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Foraging preference of barnacle geese on endophytic tall and red fescues

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Abstract: Many grasses (Poaceae) have symbiotic fungal endophytes, which affect livestock by producing unpalatable or harmful secondary compounds. Less is known about the repelling effects of fungal endophytes on avian grazers despite potential wildlife management implications. Herbivorous goose (*Branta* spp.) species may become a nuisance in recreational use areas via fecal littering. Planting these areas with grasses that avian grazers avoid may help mitigate this damage. In 2016, we studied the foraging preference of the barnacle geese (*B. leucopsis*) with endophytic (E+) or endophyte-free (E-) red fescue (*Festuca rubra)* and/or tall fescue (*Schedonorus phoenix*) in 2 sites in Finland that had a history of nuisance geese damage. In the high grazing pressure site, we planted both grass species, while in the low grazing pressure site only tall fescue was used. Geese preference was measured as the percentage of the area grazed, the height of the residual grass grazed, and the number of fecal droppings in the grass plots. Geese foraging did not differ between E- and E+ grasses, but red fescues were preferred over tall fescues. This supports previous findings that tall fescues or other coarse species could reduce the attractiveness of recreational areas to geese.

Key words: barnacle goose, *Branta leucopsis*, Finland, fungal endophyte, grass, herbivory management, human–wildlife conflict management, Poaceae, trophic interaction

Grasses (Poaceae) are tolerant to herbivory due to their excellent regrowth capacity, underground storage organs, and silicon-based physical defense (Dyer et al. 1991, Vicari and Bazely 1993, Huitu et al. 2014). In addition, many temperate Pooideae grasses, including economically important forage species, are protected against herbivores by symbiotic endophytic *Epichloë* fungi, inhabiting aboveground parts of the host grass (Siegel et al. 1985, Clay and Schardl 2002, Saikkonen et al. 2013, Schardl et al. 2013, Helander et al. 2016). For example, it has been estimated that approximately 90% of tall fescue (*Schedonorus phoenix* [Scop.] Holub. ex *Lolium arundinaceum* [Schreb.] S. J. Darbyshire, syn. *Festuca arundinaceae* [Schreb.]) pastures in the United States have symbiotic endophyte fungus *Epichloë coenophiala* (Morgan-Jones & W. Gams; formerly *Neotyphodium coenophialum* [Morgan-Jones & W. Gams] Glenn, C. W. Bacon & Hanlin; Siegel et al. 1985, Shelby and Dalrymple 1987, Ball et al. 1993, Hoveland 1993, Helander et al. 2016). Protection against vertebrate herbivores is attributable to ergot alkaloids and indole-diterpenoids produced by *Epichloë* species (Yates et al. 1985, Lyons et al. 1986, Yates and Powell 1988, Saikkonen et al. 2013, Schardl et al. 2013). The adverse effects of *Epichloë* symbiotic grasses (hereafter, E+) on vertebrate herbivores have been demonstrated to be particularly pronounced in nutrient-rich urban recreation areas and agroecosystems

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(Siegel et al. 1985; Conover and Messmer 1996; Bazely et al. 1997; Saikkonen et al. 2006, 2010).

Feeding mainly on E+ tall fescues, combined with high temperatures, can cause fescue toxicosis to livestock (*Bos* spp.; Bacon et al. 1977, Hemken et al. 1981, Porter and Thompson 1992, Ball et al. 1993, Thompson and Stuedemann 1993). Economical value of systemic *Epichloë* endophytes related to forage quality and biocontrol has been widely recognized in the agriculture and turf grass industry because the vertical transmission of the fungus via host grass seeds allows their use in grass breeding (Kauppinen et al. 2016). However, much less is known about the repellent effects of E+ grasses on vertebrate herbivores and whether E+ grasses could be used to prevent human–wildlife conflicts (Nyhus 2016).

Previous studies have reported that E+ grasses, or selected plant species, could be used to reduce the attractiveness of recreational areas to herbivorous goose species (Conover and Chasko 1985, Conover 1991, Washburn et al. 2007, Pennell et al. 2010, Washburn and Seamans 2012). For example, Conover and Messmer (1996) reported captive Canada goose (*Branta canadensis*) preference to endophyte-free (hereafter, E-) tall fescues over E+ ones. In addition, geese avoid some plants that contain secondary metabolites such as volatile terpenes, tannins, and essential oils (Buchsbaum et al. 1984, Wink et al. 1993), indicating that geese can learn to distinguish favored species through tasting and learning, although they can be tolerant to alkaloids (Wink et al. 1993).

Furthermore, Washburn et al. (2007) showed that Canada geese prefer to forage on a mixture consisting mostly of perennial ryegrass (*Lolium perenne*) and white clover (*Trifolium repens*) over tall fescue, indicating that tall fescue may be less palatable to geese. However, as only E+ tall fescue was used, and the endophyte status (E+or E-) of the ryegrass was not known, it is unclear whether the reluctance of geese to forage on tall fescue was caused by the endophytic fungi or between-species differences, such as difference in texture of the plants. Thus, as Conover (1991) suggested, it is possible that tall fescue is a less favored foraging species due to its toughness and could therefore be used to reduce the attractiveness of lawns to avian grazers.

The population sizes of many goose species have increased in the northern hemisphere, partly because agricultural fields and recreational sites provide safe and high-quality foraging sites (e.g., Si et al. 2011, Väänänen et al. 2011, Fox and Abraham 2017, Fox and Madsen 2017, Fox et al. 2017). Thus, it is not surprising that human–wildlife conflicts caused by geese have increased in several countries, impacting agricultural fields, the aviation industry, and recreational areas (Conover and Chasko 1985, Conover 1991, Little and Sutton 2013, Bradbeer et al. 2017, Fox and Madsen 2017).

Canada goose feces decreased the aesthetic appeal of recreational areas in the United States (Conover and Chasko 1985). The Egyptian goose (*Alopochen aegyptiaca*) causes similar problems in South Africa (Little and Sutton 2013). The increasing number of the barnacle goose (*B. leucopsis*) has caused littering problems in recreational areas of Helsinki and Turku, Finland (Niemi et al. 2007, Vuorisalo 2016). The population size increased during 1985–2010, likely due to human influence. In the Helsinki area alone, the number of breeding pairs increased from 1 to 1,440 during 1989–2010 (Väisänen et al. 1998; Väänänen et al. 2010, 2011). In addition to agronomic and aesthetic problems, geese and other water fowl pose severe safety risks for the aviation industry, causing approximately 20% of bird-strike aviation accidents (Bradbeer et al. 2017 and references therein).

Better understanding of goose–habitat relationships may lead to more effective management strategies based on manipulation of habitats to make them less attractive to geese. Besides providing safe roosting and foraging sites close to water, geese prefer urban grass areas because these areas are regularly maintained, providing the birds high protein and low fiber and phenolic content grass forage (e.g., Owen 1975, Durant et al. 2004, Washburn and Seamans 2012, Fox et al. 2017, Mason et al. 2018). Several methods, such as chasing or scaring the birds, which are used to reduce conflicts with geese, require frequent effort to work and often provide only temporary solutions (Conover and Chasko 1985, Smith et al. 1999, Niemi et al. 2007, Nolet et al. 2016, Simonsen et al. 2016).

The objective of our study was to investigate whether human conflicts with the barnacle goose can be reduced by landscape management using different grass species or grass associated *Epichloë* endophytes. In small-scale field studies, we tested goose preference for 2 grass species, fine-leafed red fescue (*Festuca rubra*) and the more robust tall fescue with presence and absence of *Epichloë* endophytes. These global and widely used Eurasian-origin pasture and turf grass species commonly harbour *Epichloë* endophytes (Hoveland 1993, Bazely et al. 1997, Saikkonen et al. 2000, Kvalbein and Aamlid 2012, Kauppinen et al. 2016). Foraging preference was measured as an amount of grass area eaten (visually estimated as a percentage in a pot), length of the eaten grass, as well as number of droppings.

Study area

We conducted our study in 2016 in 2 locations in southern Finland where the barnacle goose has become a nuisance during the last decade. Our study areas encompassed the grounds of Helsinki Zoo (60° 10′ N, 24° 59′ E) on the Island of Korkeasaari, Helsinki (hereafter, the high grazing intensity experiment), and in the Turku University Botanical Garden (60° 26′ N, 22° 10.4′ E) on the island of Ruissalo (hereafter, the low grazing intensity experiment). In the high grazing intensity site, approximately 150–200 pairs of barnacle geese breed annually and are present between April and August (V. Vepsäläinen, Helsinki Zoo, personal communication). Both adults and young geese forage in this area. In the low grazing intensity site, a flock of 20–40 barnacle geese was regularly observed, and this site is known as a foraging area for adult geese only. In the Ruissalo area, barnacle geese are present between mid-March and late October (Tiira database, Birdlife Finland). The geese are habituated to humans in both sites.

Methods

Plant material

In 2015, we collected seeds of red and tall fescues for this study from a common garden experiment in the fields of Turku Botanical Garden, University of Turku, Finland. The red fescue plants were originally collected from wild populations from Utsjoki, northernmost Finland (Dirihan et al. 2016), and the tall fescue plants were comprised of wild plants collected from the Åland Islands (Finland), the island of Gotland (Sweden) and the west coast of Sweden, and Kentucky-31 (KY31) obtained from the University of Kentucky (Helander et al. 2016, Saikkonen et al. 2016*a*).

The plants were either naturally symbiotic with *Epichloë* endophyte (E+) or endophyte-free (E-; Dirihan et al. 2016, Saikkonen et al. 2016*a*). The E+ plants were known to produce intermediate or high concentrations of ergovalines and ergot alkaloids in the case of red and tall fescues, respectively, when grown in the common garden experiments in Turku (B. Vázquez de Aldana, Instituto de Recursos Naturales y Agrobiología, personal communication; Helander et al. 2016). Because the *Epichloë* endophyte is maternally inherited from mother plant to offspring via seeds, we knew the endophyte status of the plants (E+ or E-) used in this study as well as their potential to produce anti-herbivore alkaloids.

We confirmed the endophyte status of the mother plants by microscopic examination of 1–3 seeds from each plant at the time of seed collection for this study. Nutritional and energy content of the forage species (e.g., nitrogen content) are known to affect the foraging preference of geese (Owen 1975; Black et al. 1991; van der Graaf et al. 2006, 2007; Fox et al. 2017), but testing of these was beyond the scope of this study.

High grazing intensity experiment

We planted tall fescue and red fescue seeds in pots and grew them in a greenhouse in the Turku University Botanical Garden 3 months before the experiment. In total, we cultivated 160 pots of tall fescue (pot size 8 × 12 cm) and 96 pots of red fescue (pot size 5 × 8 cm). The grasses were fertilized (17% N, 4% P, and 25% K) every 2 weeks and watered when needed.

We established E+ and E- tall fescue and red fescue patches in 8 sites in the high grazing intensity experiment in June 2016. Each tall and red fescue patch consisted of 10 and 6 pots, respectively, that were sunk at ground level in the soil next to each other. The distance between conspecific E+ and E- patches was 3 m, and that of tall fescue and red fescue patches was 5 m within a site. The density of conspecific E+ and E- grasses was the same by visual inspection.

As geese prefer short to intermediate height swards (Summers and Critchley 1990; Hassall et al. 2001; Durant et al. 2003, 2004; Si et al. 2011) and to mimic the height of grass in recreational areas and match the height of surrounding vegetation (mainly grass, some *Gleochoma* sp. and *Potentilla* sp.), we cut the grasses to approximately 3–4 cm in height before the experiment, and thereafter always when the grass exceeded the height of 4 cm. We watered the pots when needed and fertilized them twice during the experiment.

We measured the foraging preference of geese by measuring grazing intensity and goose visitation to pots in 3 ways at 2- to 3-day intervals between June 17 and July 6 (total of 9 times). We first visually estimated damage to plants as an area percentage in a pot where the grass was shorter than 2.8 cm (as the initial height before the experiment was approximately 3 cm minimum). Secondly, we took 5 measurements per pot to measure the height of eaten grass. From these grass height measurements, we then calculated the length of eaten grass in centimeters by subtracting the height of grass from the 2.8-cm threshold height used in damage estimation. Lastly, as an indicator of goose visitation (which we assumed to be related to foraging intensity), we counted and removed the goose droppings within a 50-cm radius of the pots. Although no direct behavioral observation was collected, we observed numerous geese foraging around and feeding on the experimental plants.

We assumed that barnacle geese would prefer E- grasses and red fescue over tall fescue because tall fescue is more coarse with a high tensile strength (Owen 1976, Owen et al. 1977, Conover 1991, Smith et al. 1999) and red fescues are known to be an important part of the barnacle goose diet (Ydenberg and Prins 1981, van der Graaf et al. 2007).

Low grazing intensity experiment

In May 2016, we established a row of 10 1 × 1.2-m fescue plots of alternating E+ and E- plants near a pond where barnacle goose flocks were frequently foraging in the botanical garden. We planted approximately 300 g of E- or 380 g of E+ seed mixture to each plot. We used a higher amount of seed material in E+ plots because this mixture had more non-seed material (seed envelopes) compared to the E- mixture. The distance between 2 adjacent plots was 2.5 m. To promote the seedling establishment, we covered the plots with white horticultural fleece that was removed after 2 weeks of seed germination.

Once the seedlings were established and vegetative propagation by the tillers had started, we cut the grass to a height of 6–7 cm. We selected this grass height to match the height of the surrounding vegetation (mainly grass, a few clovers [*Trifolium* sp.]) and because geese prefer to feed on short- or medium-height grass (Summers and Critchley 1990; Hassall et al. 2001; Durant et al. 2003, 2004; Si et al. 2011). We kept the lawn around the study plots equally short during the growing season and watered them when needed, but we did not fertilize during the experiment.

As with the high grazing intensity site, we surveyed the plots at 2–3 days, from June 18 to July 8 (total of 8 times). To estimate foraging preference of geese between E+ and E- plots, we measured the percentage of area in plots that were <5.8 cm in height (as the minimum initial height was 6 cm). In addition, we recorded 10 height measurements of the eaten grass per plot. We considered the grass to be eaten by geese if the tip was not intact and the height was <5.8 cm. Furthermore, we estimated the number of grass tillers per plot 2 days before the first cut, as well as at end of the experiment by counting tillers in 2 5 × 5-cm squares in the middle of each plot. We counted and removed goose droppings both from the plots and a 50-cm distance around them at each monitoring occasion.

Statistical analysis

To test the influence of endophyte status and grass species on goose foraging, we used a generalized linear mixed model (GLMM) and linear mixed model approaches. From the experiment in the high grazing intensity site, we set the proportion of area eaten (percentages) or length of eaten grass as response variables in generalized linear mixed model (with beta distribution and logit link function; see Fox et al. 2015) and linear mixed model (with normal distribution and identity link function, normality inspected from residuals) analyses, respectively. We used status of the pot (E+ or E-), species (red fescue or tall fescue), monitoring occasion (day in ordinal scale), and their pairwise and 3-way interactions as fixed explanatory factors. To control correlation structures of the data sets, we used area, patch, and pot as random effects (intercept) with a nested structure where pot was nested within patch, and patch was nested within an area on both analyses. Furthermore, in the grass length analysis, we treated pot as a

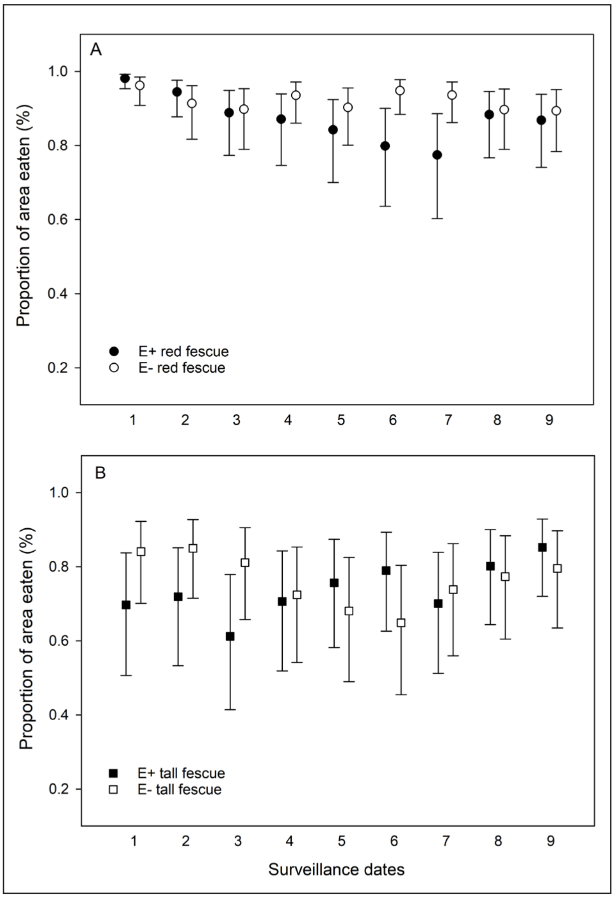

Figure 1. Proportion of the eaten endophyte symbiotic (E+) and endophyte-free (E-) red fescue (*Festuca rubra*; A) and tall fescue (*Schedonorus phoenix*; B) area by barnacle geese (*Branta leucopsis*) in the high grazing intensity site on the 9 monitoring occasions in Helsinki, Finland, 2016. Figures represent means and 95% CI:s from generalized linear mixed model. The running number on the x-axis indicates observation date: 1 = June 17, 2 = June 20, 3 = June 22, 4 = June 24, 5 = June 27, 6 = June 29, 7 = July 1, 8 = July 4, 9 = July 6.

repeated measure as multiple measures of grass height were taken from the same pot.

We conducted similar analyses for data from the low grazing intensity site, where we set endophyte status, date, and their pairwise interaction as fixed explanatory factors both in the analysis of the proportion of area eaten and in the analysis of length of eaten grass. In addition, we set the number of tillers in the beginning of the experiment as a covariate because E- plots had more tillers when the experiment started (2 sample *t*-tests, t = -3.22, df = 8, P = 0.012; this difference disappeared at the end of the experiment [t = -0.89, df = 8, P = 0.40]). To control for the correlation structure of the datasets, we set plot as a random factor in both analyses. In the grass length analyses, we again treated the plot as a repeated measure, as multiple measurements were taken from the same plot.

We analyzed the number of droppings in the GLMM analysis with negative binomial error distribution and log link function for the high grazing intensity site data, where we set status, species, observation occasion, and the interaction between status and species as explanatory variables. We set area as a random factor. For dropping counts in the low grazing intensity site, we conducted a GLMM analysis with negative binomial error distribution and log link function, where we set endophyte status of as fixed factor and plot as a random factor.

We performed GLMM models by using the GLIMMIX procedure of the SAS statistical software, ver. 9.4. To compute denominator degrees of freedom, we used the Kenward and Roger method (latest version, Kenward and Roger 2009). We present model-derived marginal means (i.e., least-squares means) with their 95% confidence interval for classifying factors throughout the results.

Results

High grazing intensity experiment

Overall, all pots were heavily grazed during the experiment (Figure 1): red fescue was 16% more intensively grazed compared to tall fescue plants (red fescue: mean 0.91 [95% CI: 0.83–0.95]; tall fescue: mean 0.76 [95% CI: 0.60–0.86]) irrespective of *Epichloë* endophyte status of the plants (Table 1; Figure 1). However, *Epichloë* endophyte differently affected the proportion of damaged area in the 2 grass species over time (indicated by the 3-way interaction between endophyte status, grass species and monitoring day [Table 1; Figure 1]). For red fescue, a high proportion was constantly eaten in E- pots, while the proportion of damage declined in E+ conspecifics until 2 weeks from the start of the experiment (Table 1; Figure 1A). For tall fescue, there was a slight decline in the proportion of damaged area from E- pots, while this proportion slightly increased in E+ pots at the

Table 1. Proportion of area eaten and length of eaten tall fescue (*Schedonorus phoenix*) and red fescue (*Festuca rubra*) grasses by barnacle geese (*Branta leucopsis*) in the high grazing intensity site, Helsinki, Finland, 2016. Explanatory factors in generalized linear mixed model and linear mixed model analyses, respectively, were status (fungal endophyte status, E- or E+), grass species (tall fescue, red fescue), and day (monitoring occasion).

	Proportion of area eaten				Length of eaten grass			
Explanatory factor	Numerator df	Denominator df	*F*	*P*	Numerator df	Denominator df	*F*	*P*
Status	1	21.78	1.06	0.32	1	20.99	0.60	0.45
Species	1	21.79	20.24	<0.001	1	20.99	5.70	0.03
Day	8	1461	11.61	<0.001	8	4699	54.13	<0.001
Status × Species	1	21.81	0.25	0.63	1	20.99	0.36	0.56
Status × Day	8	1461	4.53	<0.001	8	4699	2.09	0.03
Species × Day	8	1461	8.34	<0.001	8	4699	1.95	0.05
Status × Species × Day	8	1461	14.86	<0.001	8	4699	1.31	0.24

end of the experiment (Figure 1B).

Overall, red fescues were consumed approximately 10% more compared to tall fescues in terms of the length of the eaten grass (Table 1; red fescue: mean 1.43 cm [95% CI: 1.28–1.57]; tall fescue: mean 1.28 cm [95% CI: 1.13–1.43]). The grazing was more intensive in terms of the length of the eaten grass during the first 3 monitoring occasions on both grass species (Figure 2). The length of the eaten grass did not differ between E+ and E- grasses (Table 1). We recorded the cumulative average of droppings to be 4.0 ± SE 0.79 droppings per patch (average 0.47 ± SE 0.06 droppings per patch + 0.5-m distance around it per monitoring occasion). However, none of the fixed explanatory factors affected the number of droppings (Table 2).

Low grazing intensity experiment

In the beginning of the experiment, the tall fescue plots were heavily grazed, but the grazing intensity estimated by the percentage of the area damaged declined after the first 2 monitoring occasions (Table 3, Figure 3A). Although there appeared to be a trend indicating a higher proportion eaten form the E- plots at the start of the experiment, neither *Epichloë* endophyte status of the grasses alone, nor interactively with date, explained the proportion of the area eaten or the length of the eaten grass (Table 3, Figure 3). Instead, the density of the grasses was negatively associated with the damage of the plots; the number of grass tillers had a significant negative effect on the proportion of the area eaten (estimate -0.136 [95% CI: -0.198 to -0.074]; Table 3) as well as on the length of the eaten grass (estimate -0.036 [95% CI: -0.047 to -0.025]). We recorded on the cumulative average of 16.5 ± SE 2.2 droppings per plot (mean 2.1 ± SE 0.5 droppings per plot + 0.5-m distance around it per monitoring occasion). However, the *Epichloë* endophyte status of the grasses did not affect the number of droppings ($F_{1,75} = 0.06$, $P = 0.81$).

Discussion

Our results support the idea that strategies to mitigate human–wildlife conflicts with barnacle geese by reducing availability of attractive food plant species to control distribution and movements of geese should be tested in long-term and large-scale field studies. As predicted, barnacle geese foraged on both of the studied grass species, but they preferred red fescues over tall fescues. Tall fescue is coarse and has a high tensile strength, which likely makes it less attractive compared to softer grass species (Owen 1976, Owen et al. 1977, Conover 1991, Smith et al. 1999). Similarly, several other studies have suggested that tall fescue is not palatable for geese (Smith et al. 1999, Pennell et al. 2010, Washburn and Seamans 2012).

However, our results revealed only weak support for the hypothesis that *Epichloë* endophytes deter barnacle geese (Conover and Messmer 1996, Washburn et al. 2007, Pennell et al. 2010). The E- grasses, especially in the case of red fescues, experienced slightly higher grazing damage compared to E+ ones. Although there appeared to be a similar trend in the low grazing intensity site, the difference appeared to be associated with grazing intensity as it was detected only in the experiment conducted in the heavily grazed study site.

We acknowledge that the small size of the experimental units was probably an explanation for the lack of strong geese avoidance of E+ grass. We expected that geese would learn to differentiate between E+ and E- grasses, especially in the high grazing intensity site, because the content of alkaloids deterring vertebrate herbivores, especially in our E+ tall fescues, were known to be high (Saikkonen et al. 2010, 2013; Helander et al. 2016). Previous studies demonstrate that geese can avoid some secondary chemicals of plants through tasting and learning (Buchsbaum et al. 1984, Wink et al. 1993). The ability of geese to distinguish between E+ and E- grasses based on their alkaloid profiles, however, is proposed to be a result of post-ingestion feedback rather than the bitter taste of alkaloids (Conover and Messmer 1996). Furthermore, the purported high capacity of geese to tolerate and/or detoxify allelochemicals that are regarded as unpalatable to other animals (Wink et al. 1993) may delay the development of suboptimal food aversion (Wink et al. 1993). Thus, the size of the pots and plots possibly limited the resolution power in our short-term study to sufficiently capture the slowly developing aversion to E+ grasses in freely foraging flocks of geese.

Furthermore, accumulating studies have demonstrated that chemotypic diversity determining the nutritional quality of E+ grasses to herbivores is far more complex than the alkaloid profile of the symbiota (Saikkonen et al. 2013, 2016*b*). *Epichloë* endophytes can modulate chemotypic diversity of the symbiotum, but the outcome determining the symbiotum quality to herbivores depends on fungal and plant genotypes, abiotic

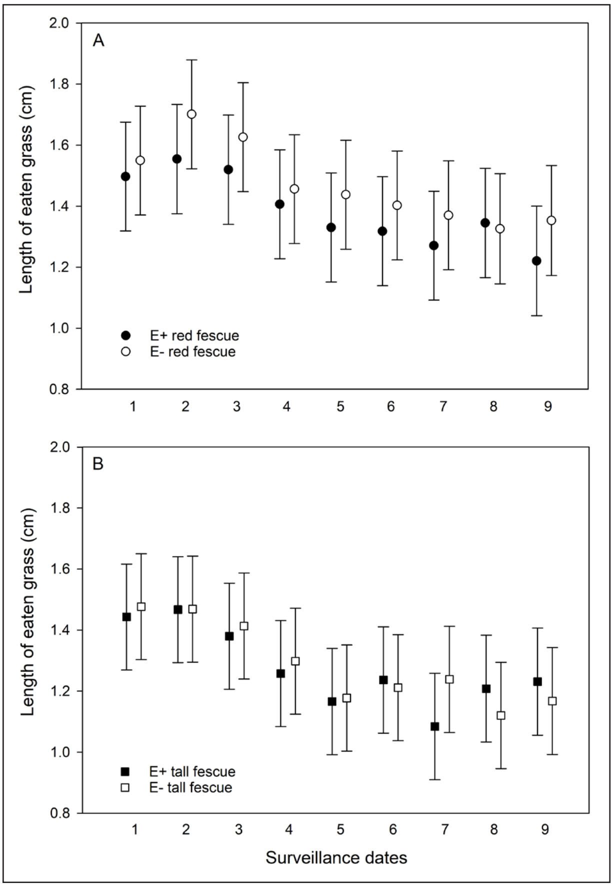

Figure 2. The length of eaten endophyte symbiotic (E+) and endophyte-free (E-) red fescue (*Festuca rubra*; A) and tall fescue (*Schedonorus phoenix*; B) grass by the barnacle geese (*Branta leucopsis*) in the high grazing intensity site on the 9 monitoring occasions in Helsinki, Finland, 2016. Figures represent means and 95% CI:s from linear mixed model. The running number on the x-axis indicates observation date: 1 = June 17, 2 = June 20, 3 = June 22, 4 = June 24, 5 = June 27, 6 = June 29, 7 = July 1, 8 = July 4, 9 = July 6.

Table 2. Number of barnacle geese (*Branta leucopsis*) droppings in the high grazing intensity site, Helsinki, Finland, 2016. Explanatory factors in generalized linear mixed model analyses were status (fungal endophyte status, E- or E+), grass species (tall fescue [*Schedonorus phoenix*], red fescue [*Festuca rubra*]), and date (monitoring occasion).

Explanatory factor	Numerator df	Denominator df	*F*	*P*
Status	1	211.7	0.05	0.83
Species	1	211.4	1.34	0.25
Day	8	241.8	1.58	0.13
Status × Species	1	211.1	1.31	0.25

Table 3. Proportion of area eaten and length of eaten tall fescue (*Schedonorus phoenix*) grass by barnacle geese (*Branta leucopsis*) in the low grazing intensity site, Ruissalo, Finland, 2016. Explanatory factors in generalized linear mixed model and linear mixed model analyses, respectively, were status (fungal endophyte status, E- or E+), day (monitoring occasion), and number of tillers (grass tiller density).

	Proportion of area eaten				Length of eaten grass			
Explanatory factor	Numerator df	Denominator df	*F*	*P*	Numerator df	Denominator df	*F*	*P*
Status	1	4.319	2.15	0.21	1	223.7	0.12	0.72
Day	7	48.61	23.64	<0.001	7	261.5	1.64	0.13
No. tillers	1	4.863	32.75	0.003	1	224.0	40.17	<0.001
Status × Day	7	49.02	0.83	0.57	7	261.5	0.31	0.95

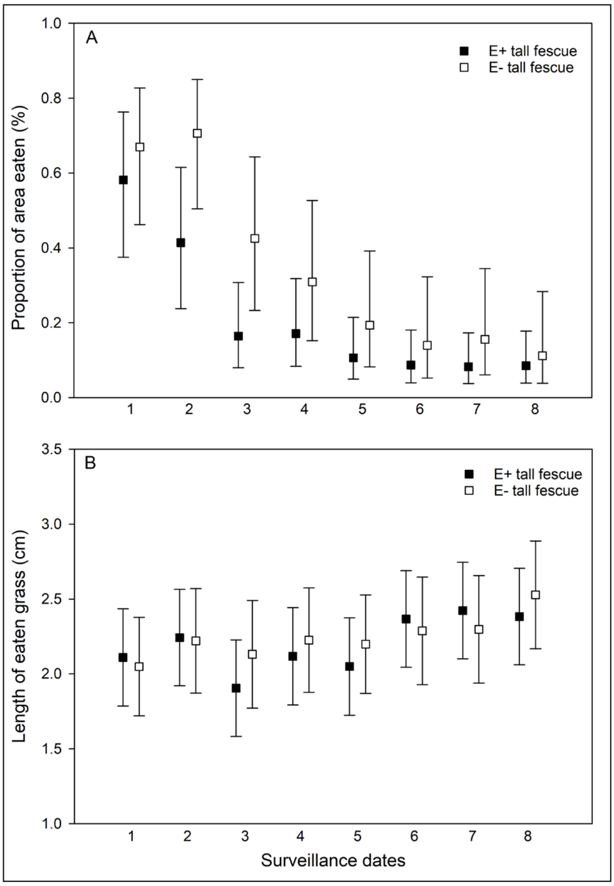

Figure 3. Proportion of the area eaten (A) and length of the eaten grass (B) of endophyte symbiotic (E+) and endophyte-free (E-) tall fescue (*Schedonorus phoenix*) by the barnacle geese (*Branta leucopsis*) in the low grazing intensity site on the 9 monitoring occasions in Ruissalo, Finland, 2016. Figures represent means and 95% CI:s from generalized linear mixed model and linear mixed model, respectively. The running number on the x-axis indicates observation date: 1 = June 18, 2 = June 21, 3 = June 23, 4 = June 25, 5 = June 28, 6 = July 2, 7 = July 5, 8 = July 8.

and biotic environmental conditions, and their interactions. For example, *Epichloë* endophytes appear to provide numerous advantages to their host plants, including higher content of nitrogen-based alkaloids (Lyons et al. 1986, Richardson et al. 1999, Krauss et al. 2007, but see Rasmussen et al. 2007) in simplified and nutrient-rich agroecosystems and other manmade ecosystems (Saikkonen et al. 2006, 2010, 2016*b*). Protein and silicon concentrations of grasses have been found to be higher in E+ grasses (Vázquez de Aldana et al. 1999, Huitu et al. 2014). Silicon especially, in addition to tolerance and high regrowth capacity of grasses, is suggested to play a significant role in their defense against herbivores (Huitu et al. 2014). Silicon increases toughness and coarseness of the grasses as well reduces their digestibility (Massey and Hartley 2006, 2009).

In some situations, these *Epichloë* endophyte mediated grass traits may have counteractive effects on the feeding preference of geese. For example, several studies indicate that protein or nitrogen content of the plant can be an important cue in determining foraging choices of geese and is likely a main reason for attraction of geese to urbanized lawn and agricultural fields (Owen 1975; Black et al. 1991; van der Graaf et al. 2006, 2007; Fox et al. 2017). In addition, fertilization and grazing may increase nutritional and silicon content of grasses, which can either improve or degrade the forage quality to geese, respectively (Sedinger and Raveling 1986, Davidson and Potter 1995, Huitu et al. 2014). Thus, the relationship between endophytic fungi and nutritional quality of the grass is clearly complex and requires further studies.

We propose that landscape management aiming to prevent human conflicts with barnacle geese requires more comprehensive understanding of goose behavior and habitat characteristics that make it appealing to geese. Access to preferred food, species community composition, height and density of vegetation, and vulnerability to predators are all factors that likely determine the goose feeding habitat selection.

Here we were able to show that barnacle geese preferred to forage on softer red fescue over coarse tall fescue. This supports the previously proposed strategy that instead of fine fescues, tall fescue or other coarse grass species could be used to reduce attractiveness, and thus grazing damage, caused by the geese (Conover 1991, Washburn et al. 2007, Pennell et al. 2010, Washburn and Seamans 2012). Further, we detected a slight indication that geese prefer to feed on E- grasses. However, vegetation height and density as well as species community composition might be a more important determinant of geese foraging behavior than alkaloids produced by *Epichloë* endophytes. For example, endophyte-promoted growth of the host grasses and thus their competitive superiority in grassland communities (Arachevaleta et al. 1989, Clay 1990, West et al. 1993, Clay and Holah 1999, but see Marks et al. 1991, Saikkonen 2000, Saikkonen et al. 2013, Dirihan et al. 2015) may create habitat less appealing to geese.

Our results suggest that the density of the grasses was negatively associated with the damage of the plots. Thus, additive benefits of using alkaloid-producing E+ grass varieties (Kauppinen et al. 2016) as well as dense, higher, and more robust grass species and varieties should be taken into account in minimizing foraging efficiency and attractiveness of habitat to geese (van de Koppel et al. 1996, van der Wal et al. 1998).

Finally, community composition should be taken into account because diverse vegetation may allow geese to balance their diet and compensate the effects of preferred but less nutritious food. For example, Washburn et al. (2007) found that geese did not show preference to plots containing mostly ryegrass and white clover over plots containing 72% of E+ tall fescues, but 2 years later when the study was repeated with different geese individuals and the coverage of E+ grasses in tall fescue plots had increased to 91%, the birds preferred ryegrass and white clover plots. As freely foraging birds, geese were also able to forage on other vegetation in our experiments. A diverse and nourishing diet can dilute the possible negative effects of fungal alkaloids to geese and enable them to successfully feed on small patches of E+ grasses in our study. Despite the scale-related limitations of our experiments, our results suggest that species composition manipulations should be incorporated into the grassland management programs aiming to change a habitat to be less appealing to barnacle geese.

Management implications

Our results revealed that barnacle geese preferred to forage on red fescue over tall fescue, suggesting that using coarse grass species instead of fine-leaved grasses should be considered in landscape management to successfully reduce human–wildlife conflicts. We found only weak support for the hypothesis that seed-borne and alkaloid-producing *Epichloë* endophytes act as feeding deterrents to barnacle geese. However, our study was unable to separate whether this reflects geese's ability to tolerate and/or detoxify fungal origin alkaloids or the small scale of the experiment. Therefore, we propose that large-scale and long-term studies are needed to test whether the alkaloid-producing and grass-growth-promoting *Epichloë* endophytes can provide additional benefits for establishing durable and easily maintained swards that are less preferred by herbivorous geese.

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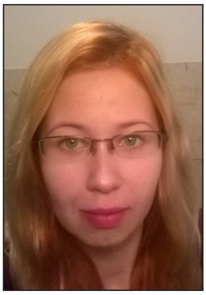

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