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The impact of waterfowl herbivory on plant standing crop: a meta-analysis.

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SUMMARY

Waterfowl can cause substantial reductions in plant standing crop, which may have ecological and economic consequences. However, what determines the magnitude of these reductions is not well understood. Using data from published studies, we derived the relationship between waterfowl density and reduction in plant standing crop. When waterfowl density was estimated as individuals ha^{-1} no significant relationship with reduction in plant standing crop was detected. However, when waterfowl density was estimated as kg ha^{-1} a significant, positive, linear relationship with reduction in plant standing crop was found. Whilst many previous studies have considered waterfowl species as homologous, despite large differences in body mass, our results suggest that species body mass is a key determinant of waterfowl impact on plant standing crop. To examine relative impacts of waterfowl groups based on species body mass, a measure of plant biomass reduction (R_s) per bird per hectare was calculated for each group. Comparison of R_s values indicated some differences in impact between different waterfowl groups, with swans having a greater *per capita* impact than smaller-bodied waterfowl groups. We present evidence that this difference is linked to disparities in individual body size and associated differences in intake rates, diet composition and energy requirements. Future research priorities are proposed, particularly the need for experiments that quantify the importance of factors that determine the magnitude of waterfowl impacts on plant standing crop.

INTRODUCTION

The quantity of living plant tissues in a given area, typically defined as 'standing crop', affects ecosystem structure, functions and service provision (Grime, 2002). Herbivores can have substantial effects on plant standing crop in aquatic ecosystems (Lodge, 1991; Newman, 1991), which may have ecological and socioeconomic consequences (Baldassarre & Bolen, 2006; Klaassen & Nolet, 2007; Elmberg, 2009). Such impacts may in turn cascade onto other organisms which use plants (*e.g.* Sammler *et al.*, 2008; Samelius & Alisauskas, 2009). Published estimates of waterfowl reductions in plant standing crop range between 0–100% (Lodge *et al.*, 1998; Marklund *et al.*, 2002; Badzinski *et al*., 2006; Rodríguez-Pérez & Green, 2006; O'Hare *et al*., 2007), yet what determines the magnitude of such reductions is unclear. In particular, how reductions in plant standing crop are related to waterfowl densities is not understood, yet much of the management of waterfowl in high value plant habitats assumes that reductions in plant standing crop will be lessened by reducing waterfowl densities (Ankney, 1996; Baldassarre & Bolen, 2006). There is a pressing need to improve our understanding of waterfowl impacts on plant standing crop as many species of waterfowl herbivores have increased recently. For example, mute swan (*Cygnus olor* Gmelin, 1789) populations have risen in many regions including Britain (Ward *et al*., 2007), Central Europe (Musil & Fuchs, 1994; Gayet *et al*., 2011a), Fenno-Scandinavia (Nummi & Saari, 2003) and North America (Petrie & Francis, 2003). Of the 21 goose species (*Anser spp*. and *Branta spp*.) for which long-term population trends in Europe are known, 16 are increasing (Fox *et al*., 2010). Most reports of waterfowl damage to plants concern consumption, trampling, and faecal deposition (Ankney, 1996; Baldassarre & Bolen, 2006; Elmberg, 2009). These impacts have led to widespread human-waterfowl conflicts and management interventions including protection of plants using fenced enclosures and controlling of waterfowl populations through culls and egg destruction (Wright & Phillips, 1991; Haramis & Kearns, 2007).

In this study, we used published values to test the relationship between waterfowl density and reductions in standing crop. Differences in plant standing crop associated with and without herbivores do not represent solely plant consumption or removal. For example a number of positive and negative feedback mechanisms, such as the stimulation of plant growth by the elevation of nutrient concentrations by herbivore faecal deposition, can also influence changes in plant standing crop (Mitchell & Wass, 1996). The differences between ungrazed and grazed treatments represent the net effects of these processes on plant standing crop. We address how such net effects vary with increasing waterfowl densities.

Differences in the species composition of waterfowl assemblages have been previously overlooked in assessments of the effects of waterfowl on plants, with waterfowl analysed typically as a homogenous group (*e.g.* Lodge *et al.*, 1998; Marklund *et al.*, 2002). Most studies quantify waterfowl densities as the number of individuals within a given area (ind. ha^{-1}). In an analysis of waterfowl reductions of plant standing crop in freshwaters, Marklund *et al.* (2002) reported that some of the greatest reductions were associated with the highest waterfowl numerical densities, but there was no statistically significant relationship between waterfowl numerical density and plant standing crop reduction. However, there is a considerable difference in body mass between the smallest (24 g; ocellated crake *Micropygia schomburgkii* Schomburgk, 1848; Taylor, 1998) and largest (11970 g; trumpeter swan *Cygnus buccinator* Richardson, 1832; Kear, 2005) waterfowl, which affects waterfowl species diet and quantity of vegetation consumed (Baldassarre & Bolen, 2006). Thus, an analysis of waterfowl impacts in which waterfowl density is based on bird biomass (kg ha^{-1}) may be more appropriate. Therefore we tested two predictions; our first prediction (P_1) was that there would be no relationship between the reduction in plant standing crop (%) and the mean number of waterfowl within a given area (ind. ha^{-1}). Our second prediction (P_2) was that there would be a significant, positive relationship between the reduction in plant standing crop (%) and the mean biomass of waterfowl within a given area (kg ha^{-1}). In the second part of this study we tested for differences in the impact on standing crop between groups of waterfowl species of different body sizes. Waterfowl species have different rates of consumption due to differences in foraging behaviour and energy requirements (Bruinzeel *et al.* 1997), and thus the quantity of vegetation removed per unit time per individual may differ between groups, being greater for larger waterfowl that have higher rates of consumption. Differences in body size amongst waterfowl groups may also lead to differences in non-consumptive destruction, as larger individuals disturb a greater area. We therefore tested the prediction that heavier waterfowl groups would have a greater impact per individual on plant standing crop (P_3). We addressed the assertion that larger waterfowl species would have higher rates of consumption *per se*, testing the prediction that the rate of food consumption would increase with body mass in waterfowl (P_4). Additionally, both the total plant material, and the proportions of specific tissues, in waterfowl diets vary between species (Baldassarre & Bolen, 2006); thus we tested the predictions that herbivory (the percentage of plant material in the diet) would be greater in heavier waterfowl (P_5), and that the proportions of vegetative tissues (leaves and stems) and seeds in the diet would differ between waterfowl species of different masses (P_6).

METHODS

Study species

Waterfowl exhibit a wide range of diets (Baldassarre & Bolen, 2006). This meta-analysis focuses on waterfowl species for which plant material (*i.e.* any plant tissues) was listed in the dietary information in Taylor (1998) and Kear (2005), hereafter termed 'plant-consuming waterfowl'. Within the guild of plant-consuming waterfowl there are six principle feeding groups; Rallidae (rails, coots and allies), Anatini (dabbling ducks), Aythyini (diving ducks), Tadornini (sheldgeese, shelducks and allies), Cygnini (swans), and Anserini (geese). Previous authors have tended to disregard Rallidae (hereafter 'rails') when discussing waterfowl (*e.g.* Baldassarre & Bolen, 2006) due to their distant evolutionary relationship to ducks, geese and swans. However, rails exhibit many broad similarities in diet, foraging behaviour and effects on vegetation with other waterfowl (Marklund *et al.*, 2002) so we include them here. Based on the information given in Taylor (1998) and Kear (2005), there are 233 species of waterfowl that consume vegetation, with around three quarters of these represented by ducks and rails (**Figure 1**). Within the swans and geese all species consume vegetation, whereas within groups of smaller-bodied waterfowl some species are exclusively carnivorous (22 % for rails and 45 % for diving ducks).

Waterfowl densities and reductions in plant standing crop

We used published experimental (n = 25) and observational (n = 1) studies in any waterfowl habitats where plant standing crop (dry weight g m^{-2}) had been measured both where waterfowl were present and absent simultaneously. We limited our meta-analysis to studies where waterfowl counts were made in a defined area over a defined period of time. We analysed both single- and mixed-species assemblages, in terms of both plants and waterfowl. We analysed data from 26 suitable studies (**Table 1**), from which we calculated two measures of waterfowl density:

WID = Waterfowl Individual Density (ind. ha^{-1}) = $\sum_i N_i$

WBD = Waterfowl Biomass Density (kg ha^{-1}) = $\sum_i N_i M_i$

where N_i = mean population size of waterfowl species *i* present per hectare during the study period

M_i = mean body mass (kg) of individuals of species *i* (as given in Taylor (1998) and Kear (2005))

and the summation is over all plant-consuming waterfowl species. Where sex-related differences in mass were reported, we took the mean values of the male and female body masses. We assumed that all individuals were adults, unless the study indicated the presence of juveniles, in which case body mass values for the appropriate age were used to calculate biomass.

Waterfowl intake rates typically scale with body mass between 0.7-0.8 (Bruinzeel *et al*., 1997; van Gils *et al*., 2007). However, given that herbivore impact on plants does not represent consumption alone (Mitchell & Wass, 1996), and that the allometric scaling of non-consumptive factors is unknown, we assumed a mass exponent of 1.0 in our conversion of *WID* to *WBD* as a conservative approximation. Percentage reduction in plant above-ground standing crop (R) was calculated after Lodge *et al.* (1998) and Marklund *et al.* (2002) as $R = [(B_{\text{-herbivore}} - B_{\text{+herbivore}})/B_{\text{-herbivore}}] \cdot 100$, where $B_{+herbivore}$ and $B_{-herbivore}$ are plant standing crop with and without waterfowl herbivores present respectively. We compared values of plant standing crop at the time of peak standing crop. The use of post-peak values, when the plant is either in recession or dormant, risked confounding decreases in plant standing crop due to herbivory with seasonal recession. Where studies contained multiple values of R which were not statistically independent, for example multiple values for the same lake, or between-year replicates, we used average values for R and waterfowl density.

Differences between waterfowl taxa: implications of body mass

To examine whether reductions in standing crop varied between different taxonomic groups of waterfowl, we analysed the R values given in the previous section, and calculated a *per capita* reduction in plant biomass (R_s) standardised between different waterfowl densities, using the formula:

$R_s = R / [P / A]$

where *P* is the total number of birds present in the study area, and *A* is the study area (in hectares). Estimates of R_s were derived from published studies for flocks of rails (*Fulica spp.* only; *n* = 6 studies), swans (*n* = 5), and geese (*n* = 6). However, no studies of single-species flocks for sheldgeese or ducks could be found that reported the information required to calculate R_s.

Waterfowl size and rates of food consumption

To test whether waterfowl intake rate, and thus the removal rate of plant tissues, increases with body size we analysed 12 published values for waterfowl foraging on terrestrial pasture grasses (*Poaceae*). Selecting *Poaceae*, the plant taxon for which waterfowl intake rates have been quantified most often, allowed us to exclude the confounding effects of plant morphology on intake rate in our analysis. Intake rate is limited by food density below a threshold (*e.g.* Owen, 1972; van Gils *et al.*, 2007).Therefore calculating a mean intake rate averaged over all of the food densities tested in a study would have yielded a value biased by both which, and how many, food densities had been tested. Thus we used the maximum intake rate reported in each study to minimise the confounding effect of food density-limitation on intake rate.

Waterfowl size and herbivorous diet

Two aspects of waterfowl diet composition may affect the magnitude of impacts on plants: the proportion of vegetation (*i.e.* any plant tissue) in the diet and the proportions of different plant tissues consumed. To examine differences in the proportion of diet comprised by vegetation, we analysed 89 published dietary values (see supplementary information) for 56 of the species that consume vegetation according to Taylor (1998) and Kear (2005). Where studies sampled in different seasons we calculated mean values and where multiple studies existed for a single species we calculated mean values for that species. We further analysed the diet data by comparing the percentage of dry weight plant material consumed by each waterfowl group that is comprised of seeds and vegetative material (stems and leaves). Other plant tissues were excluded from this analysis due to lack of sufficient data.

Statistical analyses

Waterfowl herbivory meta-analysis

We used linear regression analyses to test the relationship between waterfowl density and reductions in plant standing crop (P_1 and P_2). Both sets of estimates of waterfowl density (ind. ha^{-1} and kg ha^{-1}) were log_{10}-transformed to achieve linearity of relationship and normal distribution of residuals. Linear regression analysis was also used to test the relationship between body mass and maximum intake rate of waterfowl species (P_4). We used one-way analysis of variance (ANOVA) to test for differences between waterfowl taxa in (i) impact on plant standing crop (P_3), (ii) percentage of plant matter in diet (P_5), and (iii) percentages of seeds or vegetative tissues in diet (P_6). Statistical analyses were carried out using SPSS version 18 (IBM, US) , with a statistically significant result attributed where $p < 0.05$. Normality of the residuals was confirmed for all data.

RESULTS

Waterfowl densities and reductions in plant standing crop

We found no relationship between *WID* and *R* ($F_{1,24} = 1.51$, $p = 0.2315$, $R^2_{adj} = 2.0$ %) (**Figure 2a**), supporting our first prediction (P_1). However, we found a significant, positive relationship between *WBD* and *R* ($F_{1,24} = 12.77$, $p = 0.0015$, $R^2_{adj} = 32.0$ %) (**Figure 2b**), described by the regression equation (coefficient s.e. in brackets):

$$R = 28.24\ (\pm 6.00) + 23.88\ (\pm 6.68) \cdot \mathrm{Log}_{10} WDB$$

Thus our results support our second prediction (P_2).

Differences between waterfowl taxa: implications of body mass

A one-way ANOVA indicated that R_s differed significantly between waterfowl groups ($F_{2,14} = 13.81$, $p < 0.001$); *post-hoc* Tukey's tests indicated that swan R_s values were significantly greater than those of geese ($p = 0.002$) and rails ($p = 0.001$), but no other comparisons were significantly different (**Figure 3**). Thus, our results give partial support to our third prediction (P_3), as differences in impact on plant standing crop were observed between the largest and smallest waterfowl groups, but not between all groups.

Waterfowl size and rates of food consumption

Waterfowl herbivory meta-analysis

There was a significant, positive relationship between species $\log_{10}$-transformed maximum intake rate I_{max} (dry weight g s^{-1}) and species $\log_{10}$-transformed body size *M* (g) ($F_{1,10} = 28.75$, $p = 0.0003$, $R^2_{adj} = 71.6$ %) (**Figure 4**), described by the regression equation (coefficient s.e. in brackets):

$$I_{max} = -4.89\ (\pm\ 0.50) + (0.81\ (\pm\ 0.15) \cdot M)$$

These results support our fourth prediction (P_4); a larger species will typically consume vegetation at a faster rate than a smaller species, and thus may have a greater *per capita* impact on plant standing crop per unit time.

Waterfowl size and herbivorous diet

The proportion of vegetation in diet was significantly different between the six waterfowl groups ($F_{5,55}$= 6.62, $p < 0.001$). A *Post-hoc* Tukey's test indicated that the percentage of vegetation in diet were significantly lower in diving ducks compared to dabbling ducks ($p = 0.007$), sheldgeese ($p < 0.001$), swans ($p = 0.001$) and geese ($p = 0.047$), but no other comparisons were significantly different (**Figure 5a**). These results offer partial support for our prediction (P_5) that heavier waterfowl are more herbivorous. The proportion of seeds of total plant material consumed in the diet was significantly different between waterfowl groups ($F_{5,23} = 5.94$, $p = 0.001$). A *Post-hoc* Tukey's test indicated that seed consumption was significantly higher in dabbling ducks relative to swans ($p = 0.009$) and geese ($p = 0.002$) (**Figure 5b**). The proportion of stems and leaves of total plant material consumed in the diet was significantly different between waterfowl groups ($F_{5,23} = 7.91$, $p < 0.001$). A *Post-hoc* Tukey's test indicated that consumption of stems and leaves was significantly higher in swans relative to dabbling ducks ($p = 0.003$), diving ducks ($p = 0.007$) and rails ($p = 0.014$), and significantly higher in geese relative to dabbling ducks ($p = 0.002$), diving ducks ($p = 0.007$) and rails ($p = 0.022$), but no other comparison was significantly different. These results offer partial support for our prediction (P_6) that waterfowl mass would affect the proportions of different plant tissues in diet.

DISCUSSION

Waterfowl herbivory meta-analysis

From our meta-analysis of waterfowl impacts on reductions in plant standing crop we present the first demonstration of a significant linear relationship between reductions in plant standing crop and waterfowl biomass density. This relationship enables practitioners to estimate the likely impact on plant standing crop of both natural and managed changes to waterfowl populations. That reductions in plant standing crop were related to waterfowl density estimated as kg ha^{-1}, but not waterfowl density estimated as ind. ha^{-1}, suggests that it is the biomass of waterfowl rather than the number of individuals which is the more important determinant of waterfowl effects on plant standing crop (Gyimesi *et al*., 2011). The largest reductions in plant standing crop should thus be observed at sites where high-densities of large-bodied waterfowl congregate, such as annual moult sites and other areas where large non-breeding flocks gather to feed (Kear, 2005; Baldassarre & Bolen, 2006). Currently, most studies of waterfowl herbivory analyse the impacts on plant standing crop based on the number of waterfowl present, regardless of species. Greater recognition amongst waterfowl biologists is therefore needed of the importance of body mass when determining waterfowl impacts on plant standing crop. However, the relationship with biomass should be used cautiously as the spread of data around the mean regression line is considerable. Future research could incorporate factors other than waterfowl density that may influence waterfowl impacts on plant standing crop, such as plant life-history (*e.g.* growth rate, age, competitiveness, anti-herbivore defences) and environmental factors (*e.g.* water depth, light, temperature, CO_2 availability; Bornette & Puijalon, 2011; Gayet *et al*., 2011b). Intraspecific differences in body mass also exist, for example between sexes and between age classes; whether intraspecific differences in body mass also affect reductions in plant standing crop should be investigated further.

Swans had significantly higher *per capita* impacts on plant standing crop relative to geese and rails, probably due to the greater body mass and associated greater energy requirement, intake rate, and proportion of plant tissues in the diet. We were unable to estimate the *per capita* impacts on plant standing crop of sheldgeese, dabbling ducks, or diving ducks as there were no published single-taxon studies of these groups. Future studies could quantify the *per capita* impacts of these groups and compare the values to those presented in this study for swans, geese, and rails. Such *per capita* impacts are difficult to measure in wild waterfowl populations as individuals often live in mixed-taxon flocks (Baldassarre & Bolen, 2006). The impacts of small duck species could be assessed with the use of fencing that excludes larger-bodied waterfowl from the study area (*e.g.* Badzinski *et al*., 2006). Alternatively, *per capita* impacts on plant standing crop could be measured for a species or taxon (a flock of individuals of different species but the same group, *i.e.* dabbling ducks) under controlled *ex situ* conditions such as artificial pools in a laboratory.

Large waterfowl (> 2500 g) are almost exclusively vegetarian, whilst smaller species exhibit a range of diets from omnivory to exclusive herbivory. Bruinzeel *et al.* (1997) analysed waterfowl allometry and found that waterfowl energy intake rate scales with a power of body mass of between 0.78 and 0.85, whereas daily energy expenditure scales with the power 0.68. In this study we found that maximum intake rate scaled with a power of body mass of 0.81. Thus small waterfowl such as dabbling ducks must devote more time to foraging than larger waterfowl, or seek food of higher nutritional quality (Demment & van Soest, 1985). Vegetation is typically low in nitrogen and high in fibre relative to animal tissue (Baldassarre & Bolen, 2006). Our results suggest that smaller waterfowl rely less on lower quality vegetation and more on higher quality animal matter. Thus an individual of a small species will consume a lower quantity of vegetation, due to both a lower total energy requirement and a lower proportion of vegetation in their diet, than an individual of a larger species. As leaves and stems comprise a greater proportion of plant standing crop relative to seeds (Grime, 2002), consumption of the former will likely have a greater impact on plant standing crop than consumption of the latter, at least in the short term (Maron & Gardner, 2000).

How reductions in plant standing crop affect the abundance and behaviour of other organisms is currently poorly understood. There is a particular need to study the potential impacts on organisms with ecological and economic importance, such as fish. Several studies have demonstrated that populations of birds, small mammals, and invertebrates have been reduced due to waterfowl herbivory (*e.g.* Sammler *et al*., 2008; Samelius & Alisauskas, 2009), but whether these reductions are typical or exceptional requires further investigation. The mechanisms by which vegetation losses caused by waterfowl herbivory alter animal abundances are unclear. Several mechanisms have been proposed, including loss of refugia, reduced food availability, and physical disturbance caused by grazing. Future experiments that demonstrate the relative importance of these and other mechanisms are needed.

The ability to predict the effects of waterfowl on plant standing crop would aid management and conservation of both taxa and their associated habitats. Ecological modelling represents a potential tool for predicting the consequences of waterfowl foraging on plants. Resource-consumer models, such as individual-based models (IBMs), can generate predictions of plant biomass depletion, waterfowl foraging effort, waterfowl distribution, and habitat carrying capacity, from data on waterfowl energy requirements, food intake rates, plant distributions, and plant energy content and digestibility (Stillman & Goss-Custard, 2010; Wood *et al.*, accepted). Such predictions allow the spatiotemporal patterns of plant depletion to be quantified and strategies for both herbivore and plant management to be tested.

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TABLES

Table 1: Information extracted from each study included in the meta-analysis of waterfowl impacts on plant standing crop. Between-site replicates refer to the number of different sites at which *R* was measured, for which a mean *R* value was derived. Between-year replicates refer to the number of different years in which *R* was measured, for which a mean *R* value was derived. [1] species codes; a = mute swan *Cygnus olor*; b = Eurasian coot *Fulica atra*; c = black swan *Cygnus atratus*; d = black-necked swan *Cygnus melancoryphus*; e = northern mallard *Anas platyrhynchos*; f = gadwall *Anas strepera*; g = common teal *Anas crecca*; h = greylag goose *Anser anser*; i = tufted duck *Aythya Aythya*; j = common pochard *Aythya ferina*; k = common goldeneye *Bucephala clangula*; l = common shelduck *Tadorna tadorna*; m = northern shoveler *Anas clypeata*; n = Eurasian wigeon *Anas penelope*; o = red-crested pochard *Netta rufina*; p = common moorhen *Gallinula chloropus*; q = snow goose *Chen caerulescens*; r = Canada goose *Branta canadensis*; s = barnacle goose *Branta leucopsis*; t = coscoroba swan *Coscoroba coscoroba*; u = red-gartered coot *Fulica armillata*; v = white-winged coot *Fulica leucoptera*; w = yellow-billed pintail *Anas georgica*; x = red shoveler *Anas platalea*; y = yellow-billed teal *Anas flavirostris*; z = Chiloe wigeon *Anas sibilatrix*; ψ = silver teal *Anas versicolor*; . [2] waterfowl densities given by Allison & Newton (1974).

Study	Species present[1]	Mean WID (ind. ha^{-1})	Mean WBD (kg ha^{-1})	Study length (days)	Study area (ha)	Between-site replicates	Between-year replicates	*R* (%)
O'Hare *et al*., 2007	a	7.2	0.7	22	18.0	1	1	49.2
Verhoeven, 1980	b	12.5	15.6	60	5.6	1	1	75.1
Sondergaard *et al*., 1996	b	5.2	6.5	60	21.0	1	1	61.0
Esler, 1989	b	5.5	6.8	75	1053.0	1	1	57.8
Perrow *et al*., 1997	b	2.7	3.4	118	5.5	1	1	23.2
Allin & Husband, 2003	a	17.5	1.7	90	84.6	3	5	55.1
van Donk & Otte, 1996	b	6.3	32.6	150	1.5	1	1	48.5
Corti & Schlatter, 2002	d	7.3	1.6	256	120.0	1	1	62.7
Sandsten *et al*., 2005	b,e,o,p	20.5	81.0	92	540.0	1	1	63.1
Hilt, 2006	a,b,e,i,j,k	1.1	1.1	91	730.0	1	1	42.9
Jupp & Spence, 1977[2]	b,e,f,g,i,j,k,l,m,n	0.6	1.8	200	1597.0	1	1	24.8
Lauridsen *et al*., 1993	b	16.0	20.0	60	15.0	4	1	62.4
Cargill & Jeffries, 1984	q	33.4	67.5	60	540.0	1	1	47.1
Esselink *et al*., 1997	h	7.2	2.1	210	1160.0	1	1	56.3
Haramis & Kearns, 2007	r	33.0	10.0	138	500.0	1	1	80.4
Masse *et al*., 2001	q	3.1	1.0	42	160000.0	1	2	32.5
Ydenberg & Prins, 1981	s	7.8	4.6	40	700.0	1	1	35.4
Smith, 2010	c	2.5	0.5	135	176.0	1	1	51.8
Dixon, 2009	c	5.2	1.0	60	600.0	3	1	57.0
Bortolus *et al*., 1998	d,t,u,v,w,x,y,z,ψ	2.3	1.5	31	82.0	1	1	16.7
Marklund *et al*., 2002	a,b,e,f,g,h,i,j,k	3.5	5.0	60	56.0	1	1	0.0
Lauridsen *et al*., 2003	b,e,j	1.5	1.5	69	44.0	1	1	40.7
Patton & Frame, 1981	h,s	20.3	3.6	85	2774.0	3	2	49.9
Rodriguez-Perez & Green, 2006	b,e,f,j,o	2.3	2.6	109	2997.0	1	1	29.0
Rodriguez-Villafane *et al*., 2007	b,e,f,n	14.8	42.0	59	4.5	1	1	36.7
Hidding *et al*., 2010	a,b,e,f,g	8.5	4.9	92	2100.0	1	4	59.6

FIGURE LEGENDS

Figure 1: The number of species in each of the six feeding groups comprising the waterfowl guild, together with the proportion that consume (dark grey) and do not consume living plant tissues indicated (light grey).

Figure 2: The relationships between reductions in plant standing crop (*R*) and waterfowl density, estimated as (a) individuals ha^{-1} and (b) kg ha^{-1}, based on data from published studies.

Figure 3: Mean (± 95 % CI) proportional reductions in plant standing crop per individual per hectare (R_s), based on the published values given in Figure 3. Different letters indicate significant *post-hoc* differences between groups.

Figure 4: Relationship between $\log_{10}$-transformed waterfowl body mass and $\log_{10}$-transformed maximum dry mass intake rate (I_{max}) on terrestrial pasture grasses. Data from (1) Ebbinge *et al.*, 1975 (barnacle goose); (2) Owen, 1972 (white-fronted goose); (3) Summers & Grieve, 1982 (ruddy-headed goose, upland goose); (4) Prop *et al.*, 1998 (barnacle goose); (5) van der Wal *et al.*, 1998 (barnacle goose); (6) Therkildsen & Madsen, 2000 (pink-footed goose); (7) Durant *et al.*, 2003 (Eurasian wigeon, greylag goose, barnacle goose); (8) van Gils *et al.*, 2007 (Bewick's swan).

Figure 5: A meta-analysis of (a) the mean (± 95 % CI) percentage of all plant tissues in the diets of 53 species from 89 published values (see supplementary information), based on dry weight, and (b) the mean percentages (± 95 % CI) of herbivorous diets comprised of seeds (dark bars) and vegetative tissues such as leaves and stems (light bars), based on dry weight. Different letters indicate significant *post-hoc* differences between groups.

FIGURES

Figure 1:

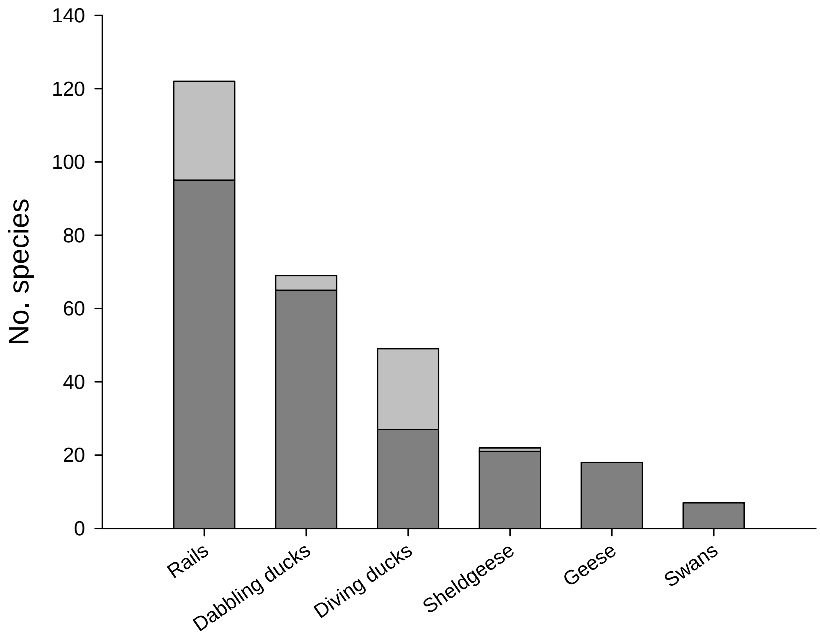
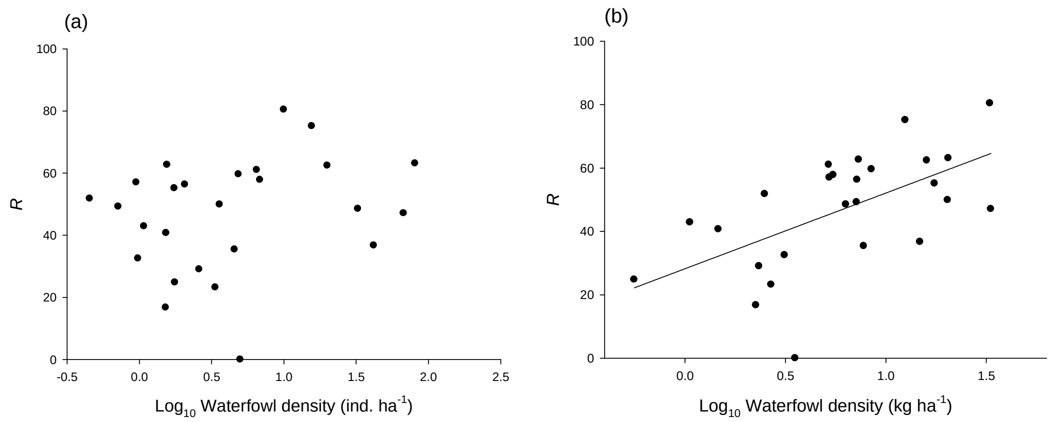


Figure 2:



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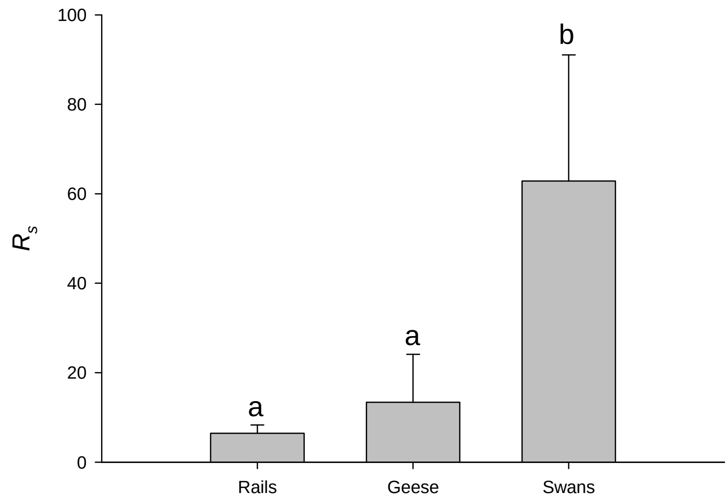

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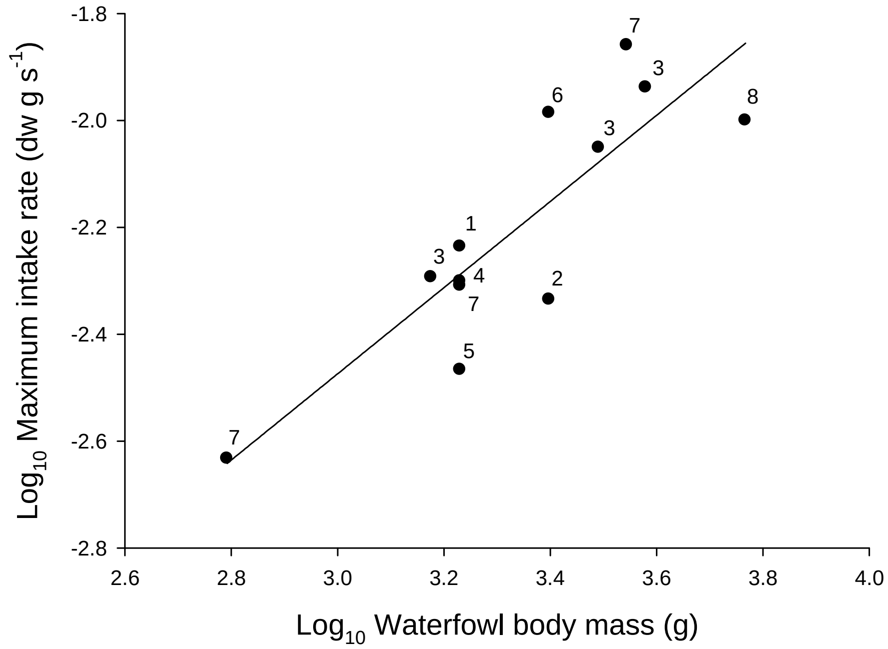
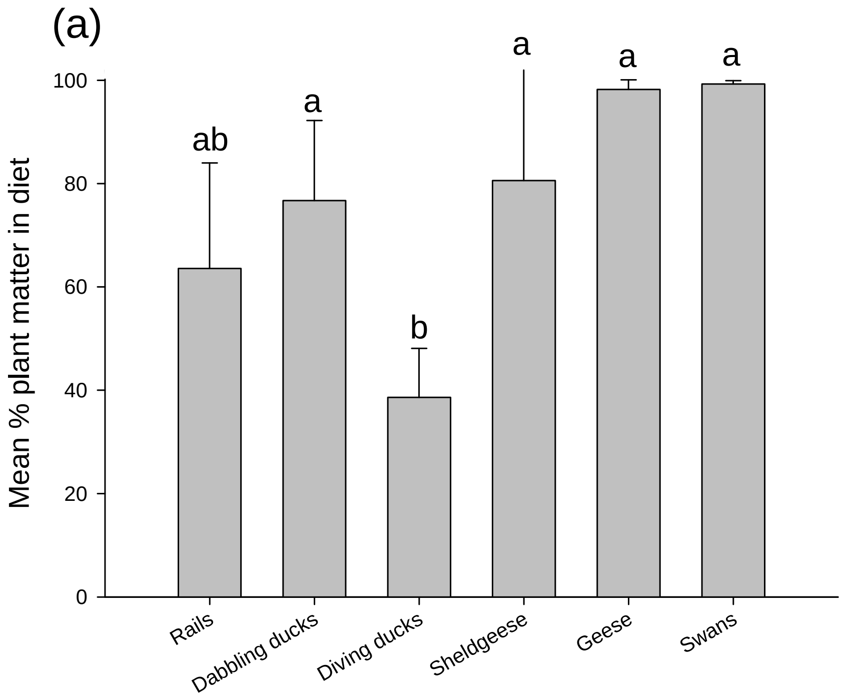
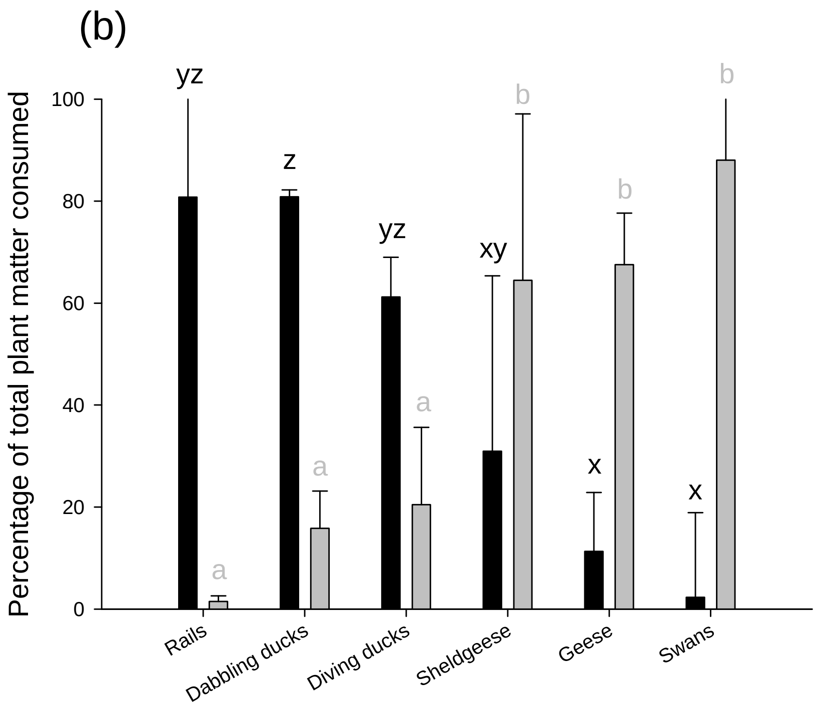


Figure 5:


(a)
Mean % plant matter in diet
0
20
40
60
80
100
ab
a
b
a
a
a
Rails
Dabbling ducks
Diving ducks
Sheldgeese
Geese
Swans


(b)
Percentage of total plant matter consumed
0
20
40
60
80
100
yz
a
z
a
yz
a
xy
b
x
b
x
b
Rails
Dabbling ducks
Diving ducks
Sheldgeese
Geese
Swans