

# Beavers and lilies: selective herbivory and adaptive foraging behaviour

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## SUMMARY

1. With the global population of beavers (*Castor* spp.) increasing, and reintroductions widespread, it is crucial to be able to predict potential impacts on flora and fauna based on defined foraging behaviours.
2. *Nymphaea alba* (white water lily) is regularly consumed by beavers and provides a model system to test selective foraging behaviour and quantify potential impacts on aquatic resources in standing-water habitats.
3. Using biometric relationships within *N. alba* pads, we accurately reconstructed the size and weight of consumed pads, demonstrating that beavers (*Castor fiber*) selected pads that were significantly larger and heavier than unselected pads. By selecting larger leaves, beavers may also avoid chemical defences associated with anthocyanin pigments that dominate in smaller leaves. Grazing was concentrated in shallow depths ( $55.7 \pm 10.7$  cm) close to the shore ( $2.95 \pm 0.62$  m) relative to ungrazed plots ( $100.5 \pm 9.2$  cm;  $4.79 \pm 0.68$  m). The level of selectivity was unchanged with increasing distance from a central feeding place.
4. Beavers removed 24–50% of pads within grazed areas, but relative to the whole *N. alba* leaf pad resource, the impact of this foraging was low (0.38–1.23% loss). Plant species diversity was unaffected by foraging, and there was no evidence of indirect effects on non-targeted *N. alba* pads or flowers.
5. When foraging in the aquatic environment, beavers are highly selective and can have a minor effect on food resources whilst feeding optimally and opportunistically. Since beavers demonstrate adaptive foraging strategies depending on their foraging environment, this knowledge should be incorporated into future decisions on further reintroduction or habitat restoration programmes.

*Keywords:* aquatic plants, *Castor fiber*, foraging, *Nymphaea alba*, selectivity

## Introduction

The ability to predict and quantify potential environmental impacts by species based on defined habitat requirements and foraging behaviours should improve judgment when species management decisions need to be made (Caro, 2007). Populations of Eurasian (*Castor fiber*) and North American (*Castor canadensis*) beavers are stable or now increasing as a result of formal and informal introductions, reintroductions and natural dispersal (Naiman, Johnston & Kelley, 1988; Halley & Rosell, 2003; Linzey, 2011). Early reintroductions were motivated by fur harvesting (Halley & Rosell, 2002), but later programmes have sought to exploit the potential of

beavers to create or restore habitat heterogeneity in degraded freshwater and riparian habitats, through dam building and selective tree felling (Burchsted *et al.*, 2010; Smith & Mather, 2013). The wider, desired impacts of beaver reintroduction are often to restore natural biodiversity and re-establish their role as a keystone organism, although benefits from ecotourism may also occur (Kemp *et al.*, 2011). As a result of their habitat restoration potential, beavers have received considerable attention in the past 20 years, with many planned reintroduction areas guided by density of preferential forage species (Nolet & Rosell, 1998; e.g. aspen and willow), interconnectivity of freshwater habitats (South, Rushton & MacDonald, 2000) and physical habitat

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characteristics (Gurnell, 1998; MacDonald *et al.*, 2000; Fustec *et al.*, 2001; Pinto, Santos & Rosell, 2009).

As semi-aquatic herbivores, terrestrial forays are energetically costly for beavers (due to time spent selecting, felling and removing items) and increase vulnerability to predation; efficient use of foraging time on land is therefore essential (Fryxell & Doucet, 1991). Depending on the distance from the water's edge, beavers exhibit selectivity for trees based on trunk size, distance from water and species (Jenkins, 1980; Gerwing, Johnson & Alström-Rapaport, 2013), transporting selected items back to the water (i.e. central place foraging; Haarberg & Rosell, 2006; Raffel, Smith & Cortright, 2009). Nevertheless, as opportunistic, generalist herbivores, beavers also spend significant periods in spring and summer supplementing a woody diet by consuming aquatic vegetation that is typically rich in protein, sodium and iron (Svendsen, 1980; Nolet, Van Der Veer & Evers, 1994; Milligan & Humphries, 2010) and has higher digestibility than terrestrial vegetation (Belovsky, 1984; Doucet & Fryxell, 1993). The importance of aquatic vegetation to beavers, and indeed other aquatic rodents, should not be underestimated. Muskrat (*Ondatra zibethicus*), coypu (*Myocastor coypus*) and capybara (*Hydrochoerus hydrochaeris*) all consume significant volumes of preferred aquatic plants, often significantly reducing their abundance (Danell, 1996; Johnson & Foote, 1997; Corriale, Arias & Quintana, 2011), though the contribution of woody vegetation to the diet of these species is minimal. Within lentic environments, aquatic plants are an easily accessible and reliable food source to mammalian herbivores even outside the growing season. For beavers, this aquatic resource requires less search and handling time than woody material on land since the cost of travel to foraging areas and in conveying selected items is reduced due to their buoyancy in water, whilst predation risk is lowered (Fryxell & Doucet, 1993; Severud *et al.*, 2013). As yet, no beaver reintroduction programmes have formally considered aquatic vegetation as an important resource or studied any associated foraging behaviours. This is perhaps because the aquatic resource can be more difficult to quantify (Howard & Larson, 1985) relative to conspicuous tree coppicing. Therefore, population and energetic models are likely to be underestimating the dietary importance of aquatic vegetation when predicting survival and persistence (Webb, French & Flitsch, 1997; South *et al.*, 2001).

The consumption by beavers of water lilies (Nymphaeaceae spp.), particularly *N. alba* or its North American equivalent *Nymphaea odorata*, provides a model system in which to study aquatic foraging behaviour

and associated impacts. Lilies are a major component of the vegetation of shallow lakes and ponds in temperate and boreal regions, with leaves, rhizomes and flowers all frequently mentioned in accounts of the diet of beavers (Northcott, 1972; Jenkins, 1980; Roberts & Arner, 1984; Doucet & Fryxell, 1993; Nolet *et al.*, 1994; Severud *et al.*, 2013). The floating blades (henceforth referred to as pads) are typically severed by beavers and then transported to a central place (e.g. shoreline or lodge) for consumption, leaving the petiole projecting above the water surface and still attached to the buried rhizome. These petioles are easily recognised and, through simple biometric relationships, provide a means to reconstruct the size of pads removed by beavers.

We tested the following hypotheses: (i) beavers forage selectively on *N. alba* pads based on their size and weight; (ii) pad selection is based on depth and distance; (iii) the impact of foraging on the *N. alba* resource occurs at different scales and (iv) aquatic foraging behaviour of beavers is different to that of accepted foraging models developed for terrestrial environments.

## Methods

### Site

The study took place in the Taynish and Knapdale Woods, on the west coast of Scotland (Lat: 56°2'32.06"N, Long: 5°33'22.21"W). This is a designated Special Area of Conservation due to the occurrence of western acidic oak woodland (*Quercus petraea*) and clear-water oligotrophic to mesotrophic lakes with aquatic vegetation. The site receives approximately 1787 mm of rainfall annually, with a mean maximum temperature of 11.3 °C and mean minimum temperature of 4.8 °C (Meteorological Office UK, 2012). In spring 2009, Eurasian beaver families were released as part of a trial reintroduction, and by summer 2010, family groups (2–4 individuals) occupied four lakes ranging in size from 0.4 to 16.5 ha. Subsequently, animals have become established within these or surrounding lakes, exhibiting typical foraging and engineering activities (e.g. felling trees and constructing lodges). To date, incidences of large-scale dam building have been rare. The surrounding riparian forest is composed of mixed deciduous species (mainly *Betula pubescens* and *Salix* spp., plus *Sorbus aucuparia* and *Corylus avellana*) backed by *Q. petraea* or commercially planted conifers (*Picea* spp. and *Larix* spp.). The aquatic vegetation of these lakes comprises substantial stands of emergent (e.g. *Cladium mariscus*, *Schoenoplectus lacustris*, *Phragmites australis*, *Equisetum fluviatile* and *Carex*

*rostrata*) and floating-leaved species (mainly *N. alba* and *Potamogeton natans*) plus a range of submerged plants, in particular the isoetids *Littorella uniflora* and *Lobelia dortmanna* (Willby & Mulet, 2010).

### Survey

Stands of *N. alba* in the 11 lakes of the Knapdale Forest were surveyed in late summer for two consecutive years using a 2 × 2 m floating quadrat. Beavers were regularly present in five of these lakes throughout the study period and absent from or only intermittently present in the remaining lakes. In each lake, 20 healthy and ungrazed *N. alba* pads of a range of sizes were removed, and the midline distance (petiole junction to pad tip) and petiole diameter of each pad were measured to the nearest mm and nearest 0.01 mm, respectively, using digital callipers. Petiole diameter of these pads was measured 5–10 cm from the base of the pad in accordance with the position at which beavers typically sever the pad. The change in petiole diameter over this length range was negligible (<0.05 mm). The remaining sections of petiole were then removed from these pads with a scalpel prior to measuring the wet weight of the pad. Pads were then dried at 60 °C for 48 h and re-weighed. All weights were determined to the nearest 0.01 g.

Beaver-grazed patches of *N. alba* only became apparent in mid-summer (late July to August) with no evidence of prior feeding. Within those patches of *N. alba* where beavers had been actively grazing, between 10 and 20 2 × 2 m quadrats were randomly placed depending on the size of the foraged area. The petiole diameter of each beaver-cut *N. alba* stem in the quadrat was measured. There was no sign of senescence or shrinkage of the remaining petiole, confirming that all leaves had been recently grazed. In addition, the water depth, distance from shore, number of *N. alba* flowers, presence of other aquatic macrophyte species and number of surviving *N. alba* pads based on three size categories of midline distance (large (>100 mm), medium (50–100 mm) and small (<50 mm)) were recorded per quadrat. To predict the dry weight of ungrazed pads, ten *N. alba* pads were randomly selected within each quadrat for measurement of midline distance. In each lake, a further 20 quadrats were randomly placed within ungrazed *N. alba* stands with the aforementioned variables measured. The midline distance of a further 120 pads was measured, and the colour, expressed in terms of percentage green versus red pigmentation, of the dorsal side of each pad was independently visually estimated by three surveyors.

### Statistical analyses

Relationships between petiole diameter, midline distance and dry weight of ungrazed pads were determined using generalised linear mixed effect models (GLMMs) with a log-link and Poisson error distribution (Winkelmann, 2008) to account for underlying heteroscedasticity of the data (Zuur *et al.*, 2009). Using these models, we could predict, with high precision (mean ± 11.5%), the midline distance and dry weight of pads removed by beaver, based on the diameter of the projecting petiole from which the pad had been removed. Pad selection was analysed using a GLMM with binomial error distribution and logit-link. Quasibinomial distributions were used to correct for overdispersion within predicted pad selection models. The relationship between midline distance and the mean proportion of pad area pigmented green was derived using a logistic regression.

A weighted mean of pad size and biomass per quadrat was calculated using the number of pads in each size category and the mid-value of each size class. These values were then log-transformed to meet linear requirements of general linear and linear mixed effect models to assess possible relationships between estimated mean pad size, water depth and grazing impact. Predicted pad sizes and biomass from model outputs was then exponentially back-transformed. Count data of species number and *N. alba* flower density were analysed using GLMM with Poisson error distribution and log-link. Within all mixed models, lake identity and year sampled were treated as random effects to control for pseudoreplication in the data (Zuur *et al.*, 2009). The best performing models were selected using an information-theoretical approach (Akaike information criterion; Burnham & Anderson, 2002). Where model explanatory factors were correlated ( $P < 0.05$ ; e.g. pad midline distance with dry weight and depth with distance), one factor was removed from the model (i.e. dry weight and distance). Significance in all models was taken to be  $P < 0.05$ . Statistical analyses and graphics were produced using R Studio version 0.97 (R Development Core Team, 2012) using the packages lme4 (Bates, Maechler & Bolker, 2012), AED (Zuur *et al.*, 2010) and languageR (Baayen, 2011).

## Results

### *N. alba* biometric relationships

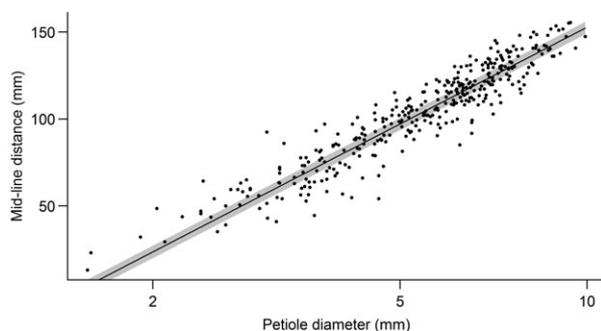
Based on pads collected from lakes where beavers are absent or where there is no evidence of grazing on

*N. alba*, there was a strong positive relationship between the petiole diameter and midline distance of *N. alba* pads ( $Z_4 = 647.8$ ,  $P < 0.001$ ; Fig. 1). The model-predicted midline distance was on average within 11.5% of the observed values. There was also a significant positive relationship between *N. alba* petiole diameter and dry weight ( $Z_3 = 123.9$ ,  $P < 0.001$ ), and between pad midline distance and dry weight ( $Z_3 = 125.6$ ,  $P < 0.001$ ; see Appendices S1 and S2).

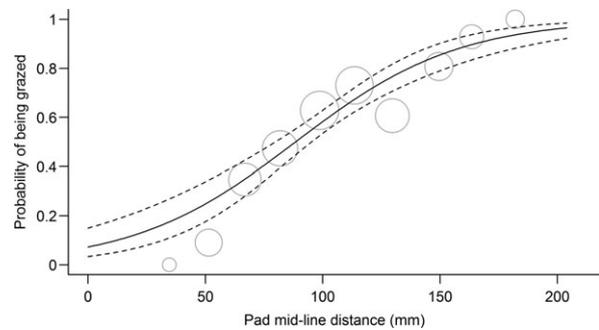
### Selection of *N. alba* pads by beavers

When a pad is encountered, the probability of it being grazed increased significantly as pad midline distance increased ( $Z_{480} = 7.12$ ,  $P < 0.001$ ; Fig. 2). From field measurements, pads removed by beavers were of a significantly larger size ( $114.2 \pm 1.6$  mm; mean  $\pm$  SE) relative to unselected pads ( $92.4 \pm 2.0$  mm). Predicted biomass of selected pads ( $2.77 \pm 0.09$  g) was also greater than that of unselected pads ( $1.75 \pm 0.09$  g). Selected pads were also larger relative to the measured global mean pad size available ( $106.1 \pm 2.7$  mm,  $2.29 \pm 0.12$  g), and larger pads also had significantly more extensive green pigmentation ( $Z_{115} = 4.627$ ,  $P < 0.001$ ; Fig. 3).

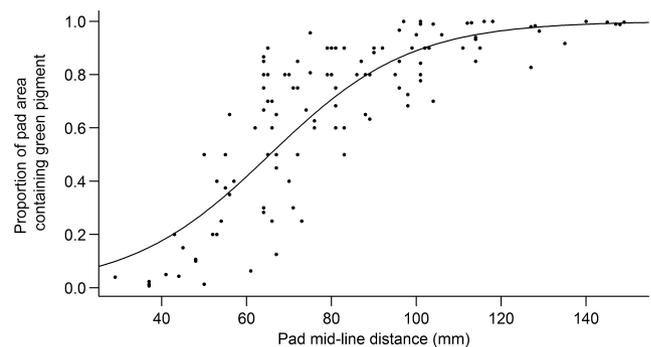
The observed mean percentage of pads per size category varied within plots, with medium-sized pads being the most dominant size class:  $>100$  mm = 40.2%, 50–100 mm = 52.9% and  $<50$  mm = 6.9%. Regardless of the proportion of available pads in each size category, beavers selected a significantly greater number of large pads compared to medium ( $t_{57} = -7.35$ ,  $P < 0.001$ ) and small pads ( $t_{57} = -2.71$ ,  $P = 0.008$ ). The observed percentage of consumed pads was large  $58.4 \pm 5.5\%$ , medium  $12.5 \pm 2.2\%$  and small  $0.7 \pm 0.7\%$ .



**Fig. 1** The relationship between *Nymphaea alba* petiole diameter and midline distance (solid line with 95% confidence intervals, on a log scale) based on pads collected from lakes where beavers are absent or where there is no evidence of grazing.



**Fig. 2** Estimated probability of grazing based on unselected and reconstructed *Nymphaea alba* pad midline distances. Dashed lines indicate 95% confidence intervals. Original data on the proportion of grazed pads are superimposed as grey circles with diameter proportional to the total number of pads.



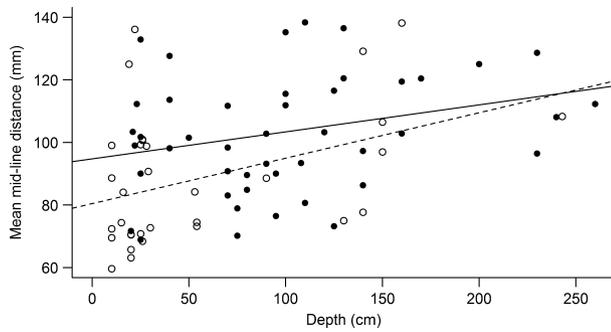
**Fig. 3** The observed (solid circles) and modelled (solid line) relationship between *Nymphaea alba* midline distance and visually assessed proportion of pad area containing green pigment.

### Factors influencing pad selection

As water depth increased, mean pad size increased significantly ( $t_7 = 2.3$ ,  $P = 0.025$ ), despite large variation in mean pad size at water depths less than 150 cm (Fig. 4). However, beaver grazing was concentrated at shallower depths ( $55.7 \pm 10.7$  cm) and closer to the shore ( $2.95 \pm 0.62$  m) relative to ungrazed areas ( $100.5 \pm 9.2$  cm;  $4.79 \pm 0.68$  m). The difference in depth between grazed and ungrazed plots was significant ( $Z_{72} = -3.03$ ,  $P = 0.002$ ), but weighted mean pad size had no effect on selectivity ( $Z_{72} = 0.03$ ,  $P = 0.974$ ). Thus, as depth increased, there was no increase in pad size selectivity ( $t_{36} = -0.26$ ,  $P = 0.80$ ) and no interaction between pad size  $\times$  depth and the proportion of pads grazed ( $t_{36} = 0.65$ ,  $P = 0.52$ ).

### Scale and impact of feeding on *N. alba* by beavers

Preference for grazing on large pads in shallower waters led to a reduced mean pad size within grazed



**Fig. 4** The relationship between *Nymphaea alba* pad mean midline distance and water depth between grazed (open circles, dashed line) and ungrazed quadrats (solid circles, solid line) within lakes with active beaver foraging on pads.

quadrats ( $t_7 = -2.28$ ,  $P = 0.028$ ; Fig. 4), but not sufficient to produce a significant interaction effect between grazing and depth ( $t_7 = 0.63$ ,  $P = 0.534$ ). At the quadrat scale, beavers removed between a quarter and a half of *N. alba* pads (Table 1), but impacts were barely evident at a coarser scale (lake level). The total grazed area per lake was small relative to the resource size, and hence, there were no significant differences in total pad density per metre square between lakes with beavers present and grazing *N. alba*, and lakes where beavers were present but did not feed on *N. alba* ( $Z_5 = 0.72$ ,  $P = 0.47$ ), or lakes with no beavers present at all ( $Z_5 = 1.45$ ,  $P = 0.15$ ).

Excluding *N. alba*, the total number of aquatic plant species present per quadrat did not differ between lakes with and without beavers present ( $Z_3 = -1.22$ ,  $P = 0.221$ ). Within lakes with active feeding, there was also no difference in species number between grazed and ungrazed plots ( $Z_3 = 0.22$ ,  $P = 0.824$ ). In lakes where beavers actively grazed on *N. alba*, there was no significant impact on *Nymphaea* flower density ( $Z_4 = -1.33$ ,  $P = 0.184$ ). Also, in lakes where beavers were present, there was a higher flower density per square metre than sites without beaver, but not significantly so ( $Z_4 = 1.09$ ,  $P = 0.28$ ).

**Table 1** Foraging impacts by beavers on *Nymphaea alba* pads per lake and year

Lake	Year	Area of <i>N. alba</i> (ha)	<i>N. alba</i> pads removed per grazed quadrat (%)	Estimated total <i>N. alba</i> pad biomass removed (gDW)	Grazed area (% of total resource)
Buic	2011	0.329	50.4	725	0.38
Beag	2011	0.224	24.4	671	0.54
Beag	2012	0.224	39.3	787	1.23

## Discussion

In comparison with terrestrial feeding, foraging on aquatic vegetation by beavers is understudied, yet can be equally pronounced (Parker, Caudill & Hay, 2007). In the present study, beavers selectively fed on larger and heavier pads, but there was no evidence that this selectivity changed with distance from shore or foraging depth. The availability of edible and palatable organs of *N. alba* will vary seasonally, thus contributing to selection by beavers (e.g. switching to plant rhizomes in winter in the absence of above-ground biomass). Temperate species of Nymphaeaceae peak in biomass and standing crop during August with pads then containing significantly more phosphorus and nitrogen per unit dry weight than the rhizome (Smart, 1980). This timing coincides with observations in this study whereby beavers grazed larger *N. alba* pads predominantly in late summer, with no evidence (from senescence or shrinkage of cut petioles) of pad removal earlier in the season, despite pads being available. During the early developmental stage, pads are red in colour due to cell pigments, notably anthocyanins (Bendz & Jönsson, 1971), that share the same phenylpropanoid biosynthetic pathway as many defensive phenolic compounds (e.g. tannins, terpenoids, alkaloids and flavonoids). The extensive red pigmentation observed only in smaller pads in this study could provide both direct (internal chemical repellents; Lev-Yadun & Gould, 2009) and indirect defences against foraging by beavers (e.g. visual aposematic stimuli) as beavers demonstrate selection of food items of higher contrast to their background (Richard, 1979). *N. alba* delays greening until full leaf expansion due to delayed chlorophyll synthesis or chloroplast development (Coley & Kursar, 1996). As the expression and importance of anthocyanin pigments, and associated secondary compounds, declines during pad maturation, this could be contributing to selection of larger, more visible or more palatable pads by beavers.

Aquatic plants will provide complementary nutrients to herbivorous mammals, particularly to gestating females; for example, moose consume aquatic plants rich in sodium and iron during the summer to correct an accumulated deficiency during winter and spring (Belovsky, 1978; Fraser, 1984). Yet without water lily in their diet, Nolet *et al.* (1994) found that beavers had sufficient concentrations of sodium for nutritional needs, and in the present study, lilies were utilised to a similar degree by both sexes (A. Law, pers. obs.). Some studies have noted that water lilies are grazed infrequently by

beavers (Roberts & Arner, 1984; Krojerová-Prokešová *et al.*, 2010), and since other family groups within the present study area have successfully bred annually without utilising the lily resource, it is most likely that water lilies are a substitutable food source.

According to central place foraging theory, beavers should become more selective as the distance from the central place increases (McGinley & Whitham, 1985; Haarberg & Rosell, 2006). Our results are contrary to this expectation. Beavers were consistently highly selective regardless of distance from the central place (shoreline or lodge). Pad size was not uniformly distributed, with the density of pads of the preferred size increasing with depth, but the large variance in pad size at all depths ensured that the encounter rate with large pads in shallow water was sufficiently high that beavers did not need to forage far from a central place. Transportation costs of removed pads are assumed to be minimal due to buoyancy, and consequently, the longer handling and digestion times associated with selection of larger and heavier pads are presumably outweighed by greater nutritional value and/or palatability compared to smaller pads. By selecting relatively larger and heavier pads, we speculate that beavers maximise energy gain and, whilst foraging at shallower depths and travelling minimal distances to obtain preferred food items, also minimise energy expenditure. Also, as beavers are often observed consuming the pads of Nymphaeaceae *in situ* rather than severing the whole pad from the petiole (P. Busher, pers. comm.), an individual does not need to return to a central place to feed. These feeding constraints are more closely associated with optimal foraging theory (Schoener, 1979; Belovsky, 1986) than central place foraging, a special case of optimal foraging theory (Orians & Pearson, 1979), as described for terrestrial habitats. Observations of beavers returning with harvested *N. alba* pads to feed at a central place are likely to be associated with the ease of feeding on preferred pads close to the shore in a stationary position, further maximising net energy gain. Similar optimal feeding behaviour occurs in other semi-aquatic rodents whilst consuming aquatic plants, including muskrat (Lacki *et al.*, 1990; Connors & Kiviat, 1999), coypu (Guichon *et al.*, 2003) and capybara (Corriale *et al.*, 2011), where individuals consume a greater volume of material in close proximity to the shoreline, lodge or burrow.

Removal of plants or specific plant organs has the potential to alter the composition and richness of surrounding vegetation (Northcott, 1971; Lodge, 1991; Ray, Rebertus & Ray, 2001). Beaver foraging did significantly reduce lily pad density in areas of feeding, but this

effect was negligible at the scale of the waterbody. Beavers fed at low average intensity despite the ready availability of *N. alba* pads. With no differences in patch-scale species richness between grazed and ungrazed areas, there was no evidence for colonisation by other species following selective removal of larger *N. alba* pads by beavers. This may reflect the low number of available species within a site that could quickly colonise such gaps since oligotrophic lakes tend to support stress-tolerant rather than ruderal species. However, it is more probable that beaver foraging did not create large enough gaps for other species to colonise and that lily rhizomes that remain in place further preclude establishment of other species. Floating leaves are essential to the functioning of the internal ventilation system of lilies, with stomata on the upper side of the pad supplying the buried rhizomes with oxygen, as well as providing access to atmospheric carbon dioxide. However, there was no evidence of compensatory growth by smaller pads following the removal of larger pads, as might have been expected to meet physiological requirements. Prior to winter, assimilated compounds in lily pads are translocated to the rhizome; investing energy into new growth after the peak of the growing season is therefore neither essential nor efficient. These findings are in accordance with Kouki (1991), who found that *Nuphar lutea* (Nymphaeaceae) also did not exhibit a compensatory regrowth response in relation to herbivory by waterlily beetles (*Galerucella nymphaeae*) during the peak of growth.

In the terrestrial environment, felling and transportation of trees by beavers may be detrimental to other vegetation as this action creates patches of trampling and disturbance. When selectively removing and transporting pads in the water, there was no visible evidence of collateral damage to unselected pads or flowers. On the contrary, those sites where beavers consumed *N. alba* pads had a greater density of flowers, although this is more likely related to the slightly higher productivity of the lakes occupied by beavers. Various authors refer to feeding by beavers on the flowers of Nymphaeaceae species (e.g. Histol, 1989), but no evidence of consumption of the flowers of *N. alba* was found in any of the lakes in this study. Anecdotal reports and photographs suggest that this habit may be commoner in *Nuphar*-dominated lakes where flowers are smaller and perhaps easier to handle and therefore more profitable as food items than those of *Nymphaea*. As the impacts of beaver feeding were low, feeding occurs over short periods, and the resource is diet-complementary, we conclude that increasing numbers of beavers will probably not

severely alter the abundance of Nymphaeaceae species through direct foraging; attendant effects on associated species are also unlikely at the lake scale. However, as beavers are territorial, generalist herbivores, it is likely that they exhibit subtle selection behaviour when feeding on other aquatic plants, the effects of which have not yet been documented.

Planned reintroductions of beavers often base the predictions of survival models on population dynamics and terrestrial foraging behaviour. Impacts on other flora and fauna should, however, be fully considered pre-release if reintroductions are to be classed as 'successful' from a more holistic conservation perspective. The highly selective, optimal foraging behaviour on *N. alba* observed in this study has not been previously described in freshwater systems for beavers. This differs from accepted principles of central place foraging behaviour in the terrestrial environment and may also apply to foraging on other aquatic plant species. Since beavers evidently demonstrate adaptive foraging strategies depending on their foraging environment, this knowledge should be incorporated into future decisions on reintroduction or habitat restoration programmes.

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### Supporting Information

Additional Supporting Information may be found in the online version of this article:

**Appendix S1.** Estimates and standard errors (SE) from generalised mixed, linear mixed and generalised linear models used in the study.

**Appendix S2.** The graphical relationships between *Nymphaea alba* organs and dry weight.

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