9

The relationship between preferred food density and grazing White-fronted Geese: an example of an asymptotic aggregative response.

Kristiansen, J.N., Fox, A.D., Boyd, H., Nyegaard, T. & Nachman, G.

The relationship between preferred food density and grazing white-fronted geese: an example of an asymptotic aggregative response

Jens Nyeland Kristiansen, Anthony D. Fox, Hugh Boyd, Timme Nyegaard & Gösta Nachman

Abstract

1. We describe the aggregative response of the Greenland white-fronted goose *Anser albifrons flavirostris* to the main food plant *Phleum pratense* during spring staging in Iceland in 1997 and 1999.

2. Geese aggregated more as the density of individual *Phleum* shoots increased but approached an asymptotic level at shoot densities above c. 10-20 shoots per 100 cm^2.

3. There was a significant increase in aggressive encounters with increasing goose aggregation in 1999 but not in 1997, and no correlation between aggression and food abundance. Hence, weak interference (such as resource guarding) may influence the aggregative response.

4. At lowest shoot densities the geese took most laminae present. As shoot densities increased the proportion of laminae taken decreased exponentially reaching an asymptotic level of c. 25-30% taken.

5. Mean lamina size decreased exponentially with increasing shoot density (i.e. many small laminae occurred at high densities), suggesting density dependent effects on shoot size.

6. At shoot densities above 10 shoots per 100 cm^2, the number (density) of laminae preferred by the geese (i.e. those > 13.7 mm) remained constant. However, the percentage of preferred laminae present declined exponentially.

7. Because geese prefer larger laminae, we suggest that the asymptotic nature of goose aggregation may be due to the constant number (density) of preferred lamina present at high densities.

8. The results suggest that measures of food density needs to take food availability and unit size into account to fully understand the mechanisms underlying the aggregative response of consumers.

Introduction

One of the main mechanisms determining the spatial and temporal distributions of consumers is the relationship between their density and that of their food – the so-called aggregative response. This has been demonstrated for a number of invertebrates (e.g. Hassell 1971; Hassell & May 1974; Driessen & Hemerik 1991) and birds; e.g. for woodpigeon *Columba palumbus* (Murton, Westwood & Issacson 1964), redshank *Tringa totanus* (Goss-Custard 1970) and herbivorous geese (Ydenberg & Prins 1981; Fox 1993; Sutherland & Allport 1994; Fox, Kahlert & Ettrup 1998; Rowcliffe, Watkinson & Sutherland 1998; Rowcliffe, Sutherland & Watkinson 1999). In these studies, consumers aggregate more as the density of their food increases. However, if the aggregative response should have some practical application, such as a predictive function, it is important to understand the nature of the relationship between the density of food and consumers, for example, whether it is linear or not. Often increasing food density above a certain threshold does not result in further increases of consumers. The general explanation for this is that higher consumer abundance increases the number of aggressive encounters (see Hassell 1978; Sutherland 1996), which counteracts the advantage of aggregating in otherwise profitable areas. Generally, agonistic interactions between feeding geese are rare and the strength of interference consequently is relatively low. Rowcliffe *et al.* (1999) suggested that resource guarding (despotism) could be responsible for a weaker aggregation in feeding brent geese *Branta bernicla* than expected at high food densities. However, apart from this, no alternative explanation for the nonlinear behaviour of the aggregative response in such herbivores has been provided.

The theory of the ideal free distribution asserts that profitability to the individual is equal in each patch (Fretwell & Lucas 1970), but profitability is dependent on food quality and availability as well as food density. Hence, the way that consumers aggregate with regard to food density is likely to be affected by these factors as well as intra-specific interference. Previous studies have hitherto focused on the latter (e.g. Sutherland 1983; Van der Meer & Ens 1997) but less attention has been paid to food availability and quality in the context of aggregative response. For a herbivore most vegetation is inedible (Sinclair 1975, Crawley 1983, 1997) and Rowcliffe *et al.* (1998) suggested that the lack of continued aggregative response at high food densities by brent geese to the biomass of *Puccinellia* was the result of accumulation of old

Study site and methods

The study was conducted at Hvanneyri Agricultural College, southwest Iceland (64°34'N 21°46'W) during 1997 and 1999. The farm comprises some 70 hayfields, all located within 1-2 km from the roost sites of the geese. The fields are dominated by two native species *Poa pratense* and *Deschampsia caespitosa* together with the introduced *Phleum pratense* which is reseeded regularly due to its gradual displacement by the two dominant native species (Fox 1993). As *Phleum* has an earlier onset of growth in spring than any of the other potential food plant species, the above ground green biomass is almost exclusively comprised of *Phleum* during the first c. two weeks after the arrival of the geese. *Phleum* has been recorded from approximately 60% of the fields (albeit at different densities) and all these fields were included in this study. The farm is intensively grazed by up to 1,400 greenland white-fronted geese at any one time during their spring staging (Fox *et al.* 1999). On a few occasions small numbers of other goose species (greylag geese *A. anser*, pink-footed geese *A. brachyrhynchus*, canada geese *Branta canadensis* and barnacle geese *B. leucopsis*) were recorded on the fields. When feeding on *Phleum* spring staging geese in Iceland have been shown to select the middle erect youngest leaf (a0-lamina) (Fig. 1), which is the part of the plant with highest nutrient and lowest fibre content (Fox 1993).

PHLEUM DENSITY AND GOOSE AGGREGATION

Goose aggregation was assessed on 27-29 April ten to 12 days after the arrival of the geese in 1997 and 1999 by relating dropping densities to shoot density of *Phleum* in 44 fields in 1997 and 42 fields in 1999. Droppings, which are produced at a rate of 0.315 droppings minute^{-1} ($\pm$ 0.04 SE, $n = 23$) by geese, give a good measure of goose use within individual fields (Owen 1971). We therefore used counts of cumulative droppings on each field as an index of grazing intensity, by counting the number of droppings in 25 randomly placed one m^2 quadrats in each field. Since goose droppings persist for 2-3 weeks (Percival 1993) it was considered unlikely that any droppings had disappeared. The density of *Phleum* shoots was assessed by counting the number of shoots in 25 randomly selected 100 cm^2 (10 cm x 10 cm) quadrats in each field. Because of differing intensity of goose use of the fields at Hvanneyri in the two studied years, we related the use of particular fields to the use of the whole farm.

We constructed a simple model to predict the proportion of geese (expressed as dropping density) in the *i*th field: $D_i/D_{tot} = N_i^c/\Sigma N_i^c$ where D_i is the number of geese (expressed as dropping density) in the *i*th field, D_{tot} is the total number of geese (expressed as dropping density), N_i is the shoot density in the *i*th field and c is a constant. In addition, to assess the proportion of shoots eaten by the geese the number of grazed shoots in each of the quadrats was counted in 1999. *Phleum* fields were evenly distributed throughout the college farm area and disturbance by occasional road traffic and farming operations is considered to have occurred to roughly similar extent on all fields. Hence we do not consider human activity or travel costs from the roost on mudflats less than 2 km from the furthest fields used to have caused any significant influence on the distribution of consumers in this study.

BEHAVIOURAL STUDIES

To assess if aggregation of the geese and/or the abundance of food (i.e. density of *Phleum*) caused an increase in aggressive behaviour among the geese, scan samples (Altmann 1974) of goose behaviour were conducted in 1997 and 1999. These were compiled at least three times every day on all of the farm fields. Only frequency of aggression (i.e. the number of encounters per goose) are considered here and this was related to observed goose density at each field unit expressed as geese ha^{-1} and to the shoot density of *Phleum* in the particular field. Logistic regression (PROC GENMOD in SAS) was applied to assess the effect of goose density, shoot density and the interaction between goose density and shoot density (independent variables) on the level of aggression among the geese (dependent variable).

SHOOT SIZE AND SHOOT DENSITY

To relate size of the a0 lamina (i.e. the youngest lamina) to shoot density, 22 randomly placed 100 cm^2 quadrats were selected from one field (field 1) to reflect the range of different shoot densities. All shoots in each quadrat were harvested by clipping to soil level and the lengths of all a0 laminae were measured. Average a0 length per quadrat was then related to the shoot density of that quadrat.

NUMBER OF PREFERRED LAMINAE AND SHOOT DENSITY

Greenland white-fronted geese select only a0 laminae above a certain size when feeding in Icelandic hayfields, however, the choice depends on the size distribution of laminae in the particular field (Kristiansen *et al.* 2000). To relate number of these preferred laminae to shoot density we used the shoot densities from one field (field 1) from which the geese select laminae larger than 13.7 mm (Kristiansen, *et al.* 2000). We then related the number of laminae >13.7 mm to shoot density and percentage of laminae >13.7 mm against shoot density.

Results

Based on the model $D_i/D_{tot} = N_i^c/\Sigma N_i^c$ a good fit to the observed data was achieved in both 1997 and 1999 (Fig. 2a & b). Hence we can expect geese to aggregate according to this simple model within a shoot density range 0-30 shoots per 100 cm^2.

In 1997 there was no effect of the density of geese, shoot density and interaction between these two variables on the level of aggression among geese (Logistic regression, goose density: $\chi^2 = 0.1897$, $P = 0.55$, d.f. = 1; shoot density: $\chi^2 = 0.3521$, $P = 0.66$, d.f. = 1; goose density*shoot density: $\chi^2 = 0.1841$, $P = 0.67$, d.f. = 1. $n = 173$). In 1999 however, level of aggression among geese increased significantly with increasing goose density but there was no effect of shoot density, or the interaction between goose density and shoot density on the level of aggression (Logistic regression, goose density: $\chi^2 = 13.6988$, $P = 0.0002$, d.f. = 1; shoot density: $\chi^2 = 0.1297$, $P = 0.7187$, d.f. = 1; goose density*shoot density: $\chi^2 = 2.3317$, P = 0.1268, d.f. = 1. $n = 387$).

As shoot density of *Phleum* increased, the mean length of the laminae available to the geese (a0 lamina) showed a significant nonlinear decline described by the power function $L_i = aN_i^b$, where L_i is mean lamina length (mm) in the *i*th patch, N_i is the shoot density (shoots/100 cm^2) of the *i*th patch and *a* and *b* are constants (Fig. 3).

Based on the relationship between lamina length and shoot density, $L=aN^b$, from Fig. 3, the a0 biomass, *B* (expressed as total length of a0 laminae, mm per 100 cm^2) from each field was measured using $B_i = L_i * N_i = aN_i^{1+b}$. Where B_i is the biomass per 100 cm^2 of the *i*th field, L_i is the mean lamina length of the *i*th field, N_i is the shoot density (shoots/100 cm^2) of the *i*th field and *a* and *b* are constants from the lamina shoot density relationship. Therefore, $B_i = 52.89\ N_i^{0.5575}$. The relative biomass, B_i/B_{tot} (B_{tot} is the total biomass per 100 cm^2 of all fields) was then plotted against shoot density and compared with relative goose use, D_i/D_{tot} (from Fig. 2a & b) in Fig. 4a & b. It was clear in both years that the relative density of geese did not match perfectly to the relative abundance of a0 *Phleum* laminae. Below c. 3-5 shoots/100 cm^2 the geese crowded more than expected and beyond this density the proportion of geese was less than expected if the birds were distributed in accordance with the distribution of their food resource.

Only at very low shoot densities did the geese usually exploit all available shoots, but as shoot density increased, the proportion eaten gradually decreased. Above densities of c. 40 shoots/100 cm^2 only c. 20-30% of the shoots were taken (Fig. 5).

In the range 10-80 shoots per 100 cm^2, there was no significant relationship between the absolute number of preferred laminae present and overall shoot density (r^2 = 0.0004, $n = 22$, $P > 0.05$). In this range an average of 9.6 laminae/100 cm^2 ($\pm$ 0.62 SE) were of the preferred size. Fig. 6. shows the relationship between percentage of preferred laminae present and shoot density. The percentage of preferred lamina decreased exponentially with increasing shoot density. At shoot densities above c. 30-40 shoots per 100 cm^2 an asymptote was reached where c. 20-30% of the laminae were of the preferred size.

Discussion

In contrast to most other studies which have used gross biomass to measure food density (e.g. Ydenberg & Prins 1981; Sutherland & Allport 1994; Rowcliffe *et al.* 1998), this study was able to relate unit prey (shoot) density to predator abundance (geese). Since the only green biomass available to staging geese at the time of the study was *Phleum pratense*, this system can be viewed as a simple predator/prey (consumer/resource) relationship. The Greenland white-fronted geese showed strong aggregative response to increasing shoot density. However, the relationship was not a simple linear one, but was characterized by a steady declining slope leading to a convex curve approaching an upper asymptote. This relationship between goose density and their single food item only persisted as long as no other food was available. After ten days or more, *Phleum* was exhausted while other food plants became available (e.g. *Poa pratense* and *Deschampsia caespitosa*). The geese gradually utilized these as a supplement in their diet (Kristiansen *et al.* 1998), as well as feeding on nearby *Carex lyngbye* meadows where the geese dug up the underground nutritious overwintering low stems, available only when the meadows had thawed (D. Stroud *et al.* unpublished). There was however, a clear discrepancy between relative goose aggregation and relative abundance of their actual food resource (a0 lamina). At low shoot densities the geese aggregated more than expected, possibly because geese normally feed in flocks, the smallest unit typically being a family comprising two adults with two to three immature birds. Contrary to the pattern at low shoot densities, the higher shoot density areas provided fewer geese than expected which could have been caused in two ways. First, in other studied systems, increased interference has been invoked to explain the levelling off pattern between a consumer and its prey at high density (Hassell 1978; Sutherland 1996) because at high predator densities intake rate of the individual may decrease due to increasing interference (Van der Meer & Ens 1997). Rowcliffe *et al.* (1999) suggested that the low degree of interference in some goose grazing studies may be because the geese avoid crowding at densities high enough to promote encounters, a phenomenon which has been recorded for other animals (Arditi & Akcakaya 1990). Above a certain biomass threshold, aggression among geese suddenly became evident, which supported the hypothesis that resource guarding may have caused the observed pattern of aggression (Rowcliffe *et al.* 1999). In our study we found a statistically significant relationship between density of the geese and the level of aggression in 1999 but not in 1997. Therefore, we cannot fully reject the hypothesis that this could contribute to the asymptotic nature of the aggregative response. It is however, unlikely that the pattern of the aggregative response shown here is caused purely by increased interference at high goose density.

Second, Greenland white-fronted geese select laminae above a threshold level due to profitability constraints, hence smaller shoots are ignored even when numerous (Kristiansen *et al.* 2000). Therefore, because mean shoot length decreased with increasing density, a declining proportion of shoots were of preferred size as shoot density increased. The most likely reason for this is increased intraspecific competition among *Phleum* shoots which has been found to affect individual size in many plant species –the so-called self-thinning effect- (Lonsdale & Watkinson 1982, 1983; Crawley 1997) and is a well documented effect of density dependent growth in some animals too (Branch 1975; Hughes & Griffiths 1991; Elliot 1993). In this study the net effect was a constant density of preferred shoots above a threshold of 10-20 shoots per 100 cm^2, which probably caused the lack of continued aggregative response by the geese above this threshold. Therefore, although weak resource guarding and/or increasing aggressive encounters with increasing goose densities may have been involved in this study, we suggest that an additional determinant of the stable aggregative response at high shoot densities was the constant density of preferred laminae size classes at these levels.

These results have revealed that the geese did not distribute themselves completely according to the Ideal Free Distribution (IFD) when all a0 size classes were included. However, because these geese select a0 laminae above a threshold level depending on field (Kristiansen *et al.* 2000) they must have been aggregating closer to the IFD if lamina size preference from each field was known and could be incorporated into the model.

As shown in natural salt marsh systems the aggregative response of grazing geese relative to their food resource can have consequences for community structure (Rowcliffe *et al.* 1998). In managed hayfields the effect on the prey (*Phleum*) population (and subsequently the sward community) could be considered in two ways. First, the very high proportion shoots grazed at low densities may give the later growing native species (e.g. *Poa pratense, Deschampsia caespitosa* etc.) a competitive advantage, leading to faster rates of extinction of *Phleum*, compared to the more dense *Phleum* swards where, normally, there are heavier absolute exploitation rates (in terms of goose days ha^{-1}). Secondly, because a lower proportion of a0 laminae are removed at high shoot densities, shoots in these patches suffer lower predation risk compared to the shoots in low density patches. Such inversely density-dependent mortality of a prey population implies that the effect on the prey or resource population will be highest at low prey densities (Heads & Lawton 1983; Van Eerden 1984). Inversely density-dependent prey mortality could be due to increased interference amongst consumers for example as a response of high consumer aggregation (Sutherland 1996). However, in our study this appears to be the result of the distribution and availability of preferred laminae (i.e. prey) sizes.

In recent years the management of sites for supporting goose populations on the wintering grounds has received much attention (Percival 1993; Vickery, Sutherland & Lane 1994; Vickery et al. 1997; Vickery & Gill 1999). Less attention has been given to spring staging areas, where acquisition of nutrients for onward migration and investment in reproduction is critical. The aggregative response demonstrated here had a clear and predictive function which may be applied to managing hayfields for geese. To optimise early feeding conditions for geese, *Phleum* hayfields need to support more than ten shoots/100 cm^2. Above this density, goose density remains at a high but relatively constant level, so from a goose management point of view, little is gained by increasing shoot density further. Regular reseeding of fields will maintain *Phleum* above this level protecting against the incursion of the native grass species which inevitably occurs (Fox 1993).

In summary, we have shown in this relatively simple goose/*Phleum* system an asymptotic relationship between aggregation of the geese and the shoot density of their food plants. Furthermore, we have demonstrated that there is a predictable relationship between shoot density and unit prey size. Therefore, assuming interference plays a minor role in the relationship, this study has demonstrated the importance of prey size and availability in determining the nature of the aggregative response. We suggest that this feature may be important in influencing the spatial distribution of other animals, especially those feeding on a single prey species systems which may be subject to density dependent effects.

Acknowledgements

We are grateful to the staff of Hvanneyri Agricultural University, especially Professor Björn Þorsteinsson and Ríkharð Brynjólfsson, for help and permission to work on the University farm, for laboratory facilities and for hostel accommodation there. Arnor Þ. Sigfusson and very many other members of the staff of the Icelandic Institute of Natural History, Reykjavik obtained permission for the work to be carried out and took part in the fieldwork. Financial support was provided by the Canadian Wildlife Service, Danish National Environmental Research Institute, Nordisk Forskerutdanningsakademi, the Beckett Foundation, Dansk Jagtforenings Jubilaeumsfund and British Ornithologists' Union. We thank Ian Francis, John Turner, Roy King, Alyn Walsh, John Wilson, Alistair Duncan, Nick Picozzi, Vinni Madsen and David Stroud for their help in the field.

References

Altmann, J. (1974) Observational study of behaviour: sampling methods. *Behaviour*, **49**, 227-267.

Anonymous (1997) Spring migration of Greenland white-fronted geese, Hvanneyri, West Iceland, April-May 1997. *Ibis,* **139**, 127-128.

Arditi, R. & Akcakaya, H.R. (1990) Underestimation of mutual interference of predators. *Oecologia,* **83**, 358-361.

Belovsky, G.E. (1981) Food plant selection by a generalist herbivore: the Moose. *Ecology,* **62**, 1020-1030.

Boudewijn, T. (1984) The role of digestibility in the selection of spring feeding sites by Brent Geese. *Wildfowl,* **35**, 97-105.

Boyd, H., Fox, A.D., Kristiansen, J.N., Stroud, D.A., Walsh, A.J. & Warren, S.M. (1998) Changes in abdominal profiles of Greenland White-fronted Geese during spring staging in Iceland. *Wildfowl*, **49**, 57-71.

Branch, G.M. (1975) Intraspecific competition in *Patella cochlear* Born. *Journal of Animal Ecology*, **44**, 263-281.

Crawley, M.J. (1983) *Herbivory, the dynamics of plant and animal interactions.* Blackwell, Oxford.

Crawley, M.J. (1997) *Plant Ecology*. Blackwell, Oxford.

Driessen, G & Hemerik, L. (1991) Aggregative responses of parasitoids and parasitism in populations of *Drosophila* breeding in fungi. *Oikos*, **61**, 96-107.

Elliot, J.M. (1993) The self-thinning rule applied to juvenile sea trout, *Salmo trutta*. *Journal of Animal Ecology*, **62**, 371-379.

Fox, A.D. (1993) Pre-nesting feeding selectivity of Pink-footed geese Anser brachyrhynchus in artificial grassland. *Ibis,* **135**, 417-422.

Fox, A.D. Norriss, D.W., Stroud, D. and Wilson, H.J. (1994) *Greenland white-fronted geese in Ireland and Britain 1982/83-1993/94.* - Greenland White-fronted Goose Study Research Report No. 8. GWGS/NPWS, Aberystwyth and Dublin.

Fox, A.D., Kahlert, J. & Ettrup, H. (1998) Diet and habitat use of moulting Greylag Geese *Anser anser* on the Danish island of Saltholm. *Ibis*, **140**, 676-683.

Fox, A.D., Hilmarsson, J.Ó., Einarsson, Ó, Boyd, H., Kristiansen, J.N., Stroud, D.A., Walsh, A.J., Mitchell, C., Francis, I.S. & Nyegaard, T. (1999) Phenology and distribution of ringing recoveries and resightings of individually marked Greenland White-fronted Geese Anser albifrons flavirostris staging in Iceland. *Wildfowl,* **50**, 29-43.

Francis, I.S. & Fox, A.D. (1987) Spring migration of Greenland White-fronted Geese through Iceland. *Wildfowl,* **38**, 7-12.

Fretwell, S.D. & Lucas, J.H.J. (1970) On territorial behaviour and other factors influencing habitat distribution in birds. *Acta Biotheoretica*, **19**, 16-36.

Goss-Custard, J.D. (1970) Feeding dispersion in some overwintering wading birds. *Social behaviour in birds and mammals* (J.D. Crook, ed.), pp. 3-34. Academic Press, New York.

Hassell, M.P. (1971) Mutual interference between searching insect parasites. *Journal of Animal Ecology*, **40**, 473-486.

Hassell, M.P. (1978) *The dynamics of arthropod predator-prey systems*. Princeton, New Jersey, Princeton University Press.

Hassell, M.P. & May, R.M. (1974) Aggregation of predators and insect parasites and its effect on stability. *Journal of Animal Ecology*, **43**, 567-594.

Heads, P.A. & Lawton, J.H. (1983) Studies on the natural enemy complex of the holly leaf-miner: the effects of the scale on the detection of aggressive responses and the implications for biological control. *Oikos,* **40**, 267-276.

Hughes, R.N. & Griffiths, C.L. (1988) Self-thinning in barnacles and mussels: the geometry of packing. *American Naturalist*, **132**, 484-491.

Kristiansen, J.N., Fox, A.D., Stroud, D.A. & Boyd, H. (1998) Dietary and microtopographical selectivity of Greenland White-fronted Geese feeding on Icelandic hayfields. *Ecography,* **21,** 480-483.

Kristiansen, J.N., Fox, A.D. & Nachman, G. (2000) Does size matter? maximizing nutrient and biomass intake by shoot size selection amongst herbivorous geese. *Ardea* **88,** in press.

Lonsdale, W.M. & Watkinson, A.R. (1982) Light and self-thinning. *New Phytologist,* **90**, 431-435.

Lonsdale, W.M. & Watkinson, A.R. (1983) Plant geometry and self-thinning. *Journal of Ecology*, **71**, 285-297.

Moss, R., Welch, D. & Rothery, P. (1981) Effects of grazing by mountain hares and red deer on the production and chemical composition of heather. *Journal of Applied Ecology,* **18,** 487-496.

Murton, R.K., Westwood, N.J. & Isaacson, A.J. (1964) A preliminary investigation of the factors regulating population size in the Wood Pigeon. *Ibis,* **106,** 482-507.

Owen, M. (1971) The selection of feeding sites by White-fronted Geese in winter. *Journal of Applied Ecology*, **8**, 905-917.

Percival, S.M. (1993) The effects of reseeding, fertilizer application and disturbance on the use of grasslands by barnacle geese, and the implications for refuge management. *Journal of Applied Ecology*, **30**, 437-443.

Rowcliffe, J.M., Watkinson, A.R. & W.J. Sutherland. (1998). Aggregative responses of brent geese on salt marsh and their impact on plant communiy dynamics. *Oecologia*, **114**, 417-426.

Rowcliffe, J.M., Sutherland, W.J. & Watkinson, A.R. (1999) The functional and aggregative responses of a herbivore: underlying mechanisms and the spatial implications for plant depletion. *Journal of Animal Ecology*, **68**, 853-868.

Sinclair, A.R.E. (1975) The resource limitation of tropic levels in tropical grassland ecosystems. *Journal of Animal Ecology*, **44**, 497-520.

Sutherland, W.J. (1983) Aggregation and the "ideal free" distribution. *Journal of Animal Ecology*, **52**, 821-828.

Sutherland, W.J. (1996) *From individual behaviour to population ecology*. Oxford University Press, Oxford.

Sutherland, W.J. & Allport, G.A. (1994) A spatial depletion model of the interaction between bean geese and wigeon with the consequences for habitat management. *Journal of Animal Ecology*, **63**, 51-59.

Therkildsen, O.R. & Madsen, J. (1999) Goose grazing selectivity along a depletion gradient. *Ecography*, **22**, 516-520.

Ydenberg, R.C. & Prins, H.H.T. (1981) Spring grazing and the manipulation of food quality by barnacle geese. *Journal of Applied Ecology*, **18**, 443-453.

Vickery, J.A., Sutherland, W.J. & Lane, S.J. (1994) The management of grass pastures for brent geese. *Journal of Applied Ecology*, **31**, 282-290.

Vickery, J.A., Sutherland, W.J., O'Brien, M., Watkinson, A.R. & Yallop, A. (1997) Managing coastal grazing marshes for breeding waders and overwintering geese: is there a conflict? *Biological Conservation*, **79**, 23-34.

Vickery, J.A. Gill, J.A. (1999) Managing grassland for geese in Britain: A review. *Biological Conservation*, **89**, 93-106.

Van der Meer, J. & Ens, B.J. (1997) Models of interference and their consequences for the spatial distribution of ideal and free predators. *Journal of Animal Ecology*, **66**, 846-858.

Van Eerden, M.R. (1984) Waterfowl movements in relation to food stocks. In P.R. Evans, J.D., Goss-Custard, and W.G. Hale (ed.), *Coastal waders and wildfowl in winter* (pp. 84-100). Cambridge University Press, Cambridge

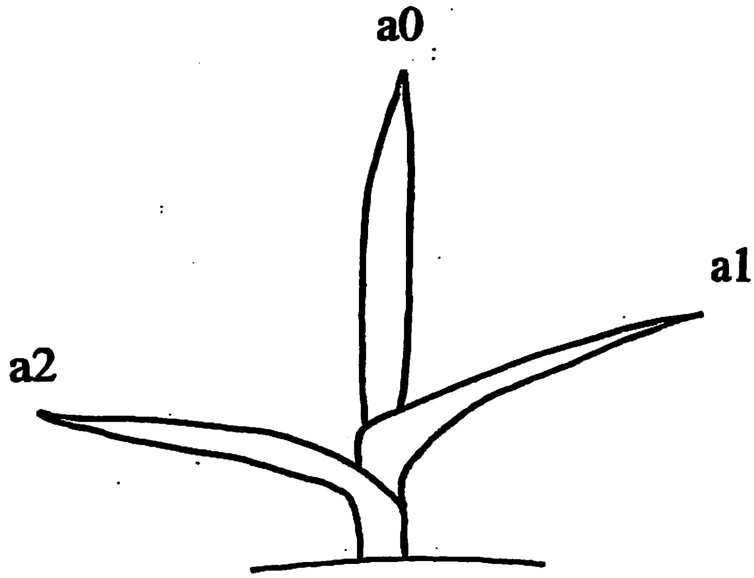

Fig. 1. Schematic illustration of a *Phleum pratense* shoot showing the youngest (middle) lamina a0, the second youngest lamina, a1 and the third youngest lamina a2. (From Kristiansen *et al.* 2000).

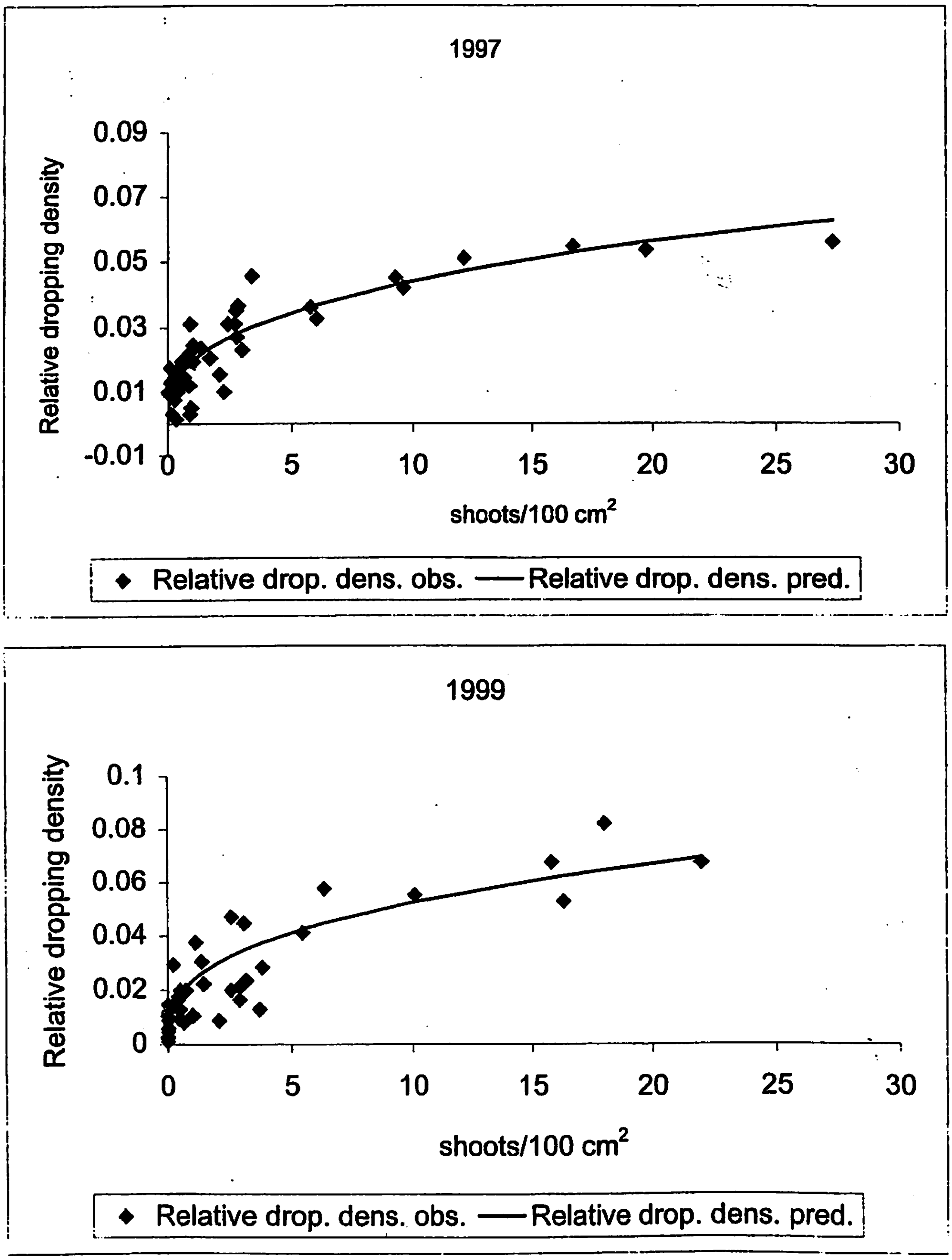

Fig. 2. Relationship between goose aggregation (relative dropping density, droppings m^{-2}) of Greenland white-fronted geese and *Phleum* shoot density (shoots/100 cm^2), at hayfields at Hvanneyri, West Iceland a) 1997, b) 1999. Each point refers to a particular field. Theoretical relationship (——) between the relative dropping density (D_i/D_{tot}) and shoot density (N_i) based on the model: $D_i/D_{tot} = N_i^c/\Sigma N_i^c$, $c = 0.3537$.

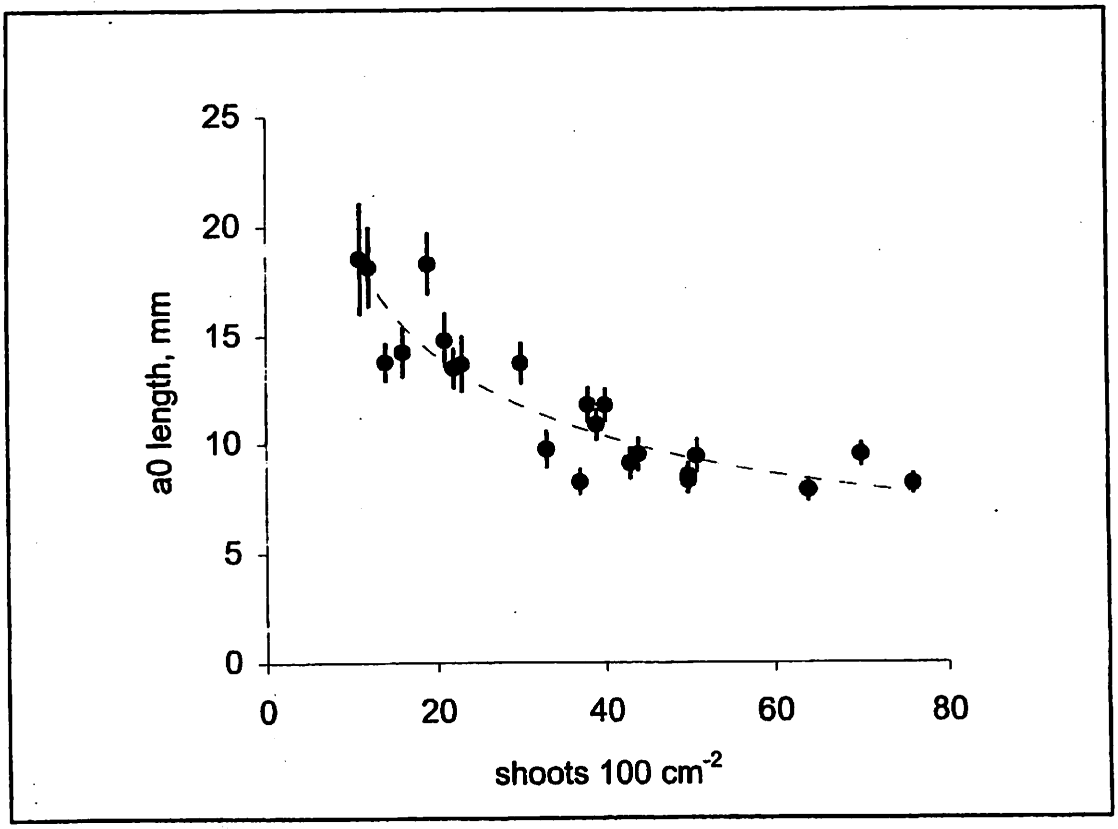

Fig. 3. Relationship between length of a0 *Phleum* laminae (mm) and *Phleum* shoot density (shoots/100 cm^2), Hvanneyri, West Iceland, 1999. The predicted curve is based on the power function $L_i = aN_i^b$, where L_i is the (mean) lamina length, in mm of the ith patch, N_i is the shoot density of the ith patch and a and b are constants. a and b were obtained from linear regression between $logL$ and $logN$: $logL = 1.7234 - 0.4425 logN$, $n = 22$, $R^2 = 0.8085$, $P < 0.0001$, thus $a = 52.89$ and $b = -0.4425$. Mean values ± SE are shown

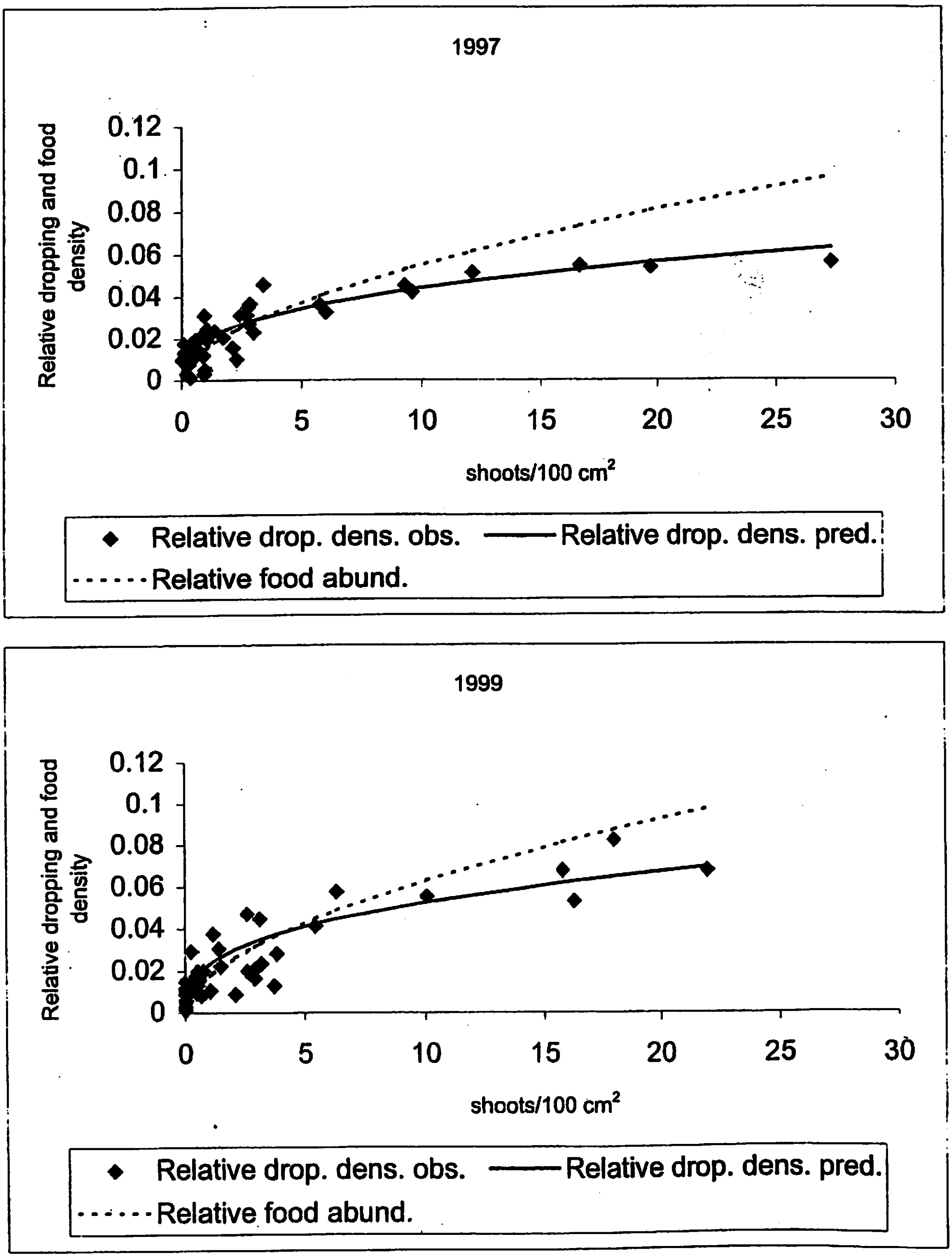

Fig. 4. Relationship between relative food abundance (----) (relative biomass of a0 laminae), relative goose aggregation, predicted (—) and observed (•) and shoot density (shoots/100 cm^2) of Greenland white-fronted geese, at hayfields at Hvanneyri, West Iceland a) 1997, b) 1999. The relative biomass B is based on the relationship: $B_i = L_i * N_i = aN_i^{1+b}$, where B_i is the biomass of the ith field (expressed as total a0 lamina length, mm), L_i is the (mean) lamina length of the ith field, N_i is the shoot density (shoots/100 cm^2), and a and b are constants obtained from the relationship between mean lamina length and shoot density $L_i = aN_i^b$ (see Fig. 3), $a = 52.89$ and $b = -0.4425$, thus $B_i = 52.89N^{1-0.4425}$. Predicted (—) and observed (•) goose aggregation curves and values are taken from Fig. 2a & b.

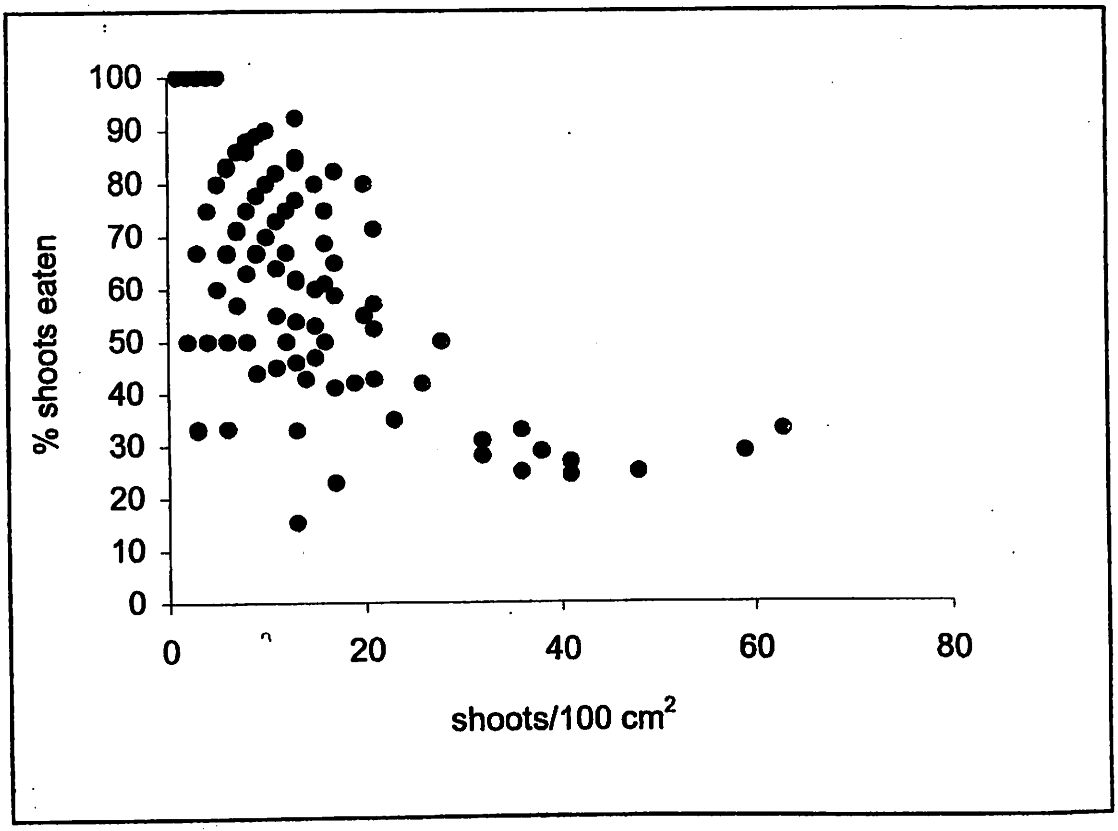

Fig. 5. Relationship between % *Phleum* shoots taken by Greenland white-fronted geese, Hvanneyri, West Iceland 1999 and *Phleum* shoot density (shoots/100 cm^2). Arcsine transformed data, ($r^2 = -0.34$, $n = 182$, $P < 0.0001$).

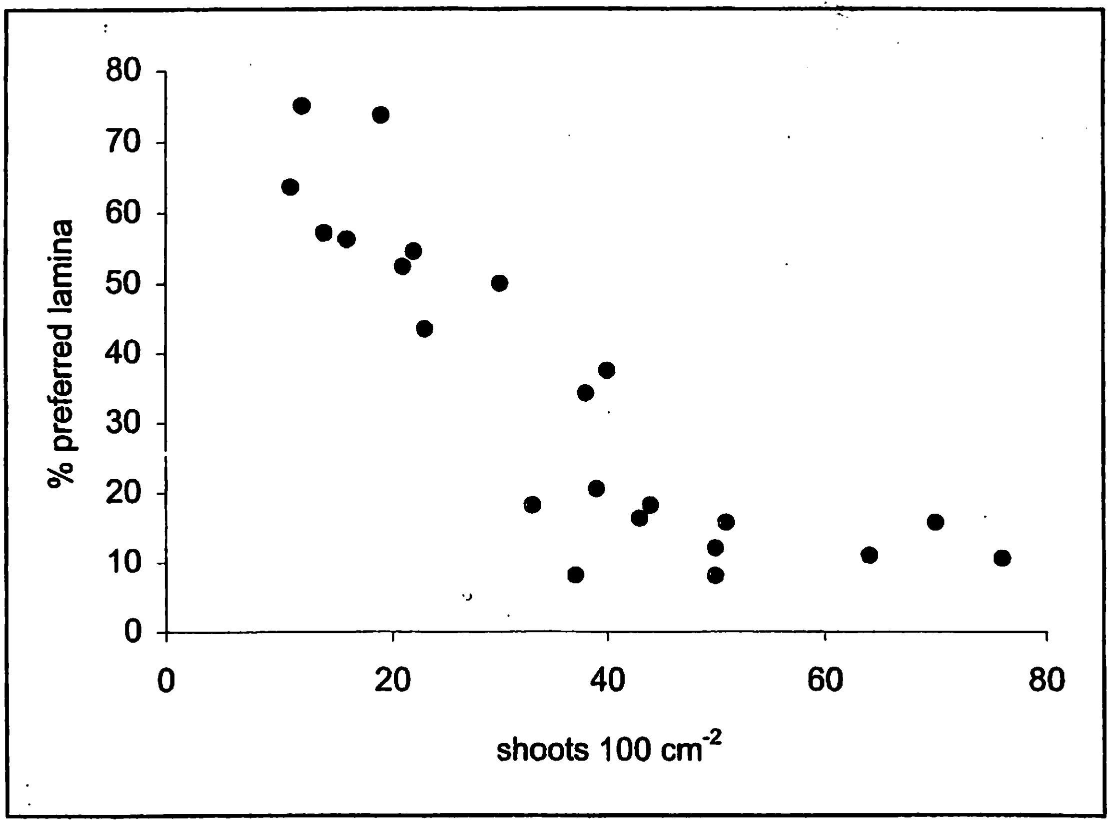

Fig. 6. Relationship between % of preferred lamina (by Greenland white-fronted geese (> 13.7 mm, see Kristiansen *et al.* 2000) and *Phleum* shoot density (shoots/100 cm^2) at Hvanneyri, West Iceland. Arcsine transformed data, ($r^2 = 0.73$, $n = 22$, $P < 0.0001$).