# Visible plot markers may bias the results of dropping counts

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Animal presence is often measured using dropping counts, and so is grazing intensity by geese and hare. Repeated counts of droppings in a plot of fixed size, and subsequent removal of the droppings, allow for a statistically robust comparison of changes in grazing pressure over time or differences in space. In many studies, the count units are marked in the field using a short stick or PVC tube in the centre of a circular plot. These markers are visible for the observer as well as for the animals. To assess the potential bias introduced by visible markers, a series of small experimental comparisons were carried out. The visibility of the marker did affect the value of the main study parameter: dropping density. Depending on the herbivore species, visible plot markers had positive, neutral or negative effects on dropping densities. European Brown Hare Lepus europaeus responded positively to very obvious markers, but these effects did not occur when markers were short. Geese did not respond to visible markers in one out of three study areas, but responded negatively in the two other areas. We assume that ecological reasons affect the degree to which different herbivores respond to the markers, e.g. habituation, relative food availability and animal species. Next to that, the vegetation structure influences the visibility of the markers. In homogeneous and short vegetation, effects of the markers are likely to be more pronounced than in heterogeneous and taller vegetation. As visible plot markers bias the results of dropping counts, the use of hidden markers should be considered, especially when absolute values of grazing intensities are required.

Key words: Geese, field methods, bias, dropping plot, dropping counts, European Brown Hare *Lepus* europaeus.

# 1. Introduction

The use of animal tracks in the assessment of distribution and numbers of wildlife is widespread. Pellet or dropping counts are one class of this technique. Counts of droppings allow for a statistically robust comparison of changes in grazing pressure over time or differences in space. The method is particularly useful for animals that defecate at regular intervals, such as small herbivores. Therefore, many studies on geese or hare have applied results of dropping counts as a measure for the time spent, or the biomass consumed, in a given habitat or time frame (OWEN 1971; YDENBERG & PRINS 1981; DERKSEN et al. 1982; AERTS et al. 1996; VAN DE KOPPEL et al. 1996; LANGBEIN et al. 1999; VAN DER GRAAF et al. 2002; Bos et al. 2004; KUIJPER & BAKKER 2005). Several factors may affect the dropping densities found at a given location at a given time. These factors are related to the animals themselves, e.g. caused by seasonal changes in diet and physiology of the animals, and patterns of habitat use in space and time. Dropping densities may also be affected, however, by factors not related to the animals themselves but to sampling errors caused by vegetation structure, observer position, the observer per se (Bédard & Gauthier 1986) or an otherwise inadequate sampling method. The data discussed in the present paper relate to that last aspect.

In many studies, dropping densities and dropping rates are assessed by repeated counts and subsequent removal at plots of fixed size. Often, the count units are marked in the field with a short stick or PVC tube in the centre of a circular plot. These markings are visible for the observer with the practical advantage that the plots can be located easily. This makes them also visible for the animals, however. This visibility could affect the behaviour of the animal and as such introduce bias in the results. In order to assess the potential effects introduced by visible markers, we have performed a series of small experimental comparisons between different types of markers and studied how these affected geese and hare dropping densities.

# 2. Methods

To evaluate the effects of visible markers, droppings were collected in plots of 4 m<sup>2</sup> (a commonly used plot size) in five small experimental set-ups. We focussed on two groups of species, geese (Barnacle Goose *Branta leucopsis*, Dark-bellied Brent Goose *Branta b. bernicla*, Greater White-fronted Goose *Anser albifrons*) and European Brown Hare *Lepus europeaus* at five different study sites in the North of the Netherlands (Table 1, Fig. 1). In the first set of three experiments paired comparisons between plots with or without markers were made to establish whether a bias occurred. In the second set of two experiments droppings were counted in concentric circles around the centre of the plot to get insight in the spatial scale over which effects occur.

#### 2.1. Paired comparisons of dropping density

In the salt marsh ungrazed by cattle on the island of Schiermonnikoog, in June 2000 hare droppings were counted during a period of 46 days in a randomised block design with four treatments 
 Table 1: Overview of the study areas and habitats where experiments were performed to evaluate the effects of visible markers on observed

 dropping densities.
 Übersicht über die Untersuchungsgebiete und Habitate, in denen die Experimente zur Untersuchung der Auswirkungen sichtbarer

 Markierungen auf die registrierten Kotstangen-Dichten durchgeführt wurden.

Species – Arten	Paired comparisons – Paarvergleiche	Concentric circles – konzentrische Probekreise	Study areas – Untersuchungsgebiete	Month – <i>Monat</i>
European Brown Hare – <i>Feldhase</i>	ungrazed salt marsh – unbeweidete Salzwiesen		Schiermonnikoog	June – <i>Juni</i>
European Brown	summer polder –	summer polder –	Noord-Friesland Buitendijks (NFB)	February –
Hare – <i>Feldhase</i>	Sommerpolder	Sommerpolder		<i>Februar</i>
Geese – Gänse	agricultural grassland –	agricultural grassland –	Oost-Dongeradeel (OD), Fraterwaard	February–March –
	Intensivgrasland	Intensivgrasland	(FW), Barsbekerbinnenpolder (BBP)	<i>Februar–März</i>



Fig. 1: Location of the five study sites. – Lage der fünf Untersuchungsgebiete.

and 6 replicate plots. The four treatments were a PVC tube of 40 cm height, a PVC tube of 10 cm, a bamboo stick of 10 cm ( $\emptyset$  0.7 cm, brown colour) and no visible marker. All PVC tubes used in all experiments in this study were yellowish-white and had a diameter of 1 cm.

In the cattle-grazed summer polder of Noord-Friesland Buitendijks (NFB), hare droppings were counted in February 2001 during a 14 days period in a paired plot design with ten repli-

cates. Half of the plots were marked with a 15 cm PVC tube, and the other half were marked with a 10 cm long inconspicuous iron peg, placed horizontally at ground level (metal colour).

For geese, data were collected in agricultural grassland in paired plots during 14 consecutive days. This was done in March 2005 at three study sites: Oost-Dongeradeel (OD, N = 2 x 50), Fraterwaard (FW, N = 2 x 26) and Barsbekerbinnenpolder (BBP, N = 2 x 38). Half the plots were marked with a PVC tube, whereas the other plots had a hidden marker. The average height of the PVC tubes was 10.0 cm in OD and 12.5 cm both in FW and BBP.

# 2.2. Dropping density in concentric circles

In order to examine the spatial scale over which effects occur, droppings have been collected in concentric circles around the centre of a series of plots. For hare this was done on agricultural grassland in the summer polder of NFB. Here, 10 plots were subdivided in four concentric circles with the outer perimeter at a distance of 0.3 m, 0.6 m, 0.9 m en 1.13 m respectively from the centre of the plot. The plots were randomly distributed in an area of 1 ha, and droppings were collected during 27 days in February 2001.

For geese, a similar exercise was performed during February–March 2006 on agricultural grassland at three study sites: OD, FW and the BBP. In this experiment, plots were subdivided in three concentric circles of equal area. Goose droppings were collected during 14 days around plots that were marked with PVC tubes of 17.5 cm height (Table 2). After that period, the height of the PVC tubes on these plots was reduced to 11.4 cm, and goose droppings were collected during two consecutive periods of 14 days (average height of markers for each study site for each period see Table 2).

#### 2.3. Vegetation height

Vegetation height was measured at all sites with a styrofoam disc ( $20 \text{ cm } \emptyset$ , 24 g). The disc was randomly dropped on the vegetation along a graduated stick. Canopy height was measured five times per plot to the nearest 0.5 cm.

#### 2.4. Study sites

The study site on the island of Schiermonnikoog is extensively described in several papers (e.g. OLFF *et al.* 1997; BOS & STAHL 2003). Our experiment was performed in unmanaged salt marsh

**Table 2:** The height of the visible markers used at the goose dropping plots at three study sites in two periods for the experimental plots that were subdivided in three concentric circles. – *Höhe der sichtbaren Markierungen in den Kotstangen-Probeflächen in drei Untersuchungsgebieten in zwei Perioden für die in drei konzentrische Kreise unterteilten Probeflächen.* 

	First period – Periode 1			Second period – Periode 2		
	Mean (cm)	s.e.	Ν	Mean (cm)	s.e.	Ν
Fraterwaard (FW)	19.6	0.4	70	12.6	0.1	70
Barsbekerbinnenpolder (BBP)	17.6	0.2	61	12.4	0.2	70
Oost-Dongeradeel (OD)	15.9	0.4	98	10.0	0.0	105
Total	17.5	0.2	229	11.4	0.1	245

dominated by Red Fescue *Festuca rubra*. The most important vertebrate herbivores in this system are hare with a year-round presence and Barnacle Goose and Darkbellied Brent Goose as seasonal grazers from October to May. At the experimental site, the vegetation comprised a homogeneous Red Fescue sward with some taller structures formed by Sea Wormsword *Artemisia maritima* of approximately 20 cm height. Average canopy height was  $6.7 \pm 0.4$  cm.

The summer polder at NFB is cattle-grazed during summer (June–October). Barnacle Geese are present here in high numbers from October to May (ENGELMOER *et al.* 2001). The polder was used for agriculture until 1996, but is managed as a nature reserve since. The area is grazed by livestock at 1 Livestock Unit/ha. The homogeneous grass vegetation was dominated by Rye Grass *Lolium perenne*, Creeping Bent *Agrostis stolonifera* and Marsh Foxtail *Alopecuris geniculatis*. Variation in plant cover yielded a little spatial variation in vegetation height with  $5.5 \pm 0.5$  cm in average.

The plots at OD were distributed in a 2,200 ha agricultural area where in the framework of a goose management plan geese were not disturbed during winter (October– April). The area mainly consisted of agricultural grassland. Barnacle and White-fronted Goose normally are the most common species with a contribution of 73 % and 23 % to total goose numbers in the area in 2004–05 (pers. obs.). The fields were fertilised and mown or cattle-grazed during spring and summer (May–November). FW and BBP were also agricultural areas. At these sites, however, Greater White-fronted Geese were the most numerous. The vegetation at all three sites consisted of a short and homogenous Rye Grass sward. Vegetation height during the experiments was 3.7, 4.1 and 4.3  $\pm$  0.1 cm for OD, FW and BBP, respectively.

At three of the study sites, Schiermonnikoog, NFB, and OD, geese have not been actively disturbed and scared for at least several consecutive years up to (including) the study season. The method of counting droppings at plots with visible markers had already been applied at these sites in the years before our study. In FW and BBP, a ban on scaring was implemented six months before the start of our study. The method of counting droppings in plots with visible markers had not been applied before at these sites.

#### 2.5. Analyses

Dropping counts have all been expressed as number of droppings/m<sup>2</sup>/day. Differences between treatments were tested with (1) ANOVA followed by Tukey-test for multiple comparison, (2) paired t-tests or (3) the nonparametric Friedman test for related samples (ZAR 1996). SPSS 12.0 was used for statistical analyses.

#### 3. Results

#### 3.1. Hare

When the marking was sizeable (40 cm), dropping density of hare was higher in comparison to controls (Fig. 2, one-way ANOVA,  $F_{3,21} = 5.4$ , p = 0.007). Small PVC tubes and small sticks did not have a measurable effect (Tukey multiple comparisons).

The same effect was found in the summer polder at NFB. Hare dropping density was higher in plots with a visible marker of 15 cm in comparison to a control with an inconspicuous iron peg (paired samples t-test, p < 0.001, df =9, Fig. 3).



**Fig. 2:** Dropping density of hare (mean  $\pm$  s.e.) at plots marked with different type of markers on an ungrazed Red Fescue-dominated salt marsh. – Dichte von Hasenkothaufen (Mittelwert  $\pm$  Standardfehler) auf Probeflächen mit unterschiedlichen Typen von Markierungen (Versteckt, Holzstab, PVC-Rohr 10 cm, PVC-Rohr 40 cm) auf einer unbeweideten, von Rotschwingel Festuca rubra dominierten Salzwiese.



Type of marker – Art der Markierung

**Fig. 3:** Dropping density of hare (mean  $\pm$  s.e.) at plots marked with a PVC tube of 15 cm in comparison to a control on extensively managed agricultural grassland. – Hasenkotdichte (Mittelwert  $\pm$  Standardfehler) auf Probeflächen mit einem PVC-Rohr von 15 cm Länge im Vergleich zu einer Kontrollfläche auf extensiv genutztem Grünland.



Fig. 4: Dropping density of hare (mean ± s.e.) in concentric circles around the centre of a plot, marked with a PVC tube of 15 cm on extensively managed agricultural grassland. – Hasenkotdichte (Mittelwert ± Standardfehler) auf kreisförmigen Probeflächen im Zentrum einer Fläche, markiert mit einem PVC-Rohr von 15 cm Länge auf extensiv genutztem Grünland.



Study area - Untersuchungsgebiet

**Fig. 5:** Average goose dropping density at paired plots with and without PVC tubes on agricultural grassland. Height of PVC tubes is 12.6, 12.4 and 10.0 cm for FW, BBP and OD, respectively. – Durchschnittliche Dichte der Gänsekotstangen auf gepaarten Probeflächen mit und ohne PVC-Rohr auf Kulturgrünland. Höhe der PVC-Röhre ist 12,6, 12,4 und 10,0 cm für FW, BBP bzw. OD.



Fig. 6: Average goose dropping density in concentric circles around the centre of a plot, marked with a PVC tube of 17.5 cm (top), a PVC tube of 11.4 cm (middle), and with a hidden marker (bottom). – Mittlere Dichte der Gänsekotstangen in konzentrischen Kreise um das Zentrum einer Probefläche, markiert mit einem PVC-Rohr von 17.5 cm (oben), einem PVC-Rohr von 11.4 cm (Mitte) und einer versteckten Markierung (unten).

The hare dropping density was concentrated close to a visible marker (15 cm) and decreased rapidly with increasing distance from the centre of the plot (Fig. 4).

#### 3.2. Geese

In contrast with hare dropping density, goose dropping density was lower around PVC tubes at two of the three study sites: FW and BBP (Fig. 5).

At the third study site OD, the PVC-tubes did not have an effect. It should be noted, however, that the markers at this site were somewhat shorter than at the other two sites (Table 2). Overall, the effect of the marker was a 19 % decrease in dropping density (paired t-test, p < 0.001). Goose dropping density increased from the marker in the centre of a plot (Fig. 6).

On the basis of all data, this effect was highly significant (tall PVC tubes of 17.5 cm height, Friedman, n = 425,  $\chi^2 = 60$ , p < 0.001; intermediate PVC tubes of 11.4 cm, n = 241,  $\chi^2 = 62$ , p < 0.001). With a hidden marker, the effect did not occur (Friedman, n = 64,  $\chi^2 = 3.6$ , n.s.). In study area OD, a marker effect on dropping density was not found ( $\chi^2 = 0.1$ , n.s. and  $\chi^2 = 4.9$ , n.s. for markers of 15.9 and 10.0 cm height, respectively).

## 4. Discussion

The present study shows that the use of a visible marker introduces a bias in the variable to be measured. Hare seem to prefer staying or grazing close to very obvious markers, and thus dropping density of hare is higher close to a plot marker than at greater distance. Hidden or small markers, however, did not affect dropping densities of hare. Geese, on the contrary, seem to respond in the opposite way. In two out of three study sites plot markers had a negative effect on dropping densities of geese.

Several ecological reasons will affect the way in which animals respond to markers, for instance relative foodavailability, habituation, and inter-specific differences in preference or fear. The direction of the effect was opposite between the two species groups in this study and the effects were consistent among the different study areas. We therefore assume that this aspect of the bias will be systematic. But the reasons for the opposite response of the two herbivore species are not clear. Grazing pressure of Barnacle and Dark-bellied Brent Geese is affected negatively by structural elements in the vegetation (VAN DER WAL et al. 2000). The negative effect of visible markers could be related to avoidance of geese of these structural elements. Why hare showed a positive response to visible markers is unknown. Hare do not use fixed defecation places as Rabbits Oryctolagus cuniculus do. According to LANGBEIN et al. (1999), dropping counts might therefore yield a reliable estimate of hare-grazing pressure. However, in an open landscape, concentrations of hare droppings are often found close to arrays of vertical structures, such as paddock poles and grass tussocks (PE, pers. obs.). It is unclear whether these pellets are produced during feeding or another activity. One explanation could be that hare are attracted by unfamiliar objects in the field. This is in line with observations of hare eating some types of the sticks used as plot marker (R. DRENT and T. BOUDEWIJN pers. *comm*.). Our findings suggest that the positive bias will be greater when the marker is more visible and the sward more homogenous.

In contrast to a supposed systematic bias between species groups, variation caused by other ecological reasons like habituation, relative food availability, and vegetation structure will not be systematic. It will, therefore, be problematic to try and correct a-posteriori for this error. Care should be taken to use hidden markers of the plots. This is especially true when absolute values of grazing intensity need to be measured, for example in studies related to carrying capacity. If dropping counts are made merely to obtain an index of terrain use, then one need not to be concerned with the bias. In ecological studies, a biased estimator is often perfectly acceptable (BÉDARD & GAUTHIER 1986).

Our study is complementary to BÉDARD & GAUTHIER (1986), who presented a preliminary assessment of the major factors affecting accuracy and precision of goose dropping estimates. They found that dropping densities observed may be affected by the observer position and the observer per se. These authors focussed on narrow rectangular plots of 25 m length and 1m width, marked with small sticks at the beginning and the end. In many studies, plot size is chosen to be 4 m<sup>2</sup> only (VAN DE KOPPEL *et al.* 1996; STAHL *et al.* 2002; KUIJPER & BAKKER 2004) rather than 25 m<sup>2</sup> in the study by BÉDARD & GAUTHIER (1986). On smaller plots, the effect of a visible marker becomes more prominent. So, in addition to the factors mentioned by BÉDARD & GAUTHIER and the sources mentioned in their paper (NEFF 1968; SMITH 1968), we have identified yet another factor that may influence results of dropping counts. Bédard & Gauthier (1986) point at observer position, observer, vegetation structure, plot size and shape, dropping density, and effects of weather on dropping disintegration as other sources of variation. They recommend to select the most appropriate observation method based upon a preliminary run in each habitat unit, and to rule out unreliable observers. AMANO et al. (2004) propose relevant directions for improving the effectiveness of the method when wildfowl's dropping density is used as an indicator of food consumption volume. They suggest (1) to use the weight of droppings rather than dropping density, and (2) to check whether defecation and foraging occur within the same area. In addition to these suggestions, our results lead to the recommendation to use hidden plot markers. This holds especially when absolute values of grazing intensity or habitat utilisation are required.

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#### 6. Zusammenfassung

#### Bos, D, D. P. J. Kuijper & P. Esselink 2008: Sichtbare Probeflächen-Markierungen können die Ergebnisse von Kothaufen-Zählungen beeinflussen. Vogelwelt 129: 147–152.

Die Äsungsintensität durch Gänse und Hasen wird häufig durch die Zählung von Kothaufen ermittelt. Die wiederholte Zählung von Kothaufen auf einer Probefläche bestimmter Größe und die anschließende Entfernung aller Exkremente ermöglichen einen statistisch zuverlässigen Vergleich von Änderungen der Beweidungsintensität bezogen auf Zeit oder Fläche. In vielen Freilanduntersuchungen sind die kreisförmigen Probeflächen in der Mitte mit einem kurzen Stab oder PVC-Rohr markiert. Diese Markierungen sind sowohl für die Beobachter als auch für die Tiere sichtbar. Um festzustellen, ob derartige Markierungen die Ergebnisse der Untersuchungen beeinflussen, wurde eine Reihe von kleinen experimentellen Vergleichen durchgeführt. Die Sichtbarkeit der Markierungen beeinflusste den Wert der wichtigsten Parameter der Untersuchung: die Dichte der Kothaufen. In Abhängigkeit von der Herbivorenart hatten die sichtbaren Markierungen positive, neutrale oder negative Auswirkungen auf die Dichte der Kothaufen. Feldhasen reagierten positiv auf deutlich sichtbare Markierungen; dieser Effekt trat jedoch nicht auf, wenn die Markierungsstäbe kurz waren. Gänse reagierten in einem der drei Untersuchungsgebiete nicht auf die Markierungen, in den beiden anderen Gebieten aber negativ. Wir nehmen an, dass es ökologische Gründe gibt, die bestimmen, in welchem Grad die verschiedenen Herbivoren auf die Markierungen reagieren, etwa Habituation, relative Verfügbarkeit von Nahrung und Tierarten. Darüber hinaus beeinflusst die Struktur der Vegetation die Sichtbarkeit der Markierungen. Bei homogener und kurzer Vegetation sind die Auswirkungen der Markierungen wahrscheinlich wesentlich ausgeprägter als bei einer heterogenen und längeren Vegetation. Da sichtbare Markierungen von Probeflächen die Ergebnisse von Kothaufen-Zählungen beeinflussen, sollte der Einsatz von unsichtbaren Markierungen in Erwägung gezogen werden, insbesondere wenn absolute Werte als Maß der Beweidungsintensität gebraucht werden.

### 7. References

- AERTS, B. A., P. ESSELINK & G. J. F. HELDER 1996: Habitat selection and diet composition of Greylag geese Anser anser and Barnacle geese Branta leucopsis during fall and spring staging in relation to management in the tidal marshes of the Dollard. Z. Ökol. Natursch. 5: 65–75.
- AMANO, T., K. USHIYAMA, G. FUJITA& H. HIGUCHI 2004: Evaluating goose-dropping density as an index of food-consump-

tion volume along a depletion gradient. Wildl. Soc. Bull. 32: 782–785.

- BÉDARD, J. &v G. GAUTHIER 1986: Assessment of faecal output in geese. J. Appl. Ecol. 23: 77–90.
- BOS, D. & J. STAHL 2003: Creating new foraging opportunities for Dark-bellied Brent *Branta bernicla* and Barnacle Geese *B. leucopsis* in spring – insights from a large-scale experiment. Ardea 92: 153–166.

- BOS, D., J. VAN DE KOPPEL & F. J. WEISSING 2004: Dark-bellied Brent geese aggregate to cope with increased levels of primary production. Oikos 107: 485–496.
- DERKSEN, D. V., W. D. ELDRIDGE & M. W. WELLER 1982: Habitat ecology of Pacific Black Brant and other geese moulting near Teshekpuk Lake, Alaska. Wildfowl 33: 39–57.
- ENGELMOER, M., J. TAAL, E. WYMENGA & R. KUIPERS 2001: Aantalsafname bij de Rotgans *Branta bernicla* langs de Friese waddenkust. Limosa 74: 41–56.
- KUIJPER, D. P. J. & J. P. BAKKER 2005. Top-down control of small herbivores on salt-marsh vegetation along a natural productivity gradient. Ecology 86: 914–923.
- LANGBEIN, J., M. R. HUTCHING, S. HARRIS, C. STOATE, S. C. TAP-PER & S. WRAY 1999. Techniques for assessing the abundance of Brown hares *Lepus europaeus*. Mammal Rev. 2: 93–116.
- NEFF, D. J. 1968. The pellet group count technique for big game trend census and distribution: a review. J. Wildl. Manage. 32: 597–614.
- OLFF, H., J. DE LEEUW, J. P. BAKKER, R. J. PLATERINK, H. J. VAN WIJNEN & W. DE MUNCK 1997: Vegetation succession and herbivory in a salt marsh: Changes induced by sea level rise and silt deposition along an elevational gradient. J. Ecol. 85: 799–814.
- OWEN, M. 1971: The selection of feeding sites by white-fronted geese in winter. J. Appl. Ecol. 8: 905–917.

- SMITH, R. H. 1968: A comparison of several sizes of circular plots for estimating deer pellet group density. J. Wildl. Manage. 32: 585–591.
- STAHL, J., D. BOS & M. J. J. E. LOONEN 2002: Foraging along a salinity gradient – the effect of tidal inundation on site choice by dark-bellied Brent Geese *Branta bernicla* and Barnacle Geese *B. leucopsis*. Ardea 90: 201–212.
- VAN DE KOPPEL, J., J. HUISMAN, R. VAN DER WAL & H. OLFF 1996: Patterns of herbivory along a productivity gradient: An empirical and theoretical investigation. Ecology 77: 736–745.
- VAN DER GRAAF, A. J., D. BOS, M. J. J. E. LOONEN, M. ENGELMOER & R. H. DRENT 2002: Short-term and long-term facilitation of goose grazing by livestock in the Dutch Wadden Sea area. J. Coast. Cons. 8: 179–188.
- VAN DER WAL, R., H. J. VAN WIJNEN, S. VAN WIEREN, O. BEU-CHER & D. BOS 2000: On facilitation between herbivores: How Brent Geese profit from brown hares. Ecology 81: 969–980.
- YDENBERG, R. C. & H. H. T. PRINS 1981: Spring grazing and the manipulation of food quality by Barnacle Geese. J. Appl. Ecol. 18: 443–453.
- ZAR, J. H. 1996. Biostatistical analysis. 3<sup>rd</sup> ed. Prentice-Hall, Inc., N.J.

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