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Long-Term Decline in a Salt Marsh Hare Population Largely Driven by Bottom-Up Factors

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Long-term decline in a salt marsh hare population largely driven by bottom-up factors

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ABSTRACT
The widespread decline of the European brown hare (\emph{Lepus europaeus}) in Europe has been attributed to both bottom-up and top-down factors, as well as climate change. Few studies have attempted to study the relative importance of these factors considered simultaneously. In this study we tested the hypotheses that hare population density is regulated by bottom-up (food), top-down (predation) or abiotic factors including tidal floods and climatic conditions. We related data on hare population density on a relatively isolated island to changes in surface area of suitable vs. unsuitable vegetation for forage, predator densities, flooding parameters and climatic variables. During the study period (1996–2012), hare numbers decreased from 580 to 219. Estimated population density was positively correlated with the cover of short, intermediate successional vegetation types and was negatively correlated with the cover of tall, late successional vegetation types. These findings corroborate results from earlier experimental studies that reported a strong aversion of hares to tall vegetation. Additionally, we found indications that raptor population density and unusually high floods also exerted negative effects on hare population density. We conclude that bottom-up factors (the availability of suitable forage) are the main regulators of the studied hare population. This suggests that the importance of bottom-up effects has been underestimated and could explain leporid population decline in areas that have experienced a similar increase in tall, unsuitable vegetation.

RÉSUMÉ
Le déclin généralisé des populations de lièvre d’Europe (\emph{Lepus europaeus}) a été attribué à la fois à des facteurs ascendants et descendants, ainsi qu’au changement climatique. Peu d’études ont tenté d’évaluer l’importance relative de ces facteurs lorsque considérés simultanément. Dans la présente étude, nous avons testé les hypothèses selon lesquelles la densité de population de lièvre est régulée par des facteurs ascendants (nourriture), des facteurs descendants (prédation) et des facteurs abiotiques tels que les inondations dues aux marées et les conditions climatiques. Nous avons comparé les données de densité de population de lièvre d’une île relativement isolée aux changements de la superficie de végétation adéquate ou non pour le lièvre, de densité de prédateurs, des paramètres d’inondations et des variables climatiques. Pendant la période étudiée (1996–2012), le nombre de lièvres a diminué de 580 à 219. La densité de population estimée était positivement corrélée au recouvrement de la végétation courte de milieu de succession et négativement corrélée au recouvrement de la végétation haute de fin de succession. Ces résultats corroborent ceux d’études expérimentales antérieures qui ont montré une forte aversion des lièvres pour la végétation haute. De plus, nos résultats suggèrent que la densité de population de rapaces et les inondations exceptionnelles ont aussi des effets négatifs sur la densité de population de lièvre. Nous concluons que les facteurs ascendants (disponibilité de nourriture) sont le facteur principal de régulation des populations de lièvre étudiées. Cela suggère que l’importance des facteurs ascendants a jusqu’à maintenant été sous-estimée et que ces facteurs pourraient expliquer le déclin des populations de léporidés dans les régions qui ont connu une augmentation comparable de la végétation haute.

Introduction
The European brown hare, \emph{Lepus europaeus} (Pallas 1778), which was once a very common species in Western European grasslands, has declined markedly since the 1960s (Mitchell-Jones et al. 1999; Edwards et al. 2000; Smith et al. 2005). A large body of literature exists on the various factors probably contributing to this decline. Intensification of agricultural practices has
resulted in loss of crop and landscape diversity, and as such is thought to be the main cause behind the decline of hares in agricultural landscapes (Edwards et al. 2000; Smith et al. 2005). Other factors may have contributed to the decline but have probably not influenced the long-term population trends (Haerer et al. 2001; Frölich et al. 2007), and these include increased predator densities (Lindstrom et al. 1994; Schmidt et al. 2004), intensive hunting (Avril et al. 2012, 2014) and diseases (Flux et al. 1990; Mitchell-Jones et al. 1999; Newey et al. 2007). Moreover, these factors probably do not operate in isolation but strongly interact with each other. For example, habitat changes can modify predation rates in many ways (Evans 2004). At the same time, an increasing number of studies have documented the importance of climate on European brown hare populations. In short, hares seem to be negatively affected by cold winters, cold springs and wet summers (Marboutin & Hansen 1998; Van Wieren et al. 2006; Rödel & Dekker 2012).

Studies that focused on mountain hare (Lepus timidus) population dynamics in natural areas have emphasized top-down factors such as predators and diseases (Newey & Thirgood 2004; Newey et al. 2007; Townsend et al. 2009). Similarly, studies on population cycles in snowshoe hares (Lepus americanus) in boreal Canada have indicated predation as the key limiting factor causing these fluctuations (for a review, see Krebs 2011), whereas climate change may lead to the disappearance of these cycles (Yan et al. 2013). Few comparable studies have been carried out on natural populations of European brown hares, as most populations are hunted (Edwards et al. 2000; Schmidt et al. 2004; Smith et al. 2005). Hunting might prevent natural mechanisms from regulating the population size by keeping numbers low.

The survival of young hares (leverets) is crucial for understanding hare population dynamics. Both survival of leverets (Marboutin & Hansen 1998) and average hare life expectancy are generally low. For example, the average life expectancy of hares has been estimated to be 1.04 years in areas with hunting in the Netherlands (Broekhuizen 1982), and has been estimated to be 1–2 years for non-hunted snowshoe hare populations (Krebs 2001). Factors influencing the survival of leverets have been divided into three groups. Firstly, several studies have shown that bottom-up factors, such as food availability or quality, exert significant influence on leveret survival to adulthood (Brüll 1973) and seem to play a role in population dynamics (Krebs et al. 2011). For example, hares showed a decrease in grazing intensity when dominant plant species, like tall-growing, late successional species, were low in nutritional quality (Kuijper & Bakker 2008). Low food quality may indirectly affect survival by decreasing body condition and increasing vulnerability to diseases (Brüll 1973; Broekhuizen, 1982; White, 1993).

Secondly, top-down effects, such as predation and diseases, may also lead to changes in leveret survival. Predator population dynamics or disease dynamics have been hypothesized to negatively affect leveret survival (Haerer et al. 2001; Schmidt et al. 2004). However, predation may affect hare populations only when the decline has already started (Krebs et al. 2001), and therefore seems to accelerate, rather than cause, the decline. Diseases such as pseudotuberculosis, brown hare syndrome, pseudococcis and gastrointestinal parasites have been argued to also play a role in explaining population dynamics (Newey & Thirgood 2004) or fitness of adult hares (Couch et al. 2012). For other hare species, it has been shown that parasites and diseases cannot sufficiently explain demographics in mountain hares (Haerer et al. 2001; Frölich et al. 2007; Townsend et al. 2009) and snowshoe hares (Murray et al. 1998), but do seem to affect body condition and nutritional status.

Apart from bottom-up and top-down factors, abiotic factors such as climate can also influence hare population dynamics. A number of studies have reported a positive relationship between summer temperature and autumn hare densities (Andersen 1952; Brezinski 1976; Smith et al. 2005) and a negative relationship between the amount of rain in spring or summer and autumn hare numbers (Andersen 1952; Brezinski 1976; Smith et al. 2005; Seltmann et al. 2009; Rödel & Dekker 2012).

As discussed, many studies have shown how different factors can affect the survival and population level of hares. However, no study to our knowledge has simultaneously addressed the relative importance of these different bottom-up, top-down and abiotic factors for European brown hares. Besides, most studies in Europe have been carried out in agricultural areas with hunting, which potentially mask or exclude several factors from operating or largely modify the relative importance of bottom-up, top-down and abiotic factors, especially when populations are over-exploited (Edwards et al. 2000). A previous study on hare population dynamics in our study area revealed that hares were negatively affected by an increase in flooding frequency and wet springs (Van Wieren et al. 2006). However, this study did not evaluate the simultaneous effects of bottom-up, top-down and abiotic factors on hare population size.

The aim of this study was to elucidate the factors that drive long-term population dynamics in the
European brown hare population of a natural salt marsh ecosystem. We tested the three contrasting but not mutually exclusive hypotheses that hare population density is regulated by one of the following: bottom-up factors through size and suitability of foraging vegetation; top-down factors through avian predation; and abiotic factors (temperature, rainfall, wind, flooding). The natural hare population on the Dutch island of Schiermonnikoog has been monitored for the last 17 years and thus provides an excellent study system to test these three hypotheses.

Methods

Study site

The study site was situated on Schiermonnikoog, a coastal barrier island in the Dutch Wadden Sea (53°30′N, 6°10′E). Owing to the prevailing sediment transport from west to east, a well-developed vegetation chronosequence has been established, with young stages in the east and older stages towards the west of the island (Figure 1) (Olff et al. 1997; Schrama et al. 2012). The present study was performed on the eastern side of the island, which is composed of both dune vegetation and back-barrier salt marsh interspersed with 10 shallow creeks that hares can easily cross. It is the salt marsh that is most intensively used by hares (Van der Wal, Egas et al. 2000). Hares were introduced in 1896 on this island and were subject to hunting until 1995 (Van Wieren et al. 2006). Hence, the population had not been hunted for 17 years at our last count in 2012. Other mammalian herbivores were absent from the salt-marsh study area with the exception of voles (Microtus arvalis). The salt marsh is intensively used as a winter and spring staging area by Barnacle geese (Branta leucopsis) and Brent geese (Branta bernicla) (see Stahl et al. 2006).

Hare counts

Estimations of the hare population size were made on the eastern part of the salt marsh of Schiermonnikoog between 1995 and 2012. Owing to expansion of the island, the vegetated area increased during this period from 520 to 710 ha (Figure 1). Hare counts were not performed on the western, older part of the marsh where hare density is very low (Van de Koppel et al. 1996). The counts were always carried out between the last two weeks of October and the fourth week of November, except in the autumn of 2006 when a heavy storm on 1 November prevented access to the marsh. We counted the hares in autumn as numbers are expected to be highest right after the reproductive season and before the winter period, when hare numbers are probably reduced by adverse weather conditions and increased flooding frequency. A previous study on this population showed very high site fidelity for hares, with overlapping summer and winter home ranges of 28.7 ± 8.5 ha (Kunst et al. 2001), so we expect that our counts adequately reflect the dynamics of this population. The counting method consisted of directly counting flushed hares along a line transect. The number of human observers varied between 28 and 48 (average of 36). Observers were

Figure 1. Map of the island of Schiermonnikoog, the Netherlands.

Note: The eastern part consists of salt marshes (shown in red). Solid rectangle indicates the area (710 ha in 2010) in which the hare counts were carried out, and dashed rectangle indicates the area (675 ha in 2010) where the annual bird counts were carried out. Different shades of red indicate the year in which first vegetation was established in each area and represent different successional stages; most hares are found in the younger stages.
evenly spaced along a line oriented north–south between the North Sea and the Wadden Sea. All observers walked eastwards in a straight line from the fourth creek to the easternmost vegetated tip of the island, which is indicated by the large solid box in Figure 1. The widest part of the study area was 3 km, making the largest distance between two observers 100 m on average, but towards the eastern part of the island where most of the hare are usually counted the width becomes much smaller and the average distance between two observers was reduced to approximately 40 m. Each of the observers only counted hares that passed between them and their neighbour to the right.

**Bottom-up factors affecting hare population dynamics: size of suitable foraging area**

To assess the size of the foraging area we used vegetation maps, which were only available for 1984, 1992, 1997, 2004 and 2010. All vegetation maps were created based on aerial photographs, false colour images and field surveys. The vegetation types were classified according to a standard typology TMAP2004 (Trilateral Monitoring and Assessment Programme of the three Wadden Sea countries: Denmark, Germany, and the Netherlands) (for methods, see Veeneklaas et al. 2013). This vegetation typology allowed us to distinguish between three different vegetation types, which were further classified according to suitability as forage for hares. This classification of forage suitability was made on the basis of the abundance of the most positively-selected and negatively-selected food plants (based on Kuijper & Bakker 2008) in the same study area as was used for hare counts. Vegetation types with high dominance of short species, such as Festuca rubra or Juncus gerardii, are positively selected by hares, whereas vegetation types with high cover (>20%) of tall species, such as Elytrigia atherica or Atriplex portulacoides, negatively affect hare densities (Kuijper & Bakker 2008).

The short type was classified as “preferred” and the tall type as “unpreferred” (sensu Kuijper & Bakker 2008). Vegetation succession on the salt marsh follows a gradual trajectory and is deterministic in that the island extends only to the east (Olff et al. 1997; Kuijper & Bakker 2005; Schrama et al. 2012). This allowed us to use these vegetation maps to derive annual estimates of the total area of suitable and unsuitable vegetation between 1998 and 2010, by interpolating the size of both areas between 1998 and 2010. ArcGis 10 was used to analyse the vegetation maps and calculate the size of foraging areas.

**Top-down factors affecting hare population dynamics: predation**

Several bird species can predate young or adult hares. In this study we included marsh harriers (Circus aegionus), hen harriers (Circus cyaneus) (Underhill-Day 1985) and large gulls (Herring gull [Larus argentatus] and lesser black-backed gull [Larus fuscus]) (Camphuysen et al. 2010) because these species have been observed to prey upon leverets (Klemann & Kleefstra 2012; D.P.J. Kuijper, personal observation). The number of avian predators (1998–2010) was derived from standardized annual counts. All breeding gulls and raptors were counted in an area of approximately 675 ha in 2010 (indicated with a dashed box in Figure 1) that was comparable with the area where hares were counted (Kleefstra 2010; Klemann & Kleefstra 2012), according to the standardized protocol of van Dijk (2004). In this counting protocol, all data were recorded by a single experienced observer who walked a fixed line transect and counted all birds in the area over the course of a single day at least twice during the breeding season each year. Each round, the observer spent on average 3.4 minutes per hectare. The higher of the two counts was used as a proxy for the total number of breeding birds in that year.

**Abiotic factors affecting hare population dynamics: flooding variables and climate**

Floods can be a direct cause of hare mortality (Van Wieren et al. 2006; M Schrama, personal observation, Figure S1). To estimate the effect of floods on hare population dynamics, we used flooding data from a publicly available database1 to calculate the annual flooding frequency (1 December–30 November) between 1995 and 2010 at two different elevations: total number of floods >70 cm above mean high tide (MHT) and floods >90 cm above MHT. We also calculated the number of days with floods above both elevation references. At a height of 70 cm above MHT, approximately 60% of the study area becomes inundated. Approximately 75% of the study area is inundated at a flooding height of 90 cm above MHT, which means that only the highest dunes remain dry. To estimate the effect of exceptionally high floods, we also calculated the number of these floods in the months before the hare counts. These floods are defined as >140 cm above MHT, when >85% of the salt marsh is flooded.

Climate is the second abiotic factor that can directly influence hare mortality (Rödel & Dekker 2012). Climatic data were obtained from the local weather
station at Schiermonnikoog. Based on an earlier study on the same population (Van Wieren et al. 2006), we calculated the most relevant climatic variables for each of the years between 1995 and 2010, which is the last year with available data. The following predictor variables were used: number of days with strong winds (>8 ms⁻¹), number of days with high precipitation (>15 mm), total annual precipitation (1 December–30 November), number of months with high precipitation (>100 mm), average yearly temperature (1 December–30 November) and the average temperature between March and May (which is time of the year when most young hares/leverets are present).

Statistical analyses

Correlation analyses with Pearson’s $r^2$ were applied to detect temporal trends in the variables expected to predict hare population size (top-down, bottom-up and abiotic variables). A similar analysis was used to detect relationships between hare population size and habitat suitability, avian predator population size and the various abiotic predictors.

To assess the relative impact of different bottom-up, top-down and abiotic variables on hare population dynamics, we performed a multiple regression analysis using a generalized linear model with a log-link function. Model selection was performed on data between 1998 and 2010 because this was the period for which all datasets were complete. We carried out a best subset selection procedure, where we used the Akaike Information Criterion (AIC) to find the best-fitting model (Burnham & Anderson 2004). Before the analysis, all bottom-up, top-down and abiotic factors were tested for collinearity. For factors that were based on similar data (e.g. number of days with high precipitation and number of months with high precipitation), we included only the factors that correlated most strongly with the changes in the hare population numbers. All statistics were carried out in Statistica 9.0. All graphs were prepared using SigmaPlot 12.5.

Results

Long-term dynamics of hare population size on the salt marsh of Schiermonnikoog

Hare population size showed large fluctuations between years but, in general, there was a clear decrease between 1996 and 2012 after hunting had ceased in 1995 (Pearson’s $r^2 = 0.45$, $p = 0.003$; Figure 2). Between 1996 and 2012, the hare population size declined at the rate of circa 19 hares year⁻¹. The size of the counted area increased from 520 ha in 1997 to 710 ha in 2010. When corrected for the change in area size, the estimated density of hares decreased from 1.2 individuals ha⁻¹ in 1996 to 0.3 individuals ha⁻¹ in 2012.

Bottom-up factors: size of suitable foraging area

The total area covered by salt-marsh vegetation types increased relatively little during the study period (from 330 ha to 333 ha between 1997 and 2010). The total cover of unsuitable late successional vegetation types (dominated by unpreferred plant species E. atherica and A. portulacoides) increased by almost 200% between 1997 and 2010 (Pearson’s $r^2 = 0.77$, $p = 0.03$; Figures 3 and 4), while vegetation types of suitable intermediate successional stages (dominated by the food plants F. rubra and J. gerardii) decreased by 66% over the same period (Pearson’s $r^2 = 0.99$, $p = 0.01$; Figure S2). There was a significant negative correlation between hare population density and the area of unsuitable (unpreferred) vegetation, and a significant positive correlation between hare population density and the area of preferred vegetation (Table 1).

Top-down factors: predation

We found no significant pairwise correlation between hare population density and the number of breeding raptors (Pearson’s $r^2 = 0.18$, $p = 0.16$) or the number of breeding gulls (Pearson’s $r^2 = 0.01$, $p = 0.99$). The number of breeding raptors increased from two to six
breeding pairs between 1998 and 2010, but the increase in population density was not significant (Pearson’s $r^2 = 0.11, p = 0.28$; Figure S3). The population density of larger gulls also showed no temporal trend (Pearson’s $r^2 = 0.13, p = 0.24$; Figure S3).

**Abiotic factors: flooding and climate**

We found no long-term trend in maximum autumn tidal flooding height, which affects the surface area flooded, or in the annual number of flooding events and summer inundations at both reference elevations (Table 1; Figure S4). Moreover, there was no correlation between hare population size and the number of inundations either at >70 cm above MHT or at >90 cm above MHT (Table 1). We did, however, find a pattern in the extremely high tides (>140 cm above MHT) that occurred in the month prior to the annual hare count. Such tides occurred at least once before the hare counts in 1996, 1999, 2002, 2007 and 2009. All of these points coincide with hare population estimations that were lower than the long-term trend (circled points in Figure 2). However, the correlation between maximum autumn flooding height and hare population size was not significant (Table 1).

There was no linear trend in any of the climatic variables between 1996 and 2010 (Table 1; Figure S4). Moreover, there was no significant correlation between any of the climatic variables and hare population size (Table 1).

**Predictors of hare population size**

The following non-collinear factors were included in the multiple regression: “size of suitable area”, “maximum autumn flood height”, “annual number of inundations >90 cm above MHT”, “total annual precipitation”, “average temperature between March and May”, “population density of breeding gulls”, “population density of breeding raptors” and “number of days with average wind speed >8 m s$^{-1}$”. We included the last factor because the number of windy days was, perhaps contrary to expectations, not significantly correlated with the number of inundations (Pearson’s $r^2 = 0.2, p = 0.1$). Only interactions between raptor density, gull density and area of suitable and unsuitable vegetation were included because model interpretation analysis became highly problematic when more interaction factors were included. A regression model using “size of area with suitable vegetation”, “size of area with unsuitable vegetation” and the interaction between “unsuitable area” and “raptor population density” as predictors for hare population size was the best-fitting model ($AIC = -6.58$, likelihood ratio $\chi^2 = 18.6, p < 0.001, k = 3$), with the lowest AIC. Most of the 10 best-fitting models included one of more of these predictors (Table S1). Models 7, 9 and 10 all included maximum flooding height as a variable. Although many models were within the range of 2ΔAIC, which can therefore be considered competitive, only few predictors (area of suitable and area of unsuitable vegetation) were actually significant (Table S1).
Discussion

During the period 1996–2012 we observed a 75% decline in hare population density on natural salt-marsh grassland without agricultural activity and where no hunting has taken place for the past 17 years. The decline in estimated hare numbers from 580 to 219 during the study period coincided with a marked decline in the area covered by preferred vegetation types. Our results showed some evidence that top-down factors could have had an additional impact on the dynamics of this natural hare population. Additionally, high autumn floods were correlated to short-term decreases in hare numbers, but our analysis suggested that this factor was uncorrelated to the long-term trend. In contrast with previous work (Van Wieren et al. 2006), our results suggest that none of the climatic variables tested are important predictors of hare population size in our study area.

**Bottom-up: quality of suitable area and hare population density**

Our results show that the decrease in the wild hare population on the salt marsh of Schiermonnikoog is strongly correlated to a single bottom-up factor: the

Figure 4. Expansion of late successional vegetation at the expense of intermediate successional vegetation. Note: Expansion happens more rapidly towards the west, which is the oldest part of this marsh.
Table 1. Analyses of long-term trends in climatic variables, predator numbers and flooding variables between 1996 and 2010 (all variables vs. year), and pairwise correlations (Pearson’s $r^2$) between the same variables and the estimated density of the hare population.

<table>
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<tbody>
<tr>
<td></td>
<td>$r$</td>
<td>$r^2$</td>
</tr>
<tr>
<td>Size of area of preferred vegetation</td>
<td>0.78</td>
<td>0.61</td>
</tr>
<tr>
<td>Size of area of unpreferred vegetation</td>
<td>0.44</td>
<td>0.20</td>
</tr>
<tr>
<td>Maximum temperature (average March–May)</td>
<td>0.08</td>
<td>0.01</td>
</tr>
<tr>
<td>Maximum temperature (average May)</td>
<td>0.11</td>
<td>0.01</td>
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<tr>
<td>Maximum temperature (May–Sept)</td>
<td>0.13</td>
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<tr>
<td>Minimum temperature (annual average)</td>
<td>0.14</td>
<td>0.02</td>
</tr>
<tr>
<td>Minimum temperature (number of days &lt;0°C)</td>
<td>0.02</td>
<td>0.00</td>
</tr>
<tr>
<td>High precipitation (total number of months &gt;100 mm)</td>
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<td>0.04</td>
</tr>
<tr>
<td>High wind (days with average speed &gt;8 ms$^{-1}$)</td>
<td>0.44</td>
<td>0.19</td>
</tr>
<tr>
<td>Precipitation (total days with precipitation &gt;15 mm)</td>
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<td>0.20</td>
</tr>
<tr>
<td>Precipitation (mm year$^{-1}$)</td>
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<td>0.06</td>
</tr>
<tr>
<td>Precipitation (total mm April–October)</td>
<td>0.25</td>
<td>0.06</td>
</tr>
<tr>
<td>Precipitation (total mm November–March)</td>
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<td>0.02</td>
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<tr>
<td>Number of days with flooding &gt;0.7 m above MHT (April–October)</td>
<td>0.23</td>
<td>0.06</td>
</tr>
<tr>
<td>Number of days with flooding &gt;0.7 m above MHT (total of year)</td>
<td>0.12</td>
<td>0.01</td>
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<tr>
<td>Number of days with flooding &gt;0.9 m above MHT (April–October)</td>
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<tr>
<td>Number of days with flooding &gt;0.9 m above MHT (total of year)</td>
<td>-0.12</td>
<td>0.02</td>
</tr>
<tr>
<td>Max autumn flood height (month prior to annual count)</td>
<td>0.18</td>
<td>0.03</td>
</tr>
<tr>
<td>Breeding raptors* (Circus cyaneus, Circus aeruginosus)</td>
<td>0.51</td>
<td>0.11</td>
</tr>
<tr>
<td>Breeding large gulls** (Larus argentatus, Larus fuscus)</td>
<td>-0.36</td>
<td>0.13</td>
</tr>
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</table>

Note: *Numbers of breeding birds and raptors were estimated between 1998 and 2010.

area of suitable forage. The notion that suitable habitat is an important determinant of hare foraging behaviour and patch selection has been illustrated in an experiment in the same study area by removing tall, late-successional vegetation from patches of short, preferred vegetation. This led to a five-fold increase in hare visitation (Kuijper & Bakker 2008). The opposite effect occurred when unpalatable, tall plants were planted in patches of preferred vegetation. At a density of 20% artificial plants, hare visitation decreased by approximately 60% (Kuijper & Bakker 2008). The progressing vegetation succession (coinciding with increasing cover of tall plants such as A. portulacoides or E. atherica; Olff et al. 1997) on the salt marsh of Schiermonnikoog is likely to have a similar impact on hare foraging behaviour at large scales. With increasing tall plant cover, the vegetation becomes increasingly unsuitable for hares (Kuijper & Bakker 2008). Hares are predicted to track vegetation succession and move their foraging activity towards younger salt marshes as has been shown for Brent geese (Van der Wal, Van Lieshout et al. 2000). However, as the present study shows, the total surface area of suitable vegetation for hare foraging is declining, leading to an overall deterioration of foraging conditions. The clear effects exerted by area of suitable vegetation (dominated by the preferred food plant F. rubra) strongly suggest that this has important consequences for hare carrying capacity in the area. Besides decreasing carrying capacity (food availability), the increasing abundance of tall-growing late successional plants can make the area less attractive for hares even when food plants are still abundantly present (Kuijper & Bakker 2008) because late successional plant species are of inferior forage quality for hares (Van der Wal, Van Lieshout et al. 2000; Kuijper & Bakker 2008) and because vegetation change might interact with (perceived) predation risk, as will be discussed in more detail below. Hares may avoid these low-visibility areas because of higher (perceived) predation risk. Both factors can contribute to sub-optimal foraging conditions for hares.

Top-down factors as predictors of hare population size

Whether predators can influence the long-term population dynamics of European brown hare is a controversial question (Schmidt et al. 2004; Smith et al. 2005), although predation is known to have a considerable effect on snowshoe hare populations (Murray 2002). Avian predators were estimated to be abundant on the island. Results from our multiple regression analysis suggested that an increase in the population of harriers may have contributed to the decline in hare numbers. Diet observations from marsh harrier nests, the most abundant raptor species on Schiermonnikoog, confirmed that hares are part of the raptor diet (Klemann & Kleefstra 2012). However, remains of predated hares were rare, with only three leverets and one adult found over eight nests among a total of 36 food items.
(Klemann & Kleefstra 2012). A probable reason for the fact that the number of harriers is a predictor in our multiple regression analyses is that both hare and harrier react to the same driver, an increase in tall grass, from which marsh harriers are known to benefit (Johnson & Horn 2008). This suggests that although predation may have some effect on hare population dynamics, it is not necessarily the main factor regulating hare population size. Studies on gull populations have shown that gulls can be a food source for lesser black-backed gulls (Camphuysen et al. 2010; D.J.P. Kuijper, personal observation), but no direct observations of hare remains were reported in the vicinity of gull nests on Schiermonnikoog (Kleefstra 2010). Our results are in line with this: we found no effect of gull population density on hare density. On Schiermonnikoog, feral cats (Felis catus) are the only mammalian predator large enough to prey on hare. The two available population estimates of feral cats suggest that there was no change in population density over the period 1984–2010 (Langeveld 1987; Op de Hoek et al. 2012). Both censuses, which were carried out using different methods, report a feral cat population size of 0.02 individuals ha⁻¹. This suggests that cats are not the prime driver of hare population size, but data are too scarce to warrant any conclusions.

In addition to directly impacting hare population size, the presence of predators could also affect hare (foraging) behaviour indirectly. In addition to the higher food quality in the F. rubra-dominated meadows (Kuijper & Bakker 2008; Kuijper et al. 2008), a latent fear of predators could also drive hares to forage in this short, open vegetation type. Being a species of open landscapes, hares typically use their speed to avoid predation. Tall vegetation will block a good view of the surroundings, reducing the chance to react adequately to approaching predators. This might be one of the reasons why hares avoid tall vegetation (Kuijper & Bakker 2008). A similar effect was found in large ungulates in North American and African ecosystems, which were shown to be more vigilant in habitats with low visibility and high density of obstructions blocking escape routes (Underwood 1982; Ripple & Beschta 2004; Valeix et al. 2009). There is evidence from a population of snowshoe hares that similar “fear-induced behaviour” can force animals to forage in sub-optimal feeding areas, subsequently leading to population decline (Hik 1995). This notion is also supported by observations of intense grazing and high pellet counts of hares on slightly elevated, Festuca-dominated, yellow meadow ant (Lasius flavus) mounds in otherwise tall vegetation (Veen et al. 2012). Hares can both graze and be alert on top of these mounds. Hence, direct and indirect effects of predation might play a role in the observed hare population decline. However, our results suggest that it is not the main driver.

In addition to predators, pathogens could also play a role. For example, there is evidence that the parasite Trichostrongylus retortaeformis can be a contributory cause of population cycles in L. timidus populations in Scotland (Newey & Thirgood 2004; Newey et al. 2007), while another study showed that hare population cycles are not caused by the parasite (Townsend et al. 2009). Unfortunately, we were not able to address the role of pathogens and parasites in regulating hare population size (Couch et al. 2012) because of a lack of data on pathogen load.

### Abiotic factors: flooding, climate and hare population density

Other long-term studies (8–28 years) on hare population dynamics have shown a strong negative effect of wet summers or springs (Van Wieren et al. 2006; Rödel & Dekker 2012), whereas our study did not reveal a correlation between climatic variables and hare population size. This apparent difference may be caused by the fact that none of these other studies simultaneously took bottom-up or top-down factors into account. Climatic conditions are an important factor affecting leveret survival (Andersen 1952; Brezinski 1976; Smith et al. 2005; Seltmann et al. 2009; Rödel & Dekker 2012) and, as such, probably affect year-to-year variation in hare numbers at the end of the reproductive period. Since hares can reproduce quickly, they can also quickly compensate for this during the subsequent breeding season. Thus, one could expect long-term trends in population decline to coincide with deteriorating climatic conditions. We did not find any indications of this in our study. Moreover, Van Wieren et al. (2006) concluded that flooding events were responsible for strong year-to-year changes in counted hare numbers. Our results support this observation as many negative deviations from the long-term declining trend coincided with exceptionally high floods in the month prior to the counts (Figure 2). The total number of flooding events may, thus, be less important than exceptionally high autumn floods, when more than 85% of the marsh gets inundated, just before the annual hare count. Additional evidence that high floods cause mortality comes from a recent study,
which showed that higher spring floods led to lower survival of hatchlings of Oystercatchers (Haematopus ostralegus) (Van de Pol et al. 2010). In contrast to these findings, our data do not show any long-term changes in flooding height or frequency during our study period. The number of flooding events cannot therefore be regarded as a driving factor behind the observed long-term decline in hare population size, although year-to-year variation in hare numbers could well be ascribed to exceptionally high autumn floods.

**Perspectives**

An increase in the abundance of late successional, unpreferred vegetation types was also noted in other Western European salt marshes (Veeneklaas et al. 2013). On the mainland salt marshes in Germany, France, the United Kingdom and the Netherlands as well as on the back-barrier island salt marshes, ongoing succession has resulted in marshes becoming increasingly dominated by E. atherica (Veeneklaas et al. 2013). This process is, to a large extent, due to cessation of livestock grazing. A remarkably similar process has taken place in several other (semi-)natural grassland ecosystems. In many of these systems, tall (nitrophilic) grass species are promoted at the expense of short species owing to cessation of livestock grazing in combination with increased atmospheric deposition of nitrogen (Bakker & Berendse 1999; Bobbink et al. 2010). While further vegetation succession on the salt marsh is mainly driven by a nutrient increase in sediments deposited by seasonal floods (van Wijnen & Bakker 2000), the increase in nutrient load of most natural grasslands occurs through increased atmospheric deposition (Vitousek et al. 1997). If this leads to a similarly strong increase in tall grass vegetation cover, such as shown for dunes in the Netherlands (see, for example, Kooijman & De Haan 1995), the decrease in suitable foraging area may have important consequences for populations of hares occurring in natural grasslands in the rest of Europe. Until now, this explanation for the Europe-wide decline of brown hares has not been thoroughly explored, possibly due to a lack of data on the increased cover of tall grass species in natural grasslands and decline in preferred forage area across Europe. In addition to these direct negative effects, predator populations (marsh harrier) might benefit from the increase in tall vegetation (Johnson & Horn 2008), which may have a subsequent negative additional effect on hare population density. These trends can be counteracted by the introduction of large herbivores, such as livestock. Large herbivores can facilitate hares on salt marshes by increasing the area of short sward meadows with preferred food species (Olff et al. 1997, Kuijper et al. 2008) and can therefore be a useful management tool. Large herbivores may thus be able to turn the tide for hares in the losing battle with vegetation succession.

**Note**

1. See http://live.waterbase.nl/

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