full interactions. The habitat category agricultural grassland was used as reference, as it is the habitat with the most observations (Table 1). Months are ordered according to a breeding year; from July to June as the young fledge in July. As multiple observations of the same individuals were present in the data, the model predicts a probability for each individual rather than per observation. The most parsimonious model according to AIC was utilized, a full model with the following variables; rearing, month and age (Supplementary material Appendix 2 Table A1).

A multivariate logistic regression model requires an independence of alternative choices. Simply, the probability that one of dependent variables (habitat) is chosen is not due to the presence or absence of another habitat. This model has that independence (Hausman–McFadden test ($\chi = 46.599$, $DF = 24$, $p = 0.0037$)).

Habitat availability

The availability of the habitat, which occurs in the Ooijpolder, was calculated by measuring the surface area of each habitat category in hectares per year. The proportion of the suitable landscape was averaged from 1997–2013. A preference score was calculated by using the proportion of the habitat divided by the probability of individual habitat choices, then the score was log transformed. Scores above zero signify non-random foraging on the suitable habitats.

Results

Irrespective of the rearing condition, greylag geese foraged on agricultural pasture more than any other suitable habitat (Fig. 1). According to the predictions of the model, the probability of adult geese foraging in agricultural pasture was roughly 60%. Interestingly, the age of the geese and the rearing condition influenced whether geese forage on restored meadow ($t_{14,648} = -2.34$, $p = 0.01$) in the spring and on agricultural corn ($t_{14,648} = 2.08$, $p = 0.03$) and grain ($t_{14,648} = 2.08$, $p = 0.05$) in the fall (Fig. 2, 3). Throughout life, the geese from less favourable rearing conditions have a higher probability to forage in restored meadows during spring and summer. In early spring, before the breeding season, older geese from favourable rearing conditions foraged in the restored meadows. Corn was more likely to attract younger geese from favourable rearing conditions. Conversely, geese raised in less favourable rearing conditions have a higher probability to forage on grain as they grew older. If younger geese did visit the grain fields, then they were more likely to do so later in the winter. Regardless of their rearing condition, during the months after fall harvest, geese had a higher probability of foraging on agricultural tubers ($t_{14,648} = -3.39$, $p < 0.001$). Therefore, for the habitats agricultural corn, agricultural grain, and restored meadows, the influences on habitat choice are interconnected.

The habitat choice of pasture was non-random given the availability of the suitable habitats. Geese, of all rearing conditions, showed a clear preference for agricultural grassland (Fig. 4). While the model does not predict significant differences between rearing conditions with respect to agricultural tubers, geese from favorable rearing conditions had a non-random preference for them.

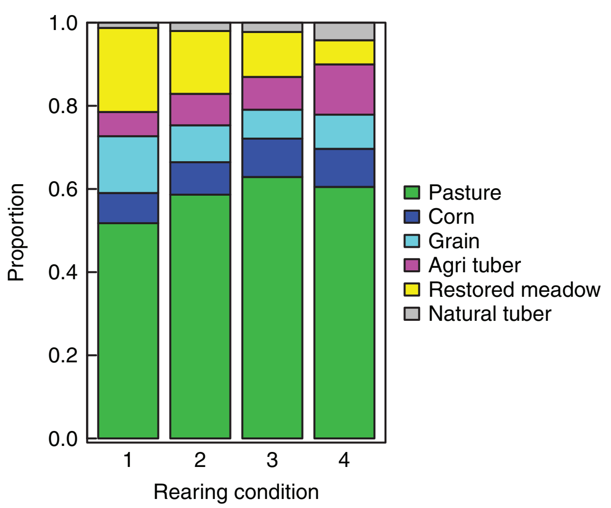

Figure 1. Relative proportion habitat choice of adult geese in relation to rearing conditions (grassland ranging from restored meadows to annual fertilizer regime).

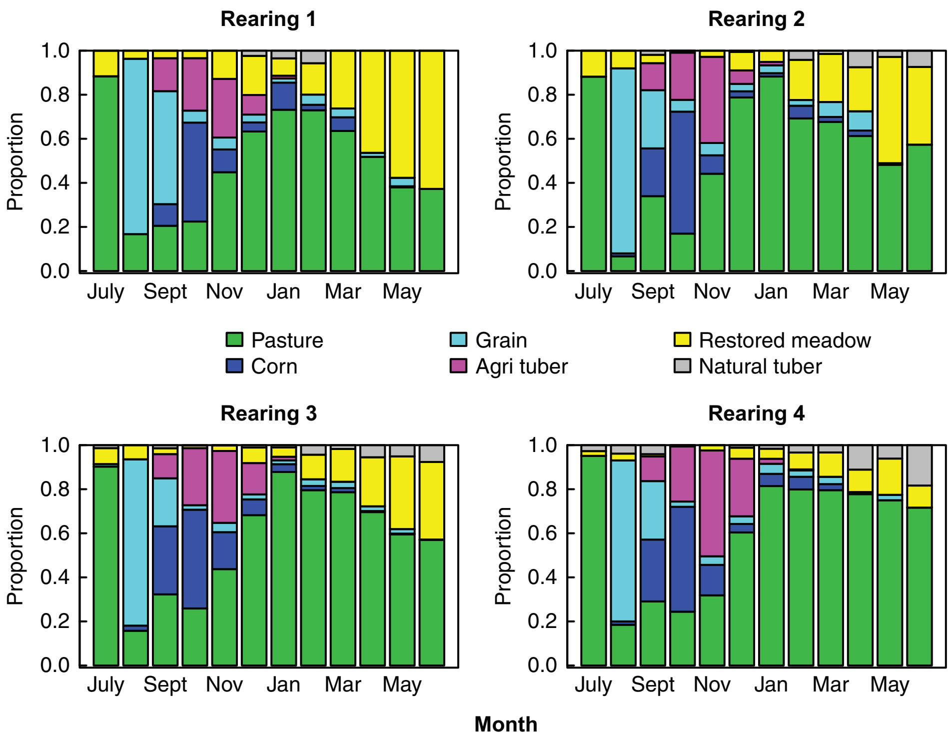

Figure 2. Relative proportion habitat choice of adult geese in relation to season and rearing conditions. The year begins with July as this is when goslings fledge.

Discussion

Improved grassland seems to be equally attractive to geese, as the different rearing conditions deployed a high probability (60%) of foraging on improved agricultural grassland. However, there was a distinct difference in preference for corn, grain, and restored meadow for geese from different rearing conditions. These differences in habitat choice correspond with the availability of food and physiological stress associated with winter. For example, in early spring geese

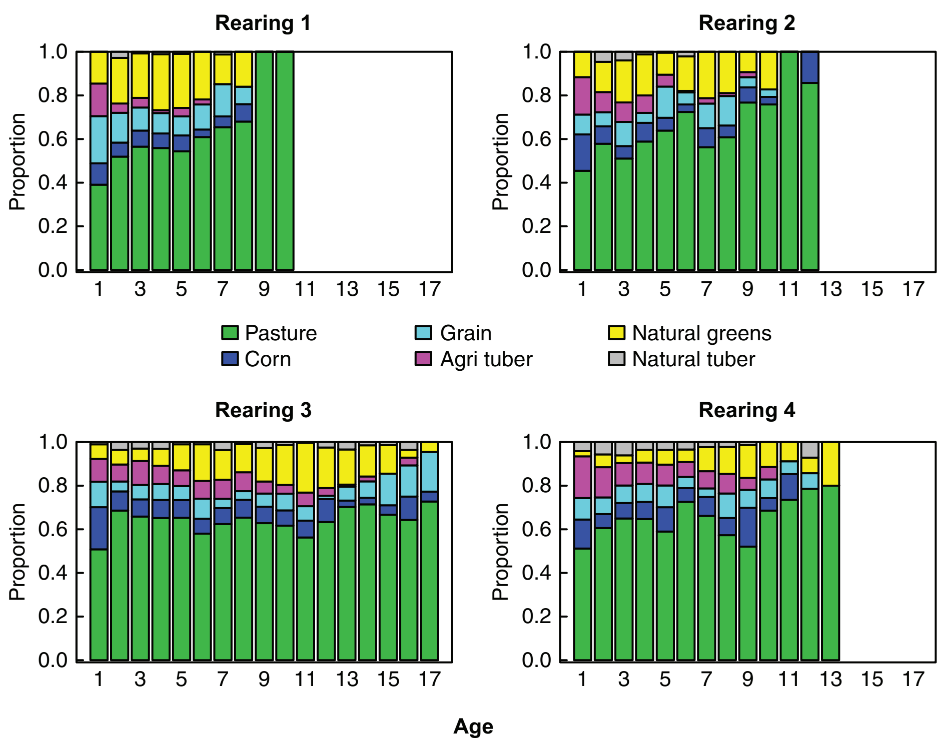

Figure 3. Relative proportion habitat choice of adult geese in relation to age and rearing conditions. Note – the graphs of rearing conditions 1, 2, and 4 stop before 17 years, because geese from these rearing condition have a shorter lifespan than geese from rearing conditions 3.

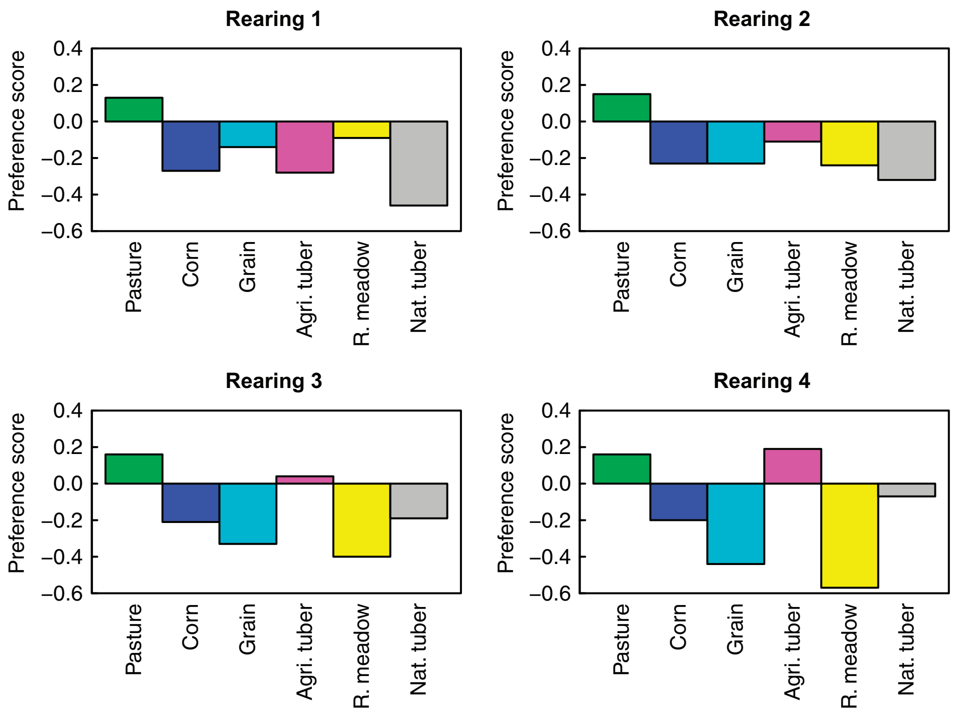

Figure 4. Preference scores with respect to habitat choice given rearing condition. Pasture consistently have a preference score above zero indicating a non-random habitat choice.

from more favourable habitats choose to forage in restored meadow habitat. Intriguingly, geese reared in less favourable habitats preferred to forage in restored meadows during the entire spring and summer. Furthermore, we observed a clear preference of young geese from favourable rearing conditions for foraging on spilled corn, an energy rich food source with a temporally limited availability. Meanwhile, areas with spilled grain were an appealing habitat for geese of less favourable rearing conditions. Our long-term observations of ringed individuals give a unique insight on the effect of rearing sites on habitat choice later in life.

The benefits of foraging on agricultural grasslands cannot be overstated. The advantages the farmers provide by improving the grasslands include: high levels of crude protein, easier digestibility, high intake rates, and a longer period of seasonal availability of grass swards (van Eerden et al. 1996, van der Graaf et al. 2006). These nutritional benefits translate into behavioural changes in geese. Application of fertilizer increases the density of geese foraging in the pasture (Hassal and Lane 2001). In addition, behavioural studies have demonstrated the preference for fertilized grass patches and shown geese guarding them (Bell 1988, Manseau and Gauthier 1993, Bos et al. 2005). Clearly, the benefits of improved grasslands for geese are distinct and can hardly be ignored as criteria for habitat choice.

Seasonal changes affect vegetation availability and physiological requirements, and therefore influence the annual variation in goose distribution (Tinkler et al. 2009). Firstly, the changes in availability of food resources is caused by peaks in availability of highly digestible, highly nutritious grass in spring and the temporal availability of spilled harvest crops in fall (McLandress and Raveling 1981, Amano et al. 2004, van der Graaf et al. 2004, Hassal and Lane 2005). Secondly, important peaks of physiological energy demands are present due to thermoregulation in winter and reproduction in spring. Nutritionally rich food resources are essential, as geese are restricted by their poor digestion (Bos et al. 2005). The birds need to build up fat before and during the winter in order to survive (Biebach 1996). Moreover, the breeding season shows the highest energy demand of the year (Dawson and O'Connor 1996). Female birds exhibit higher breeding success when they have access to energy rich crops during the winter and pastures during the breeding season (Carey 1996). It is expected that greylag geese utilize the different high-energy habitats available during the year to maximize survival and reproductive output.

Spring habitat choice displayed by geese reared in less favourable rearing sites can potentially be explained with habitat fidelity. Individuals that consistently return to a habitat to rear their young or forage demonstrate breeding fidelity and foraging fidelity (Larsson and Forslund 1992, Lowther et al. 2012). In the Ooijpolder, 72% of the ringed breeding females favour sites that resemble rearing conditions they experienced and they return to them with their own offspring. Fidelity to a habitat is heightened with each successful breeding attempt experienced (Hoover 2003). Nevertheless, at a population level variation in foraging fidelity is advantageous when habitat conditions are fluctuating, i.e. during habitat degradation or improvement (Lindberg and Sedinger 1998, Bos and Stahl 2003). However in this study, geese raised in restored meadows are faithful to that habitat for foraging as well as rearing their young.

The influence of age and rearing condition on habitat choice is due to the dual importance of age and size for the dominance structure in goose groups. Both, larger body weight as well as its position as a breeding bird increase an individual's dominance and positively correlate with individual competitive capabilities (Poisbleau et al. 2006, Weiß et al. 2011). Dominance increases access to profitable food resources, which impacts foraging behaviour of geese (Newton 1998). Unlike pasture, spilled corn and grain have patchy distributions, which allows dominant geese to monopolize the spilled crops found by the subordinate geese (Stahl et al. 2001). Therefore, younger geese from favourable rearing conditions have an advantage of their size over geese from less favourable conditions (Aubin et al. 1993). Likewise, younger geese from the less fertilized habitat had to compete for grain with breeders from the same rearing condition. Further study is needed to distinguish a possible difference in the intake rate between grain and corn, which could indicate an advantage for one of the harvest crops. It is plausible that a higher predation risk is perceived in the arable land than in pasture and restored meadow, as grassland is preferred when geese age (Whittingham et al. 2006). Understanding the past rearing conditions of geese allows for a closer examination of the effects of size on competition in habitat choice.

The results of the present study have to be considered in relation to habitat availability in the Ooijpolder. Note that the area of agricultural grassland did not increase during our long-term study period. The preference score is an important tool in examining the relative importance of different habitats, as it depicts non-random movements when a particular habitat is favored. Agricultural grassland is highly favored, and foraging in that habitat was not random. This corresponds with earlier findings in observational and experimental field studies on geese (Mulder et al. 1995, van der Graaf et al. 2007). It is conceivable that the area covered by the other crops do not provide the same evenly distributed benefits as agricultural grassland.

Currently, the literature on goose habitat choice consists of migrant populations and if the rearing effects on goslings are examined, there is a focus on differences in the time of hatching or gosling movements. Most habitat choice studies focus on geese that migrate from their artic breeding grounds to their temperate wintering grounds (Merkens et al. 2012). In North America, the body mass differences between lesser snow geese have resulted from seasonal variation, as the late goslings have inferior access to food (Cooch et al. 1991, Cooke et al. 1995). Furthermore, greater snow goose families that traveled to rearing sites of improved quality exhibited heavier fledglings (Mainguy et al. 2006). However, in a study examining seven comparable unimproved rearing sites there was no significant difference in lifetime fitness of black brant geese between rearing sites (Nicolai et al. 2014). This study is unique with its long-term observation of resident population of geese whose goslings are reared in distinct habitats which range from restored meadow to intensively managed pasture.

Goose habitat choice gives several insights in managing non-migrant geese populations. Firstly, it would be a prudent method for population reduction to restrict the access of geese with young to improved grassland. Geese reared on improved grassland have an increased nesting success, which contributes to population growth (van der Jeugd and Larsson 1998, Feige et al. 2008). Secondly, a management method aimed to reduce foraging levels on pastures would be to lure geese to fields with harvest crops, however this is predicted to increase crop damages in the long run as it increases the carrying capacity (Hill and Frederick 1997, Merkens et al. 2012). Instead, it would be advisable to diversify crops and reduce field size, as these are less preferential to geese (Rosin et al. 2012). Lastly, it would be beneficial to continue disturbance when improved pastures are abandoned, as the combination of previously fertilized fields and the lack of disturbance is in itself advantageous (Madsen and Fox 1995, Bos and Stahl 2003, Beaumont et al. 2013). Knowledge of foraging differences between rearing conditions offers a tool box for managing goose populations.

Habitat choice is a complex behaviour that is influenced by rearing conditions, age and season. In spring, geese raised in the restored meadows exhibit habitat fidelity. Later in the season, the habitat choice of spilled harvest crops illustrates the potential importance of social interaction and costs associated with foraging in different habitats. The benefits of improved pastures for geese are noticeable, as geese from all rearing conditions show a preference for that habitat. Our study demonstrates that rearing condition does affect where the geese forage later in life. Further study is required to understand how rearing conditions affect habitat fidelity in relation to reproduction success in the light of the conflict between the human interests and the greylag goose population explosion.

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Supplementary material (available online as Appendix wlb-00204 at <www.wildlifebiology.org/appendix/wlb-00204>). Appendix 1–2.