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Satellite- versus temperature-derived green wave indices for predicting the timing of spring migration of avian herbivores

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ABSTRACT

According to the green wave hypothesis, herbivores follow the flush of spring growth of forage plants during their spring migration to northern breeding grounds. In this study we compared two green wave indices for predicting the timing of the spring migration of avian herbivores: the satellite-derived green wave index (GWI), and an index of the rate of acceleration in temperature (GDDjerk). The GWI was calculated from MODIS normalized difference vegetation index (NDVI) satellite imagery and GDDjerk from gridded temperature data using products from the global land data assimilation system (GLDAS). To predict the timing of arrival at stopover and breeding sites, we used four years (2008–2011) of tracking data from 12 GPS-tagged barnacle geese, a long-distance herbivorous migrant, wintering in the Netherlands, breeding in the Russian Arctic. The stopover and breeding sites for these birds were identified and the relations between date of arrival with the date of 50% GWI and date of peak GDDjerk at each site were analyzed using mixed effect linear regression. A cross-validation method was used to compare the predictive accuracy of the GWI and GDDjerk indices. Significant relationships were found between the arrival dates at the stopover and breeding sites for the dates of 50% GWI as well as the peak GDDjerk ($p < 0.01$). The goose arrival dates at both stopover and breeding sites were predicted more accurately using GWI ($R^2_{cv} = 0.68$, $RMSD_{cv} = 5.9$ and $R^2_{cv} = 0.71$, $RMSD_{cv} = 3.9$ for stopover and breeding sites, respectively) than GDDjerk. The GDDjerk returned a lower accuracy for prediction of goose arrival dates at stopover ($R^2_{cv} = 0.45$, $RMSD_{cv} = 7.79$) and breeding sites ($R^2_{cv} = 0.55$, $RMSD_{cv} = 4.93$). The positive correlation between the absolute residual values of the GDDjerk model and distance to the breeding sites showed that this index is highly sensitive to latitude. This study demonstrates that the satellite-derived green wave index (GWI) can accurately predict the timing of goose migration, irrespective of latitude and therefore is suggested as a reliable green wave index for predicting the timing of avian herbivores spring migration.

1. Introduction

The green wave hypothesis predicts that herbivores time their spring migration to take advantage of the flush of nutrient-rich plants at each stopover site toward their breeding grounds (Owen, 1980). In support of the green wave hypothesis, it was observed that the timing of the annual northern migration of geese coincided with plant phenology (Van der Graaf et al., 2006). Arrival to the breeding site usually happens prior the peak of nutrient biomass, since it provides a better chance to profit from high food

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quality for hatched goslings and molting adults (Prop and de Vries, 1993; Sedinger and Flint, 1991; Van der Graaf et al., 2006). The phenological patterns of migratory animals (including birds) such as migration timing are responsive to climate change (Root et al., 2003). However, it still remains unclear whether timing of avian herbivores migration coincides with the phenology of food source, i.e. the date of first spring flush of plants, which in turn determines food availability for migratory birds (Visser and Both, 2005). Spring advancement, which results from climate change, is more rapid in high-latitude Arctic regions than further south. This may advance food availability more at higher latitude compared to lower latitude, where spring migration begins (IPCC, 2007; Stone et al., 2002). Therefore, Arctic nesting geese may miss the rapid seasonal development because of late arrival relative to plant growth phenology at the breeding ground. The mismatches between arrival time at the breeding ground and the initiation of plant growth can affect the timing of optimal breeding conditions (Pearce-Higgins et al., 2005). Therefore, an accurate understanding of the timing of the spring migration of avian herbivores such as geese to both stopover and breeding sites with respect to the green wave of plant phenology might help to predict the consequences of future climate change on migration patterns on individuals and therefore also on populations.

Satellite imagery provides a potential tool for ecologists and conservation biologists to investigate vegetation productivity and phenology for large regions and long time-frames (Kerr and Ostrovsky, 2003; Pettorelli et al., 2005). The normalized difference vegetation index (NDVI) is a measure of the presence and vigor of green vegetation and is calculated from the near-infrared (NIR) and red reflectance that can be captured by satellite sensors (Myneni et al., 1995; Reed et al., 1994). Photosynthetically active green vegetation has a high NIR reflection and low red reflection resulting in a high NDVI. Because clouds may obstruct the visibility of the land cover, frequent imagery is required to obtain accurate information on temporal changes of vegetation growth. Due to the trade-off between spatial and temporal resolution, daily imaging of the same site is currently only feasible with a relatively coarse spatial resolution. The most commonly used sensors for long-term monitoring of seasonal changes of green vegetation include the Advanced Very High Resolution Radiometer (AVHRR) at 8 km resolution, the Satellite Pour I'Observation de le Terre-Vegetation (SPOT-VGT) at 1 km resolution, and the Moderate Resolution Imaging Spectroradiometer (MODIS) data set at 1 km resolution (Pettorelli et al., 2005).

Satellite-derived NDVI time series yield reasonable estimates of biomass (Skidmore and Ferwerda, 2008) and may also be used to infer vegetation quality, because the nutritional quality declines as vegetative biomass increases (Fryxell, 1991). Thus, NDVI time series have been used to link plant quality with herbivore habitat use (Hamel et al., 2009; Marshal et al., 2006; Mueller et al., 2008; Tveraa et al., 2013). In a study conducted by Doiron et al. (2013) on Bylot Island, Canada, NDVI temporal changes were related to the date of peak nitrogen concentration in above-ground graminoid plants (grasses and grass-like plants, rushes, sedges). Their results showed that the date when NDVI was halfway the seasonal minimum and maximum value was the best predictor for the date of peak nitrogen in graminoids. They indicated that this date constitutes an important phenological event for herbivores such as the greater snow goose, *Anser caerulescens atlantica*, which breeds in the Arctic tundra ecosystem.

NDVI time series have been used to improve our understanding of the movements of herbivores, and how they relate to the spatio-temporal variation in the forage characteristics of their environment. For instance, a powerful predictive migration model for the migratory zebra, *Equus burchelli antiquorum*, was developed using NDVI data to evaluate how their timing and pace of movement is affected by spatio-temporal changes in the environment (Bartlam-Brooks et al., 2013). Another example also showed that elephants tracked an intermediate value of NDVI in the Marsabit protected area in Kenya, corresponding to the "surfing the green wave" hypothesis (Bohrer et al., 2014).

For animal migration studies, NDVI time series have often been transformed into the green wave index (GWI), i.e. a normalized NDVI trajectory for each pixel with a ratio output, where 0% reflects the annual minimum and 100% the annual maximum NDVI (Beck et al., 2008; White et al., 1997). The GWI has been successfully used to explain the seasonal movements of giant pandas, *Ailuropoda melanoleuca*, in relation to plant phenology (Beck et al., 2008). Moreover, using the GWI, Bischof et al. (2012) showed that ungulates can time their migration to either surf a wave of food availability (i.e. green wave) or jump ahead of the green wave as they move along the migration corridor. In addition to mammals, the migration of barnacle geese, *Branta leucopsis*, with respect to the vegetation phenology was successfully studied using the GWI index (Shariatinajafabadi et al., 2014).

An alternative parameter that may be used to test the green wave hypothesis is temperature, which is an important factor for plant phenology (Gordo and Sanz, 2009; Menzel et al., 2006). Plant phenology studies have traditionally used models based on variables, such as growing degree days (GDD), i.e. the sum of mean daily temperature above a certain temperature threshold (Wang, 1960). This measure is relevant for different phases of plant development (Cleland et al., 2007; Gordo and Sanz, 2010). Van Eerden et al. (2005) proposed to use the day at which GDD reaches 180 °C as a definition of the start of spring (using a threshold of 0 °C and a starting date of 1st January). Furthermore, the rate of change in temperature acceleration (GDDjerk) could be another proxy for the onset of spring (Fitzjarrald et al., 2001; Van Wijk et al., 2012).

The GDD and day length were found to be accurate predictors for timing the migration of pink-footed geese, *Anser brachyrhynchus* (Bauer et al., 2008; Duriez et al., 2009). Van Wijk et al. (2012) compared three green wave indices (GDD 180 °C, GDDjerk, and date of snow melt) with variables related to the accumulated photoperiod (period between sunrise and sunset) and latitude to predict the arrival date of white-fronted geese, *Anser albifrons*, at stopover sites during their spring migration from the Netherlands to Russia. The arrival of white-fronted geese at stopover sites was predicted most accurately by the peak in GDDjerk (i.e. the highest acceleration of daily temperature per site) (Van Wijk et al., 2012). Kölzsch et al. (2014) used the same index to show how much the onset of spring is correlated across successive stopover sites, and if the timing of goose migration depends on this predictability of onset of spring between sites. Based on their results, if there is high predictability between the consecutive stopover sites, the geese closely follow the onset of spring during their migration.

Air temperatures, solar radiation and water are the most critical constraints to vegetation growth in different parts of the world (Churkina and Running, 1998; Nemani et al., 2003). The relationship between temperature or growing degree days with different phases of plant development, especially spring flush of plants, is well known (Cleland et al., 2007; Schwartz, 2003). For this reason, a number of studies could identify significant relationships between temperature and NDVI (Jia et al., 2003; Maselli et al., 1998).

NDVI is closely related to the amount of photosynthetically active radiation absorbed by vegetation canopies (Slayback et al., 2003). NDVI has been used as a direct measure of plant phenology to study the effect of seasonality in plant phenology on synchrony of herbivores reproduction (Loe et al., 2005). Therefore, plant phenology can be directly studied through NDVI, and not through its proxy' growing degree days (GDD) that is an indirect measure of plant development (Kerby and Post, 2013). Based on this