Predation Danger Can Explain Changes in Timing of Migration: The Case of the Barnacle Goose

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Abstract
Understanding stopover decisions of long-distance migratory birds is crucial for conservation and management of these species along their migratory flyway. Recently, an increasing number of Barnacle goose breeding in the Russian Arctic have delayed their departure from their wintering site in the Netherlands by approximately one month and have reduced their staging duration at stopover sites in the Baltic accordingly. Consequently, this extended stay increases agricultural damage in the Netherlands. Using a dynamic state variable approach we explored three hypotheses about the underlying causes of these changes in migratory behavior, possibly related to changes in (i) onset of spring, (ii) potential intake rates and (iii) predation danger at wintering and stopover sites. Our simulations showed that the observed advance in onset of spring contradicts the observed delay of departure, whereas both increased predation danger and decreased intake rates in the Baltic can explain the delay. Decreased intake rates are expected as a result of increased competition for food in the growing Barnacle goose population. However, the effect of predation danger in the model was particularly strong, and we hypothesize that Barnacle goose avoid Baltic stopover sites as a response to the rapidly increasing number of avian predators in the area. Therefore, danger should be considered as an important factor influencing Barnacle goose migratory behavior, and receive more attention in empirical studies.

Introduction
In migratory species, flexibility allows dealing with a continuously changing environment. Illustratively, Sutherland [1] presented an overview of bird species that showed flexibility in their migratory behavior to changing environmental conditions. He described changes in the use of wintering, breeding and staging areas, occurring in a wide range of families. Recently, Jonzen et al. (2006) suggested a climate-driven evolutionary change in the timing of spring migration for a number of long-distance passerine migrants [2] but see [3]. Changes in migration can also be caused by factors other than climate. Gill et al. [4] for example, showed that an increasing population of Black-tailed godwits Limosa limosa islandica, wintering in the UK, established new wintering sites on less suitable sites than the original wintering sites. They suggested that the carrying capacity of the original sites was reached, forcing the Black-tailed godwits to winter elsewhere. Additionally, Klaassen et al. [5] adopted a dynamic state variable model and showed that Pink-footed geese Anser brachyrhynchus respond to scarring practices by farmers in Norway by changing their use of stopover sites. Alerstam & Lindstrom [6] discussed minimization of time, energy and predation during migration as the main drivers of evolution in migratory behavior. The aforementioned examples of migratory change might represent responses to changes in one or more of these factors. Identifying possible causes of these changes, is essential for understanding flexibility in migratory behavior. Since the early 1990s, an increasing number of Barnacle geese Branta leucopsis breeding in the Russian Arctic have delayed their departure from their wintering site in the Netherlands by approximately one month. The geese reduced their staging duration in the next stopover area in the Baltic (traditionally used by the entire population) according to the delay from the Netherlands, such that some migrants virtually skip the Baltic stopover site altogether [7,8]. Because of these changes, the question arose what has caused the delayed departure from the wintering site and decreased use of the Baltic stopover site. Compared to changes in (migration) phenology in other bird species [2,9,10,11], the rate of change of approximately 3 days/year as observed in the Barnacle goose is unprecedentedly large. One important consequence of the delayed migration of Barnacle geese is an increased agricultural damage in the Netherlands of approximately €350,000 annually, and this figure is growing rapidly [12]. Successful management actions require the identification of factors and processes affecting departure and staging decisions. Therefore, we have formulated three possible explanations for the delay: Barnacle geese have delayed their departure as a consequence of changes in (i) onset of spring, (ii) potential food intake rates, and (iii) predation danger [13].

(i) Advanced onset of spring
Recently, several studies have found that migratory birds responded to climate-driven changes in plant phenology with...
The dynamic state variable model

Methods

Prioritize other factors, such as safety or food quality. Therefore, of fresh plant growth along the flyway [16]. However, this thought to schedule their migration according to the "green wave" change could result in higher spring temperatures in some regions, advanced laying dates [14], advanced spring arrival dates = 0,1… .

The potential intake rate at a stopover site, i.e. the intake per day a goose can gain if foraging at maximum intensity, limits the rate at which geese can replenish their energy reserves [17]. Earlier studies have shown that decreased availability and reduced quality of food can make a stopover site less attractive [18]. Van der Graaf [19] reported lower intake rates in the Baltic as compared to the Netherlands. Moreover, as the total population of Barnacle goose passing through the Baltic has increased drastically over the past thirty years [20], the competition for food at the Baltic stopover site may also have intensified [21]. Additionally, desertion of farmland, and thus reduced facilitation by cattle grazing, in these regions may also have decreased intake rates [22].

For these reasons, decreased potential intake rates at the Baltic stopover site may cause Barnacle geese to reduce staging time or even completely skip this site. Then, the geese could fly directly to one of the next stopover sites in Russia; however, since food there becomes available only later in spring, they have to delay their departure from the Netherlands until spring starts in the arctic stopover sites in Russia.

Increased predation danger can reduce the attractiveness of a site because of its lethal and non-lethal effects [23,24]. Although safety has long been acknowledged as potentially important for successful migration [6], it has received little attention so far and the few studies on the impact of predation danger on migration have not led to unambiguous conclusions [25,26]. While a number of studies indeed demonstrated the effects of predators on body mass, stopover duration and site usage [27,28], some of the results are difficult to interpret [29], and others even deny at least some of the suggested effects of predation danger [30].

In this study, we used a dynamic state variable model to analyze whether these three hypotheses can explain the observed changes in migratory behavior of Barnacle geese.

Model parameters Barnacle geese

| Parameter | unit | Reference |
|-----------|------|-----------|
| Lean body mass | 1500 g | Eichhorn 2008 |
| Maximum body mass | 2300 g | Eichhorn 2008 |
| Potential mass reserves | 800 g | |
| Energy density | 29 kJ/g | Madsen and Klaassen, 2006 |
| Total energy reserves | 23.2 MJ | |
| Energy density per x | 232 kJ | |
| Flight speed v | 18 m/s | Green, 2001 |
| Average flight costs f | 6.23 kJ/km | Butler et al., 2000; Nolet et al., 1992; Ward et al., 2002 |
| Daily energy expenditure e | 4.7 kJ | Bruinzeel et al., 1997 |

The terminal reward was defined as the reward at T, and served as a starting point for the backward iteration. Upon arrival at the breeding site N the expected reproductive success F(x, t, i) depended on the body stores at arrival as well as the timing of arrival [36]. Additionally, a
component was added for expected future reproductive success $B_T$ because Barnacle geese are long-lived animals with many years of breeding attempts. Thus:

$$F(x,t,N) = K(t) \times K(x) + B_T$$  \hspace{1cm} (1)

where $K(t)$ was the function of the timing of arrival, $K(x)$ the function of the body stores on arrival, and $B_T$ was set to 2, representing the expected future reproductive success given that an individual actually survived at any site until $T$. Both $K(t)$ and $K(x)$ result in 0 reward if an individual had not arrived at breeding site $N$ at $T$. Subsequently, the effect of timing of arrival was incorporated by a step function, meaning that breeding was only possible if arriving at the breeding grounds within the set time-limits:

$$K(t) = \begin{cases} 
0 & \text{if } t < \text{June 6 or } t > \text{June 11} \\
1 & \text{if } \text{June 6} \leq t \leq \text{June 11} 
\end{cases}$$  \hspace{1cm} (2)

The effect of body reserves on breeding success was described by a sigmoidal shape function based on data from the Pink-footed goose [36], indicating that the chance of successful breeding success increased if body stores upon arrival at the breeding site exceeded a certain threshold $x_s$. We assumed a similar relationship for Barnacle goose. Thus:

$$K(x) = \frac{1}{2} \left( e^{w(x-x_s)} - e^{-w(x-x_s)} + 1 \right)$$  \hspace{1cm} (3)

where the shape parameter $w$ was set to 0.028 and $x_s$, the threshold for successful breeding, was set to 15060 [kJ ($x_s = 65$)]

Backward iteration. At each time step a goose decided whether to stay at its present location and forage, or to depart to another location. When staying at location $i$, the potential intake rate (defined as metabolizable energy intake according to [37]) of the goose was site- and time-dependent and had predefined stochasticity $[g(i,j), k]$ day$^{-1}$. However, the actual intake rate depended on the foraging intensity $u$, ranging from 0 (no foraging) to 1 (continuous foraging). The actual intake rate minus the energy expenditure $e$ [kJ day$^{-1}$] resulted in the energy available for the storage of reserves. However, foraging with a particular intensity and storing reserves had a cost in terms of predation risk, defined by $\beta(x,u)$:

$$\beta(x,u) = m_{g(i)} \frac{(x + u g(i,t)) - e)^{\alpha + 1} - x^{\alpha + 1}}{(a + 1)(u g(i,t) - e)}$$  \hspace{1cm} (4)

where $a$, the mass-dependent escape performance exponent, was set to 2 and the site-specific constant attack rate [33] $m_{g(i)}$ is set to $10^{-3}$. The parameter $m_{g(i)}$ is the predation danger according to the definition by [13]. Thus, the goose foraged with the intensity that maximized its expected reproductive success $F$:

$$H_f(x,t,i) = \max_u [(1 - \beta(x,u)) F(x + u g(i,t) - e, t + 1, i)]$$  \hspace{1cm} (5)

Alternatively, when departing to another site $j$, the goose chose the site $j$ that maximized $F$:

$$H_d(x,t,i) = \max_j \left[ F \left( x, t + \left( \sum_{i=1}^{\text{lag}} D_j / v_i \right), j \right) \right]$$  \hspace{1cm} (6)

This choice depended on the distance between the sites $[D_i$ (km)], the speed of flight $[v$ (km day$^{-1}$)], and the reserves upon arrival ($x_a$) at site $j$. The latter was defined by

$$x_a = \left( \frac{c^2}{(c - (1 + x_j / x_{\text{max}})^{0.5} - D_j)^2} - 1 \right) x_{\text{max}}$$  \hspace{1cm} (7)

where $D$ was the distance covered. The constant $c$ in this equation was defined by

$$c = \frac{D_{\text{max}}}{1 - (1 + x_j / x_{\text{max}})^{0.5}}$$  \hspace{1cm} (8)

where $x_j$ was the level of body reserves available for flight, which equaled $x_{\text{max}}$ for Barnacle goose, and $D_{\text{max}}$ was the maximum flight distance defined by

$$D_{\text{max}} = \frac{x_{\text{max}}}{f}$$  \hspace{1cm} (9)

where $f$ was the average flight cost [kJ km$^{-1}$] [38,39,40]. To find the fitness-maximizing decision, we calculated the fitness consequences of the behavioral alternatives, i.e., to forage or depart, for all combinations of state, location and time and chose the one with the highest fitness. The thus obtained optimal decision matrix showed the best decision for each time step and for all possible levels of body reserves and sites, namely:

$$F(x,t,i) = \max \left[ H_f(x,t,i), H_d(x,t,i) \right]$$  \hspace{1cm} (10)

Forward simulation. Based on the decision matrix, optimal migration was simulated for each goose. The simulations started at
t = 0, each goose started with a random amount of body reserves between 4640 kJ ≤ x ≤ 11600 kJ, and ended when the bird reached the breeding site, died, or passed the time limit T at any other site.

In the simulations, we assumed geese had full knowledge of the environment, i.e., the geese experienced the same conditions in the forward simulation for which the optimal decisions were calculated in the backward calculation. The actual experienced potential intake rate $g(i,t)$ for each individual was drawn from a distribution with a predefined stochasticity.

Scenarios

We analyzed the three different hypotheses by step-wisely changing the relevant model-parameters, i.e., onset of spring, intake rates and predation danger. For all scenarios, both backward iteration and forward simulations were run. First, we changed onset of spring in the Baltic staging site from 24 April to 3 June in steps of 5 days. Onset of spring was defined as the point in time when food availability $g(i,t)$ first reached its highest value. Second, we changed food availability in the wintering and Baltic stop-over site from 1392 kJ d$^{-1}$ to 2784 kJ d$^{-1}$ in steps of 232 kJ d$^{-1}$, and in all possible combinations for both sites.

Third, we increased predation danger ($m_{i0}$) in the Baltic site from $10^{-10}$ to $10^{-6}$ with 16 logarithmically equal steps ($10^{-10}$, $10^{-9.75}$, $10^{-9.5}$, …, $10^{-6.5}$, $10^{-6.25}$, $10^{-6}$). We choose this range of values based on the value of $10^{-8}$ used by Klaassen et al. [5] and the value of $2 	imes 10^{-6}$ used by Weber et al. [33].

We compared the model predictions of the three scenarios with passage data from the Ottenby bird observatory (56°11’43”N, 16°23’56”E) from 1970 until 2004 (adapted from [41], see figure 2).

Ottenby is situated on a main migratory corridor for Barnacle geese traveling from the Netherlands to Baltic stopover sites [42]. Because the total population of Barnacle geese also greatly increased during that period, we used the relative cumulative percentage of passed dates. The most plausible predictions were those that showed a delay in departure equivalent to the observed delay of one month. All results were analyzed with R 2.8.1 [43].

Results

Advancing the onset of spring in the Baltic by a given unit of time led to an equally advanced departure date from the wintering site for most of the range tested in our simulations (figure 3). Additionally, the simulations showed that the geese always depart from the Dutch wintering site just before the onset of spring in the Baltic.

Decreasing intake rates in the Baltic stopover sites by 1392kJ/day led to a delay in departure date from the wintering site of 29 days (mid April–mid May) (figure 4). If, alternatively, the intake rates in the wintering site increased, the geese delayed their departure date by only 16 days (figure 4).

Increasing predation danger in the Baltic above the predation danger of the other sites led to a rapid delay of 28 days (mid April–mid May) in departure date from the wintering site (figure 5). When predation danger was further increased, a growing proportion of geese stopped using the Baltic stopover site (figure 6). However, a small proportion geese still visited the Baltic, and stayed for a few days only. They had low energy reserves, and apparently, could not skip this site as they were in dire need of replenishing their body stores.

![Figure 2. Observed delay in onset of spring migration.](image-url)

The departure dates from the wintering grounds in the Netherlands, shown as the relative cumulative percentage of departure as a function of days since the median departure date in the 1970's. Data points represent per day the mean relative cumulative passage count at Ottenby bird observatory over a certain period (circles: 1970–1979, triangles: 1980–1989, open squares: 1990–1999, solid squares: 2000–2004). The median departure date in the 1970’s was April 12.

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Discussion

Our simulations showed that the delayed departure of Barnacle geese from their wintering grounds by up to one month can be explained by either decreased potential intake rates or increased predation danger in the Baltic stopover site. In contrast, an advanced onset of spring fails to explain such a delay. The predicted response to an advanced spring growth is opposite to a delayed departure actually observed in the field. According to our simulations, an advancement of spring of 8 days (as predicted by [19] based on growing degree days) should advance departure by 8 days too. Interestingly, also the Barnacle geese breeding on Spitsbergen have not advanced their departure from Scottish wintering grounds despite an advanced onset of spring at their Norwegian stopover site, in contrast to Pink-footed geese, which largely share the same flyway and have advanced their spring migration [44]. Tombre et al. [44] suggest that Barnacle geese breeding at Spitsbergen cannot predict spring in Norway from their wintering site in the United Kingdom because of the large overseas crossing. The Russian breeding Barnacle geese, however, do not have such a large overseas crossing, and prioritize other factors than responding to advanced onset of spring in the Baltic. Thus, although the timing of high quality food during migration is important for Barnacle geese [16], this result suggests that Barnacle geese may prioritize other factors above the onset of plant growth in spring, and that the observed delay in migration cannot be caused by climatic changes. Theory also predicts that birds should not advance their timing of migration as much as spring advances, because the timing of migration has not only evolved to match the peak of food availability but also in response

Figure 3. Predicted delay in onset of spring scenario. The delay in departure (in days since April 12, which was the median departure date in the 1970’s) from the wintering site in the Netherlands as a function of onset of spring. In the model, the geese responded to a change in the peak date of intake rate such that they advance departures with an earlier spring and vice versa, they would depart later from the wintering site if spring in the Baltic would be delayed. doi:10.1371/journal.pone.0011369.g003

Figure 4. Predicted delay in intake rate scenario. The predicted delay in departure date (in days since April 12, which was the median departure date in the 1970’s) from the wintering site in the Netherlands to a changed intake rate, ranging from 1.4 MJ to 2.8 MJ, at the wintering site and the Baltic stopover site. doi:10.1371/journal.pone.0011369.g004
to many other factors, such as competition for territories and predation risk [45].

Our assumptions on decreased potential intake rates are supported by empirical studies [16,41]. Both studies suggested a recent decrease in intake rates in a Baltic stopover site. Additionally, Barnacle geese have been observed to colonize new staging sites at several locations in the Baltic. Populations staging at traditional sites remained approximately constant [46], indicating that the traditional sites reached capacity, especially because the total population of geese increased much more than the population staging in the Baltic [7]. Besides, the ongoing urbanization in the Baltic region has led to a general decline in agricultural practice, e.g., cattle farming. Consequently, intake rates may also have decreased as facilitation by large grazers decreased. Altogether, decreased intake rates can be a plausible explanation for the observed delay.

In addition to the importance of food en route, our simulations showed a particularly strong effect of predation danger on the departure date from the wintering site. When predation danger in the Baltic was only slightly higher compared to the other sites, the geese immediately started delaying departure from the wintering site, reducing staging time at the dangerous site and ultimately, skipping the site with higher predation risk. This is in line with theoretical predictions that a migratory bird should minimize the time spent in a dangerous area [47] and that the loss of future reproductive success by predation is traded off against the benefit of increasing reserves by foraging [48]. Predators can have a strong influence on migratory strategies, e.g. by causing migrants to avoid the predator abundance peak [28]. If the whole Baltic area has become more dangerous due to the recovery of predator populations, we expect the geese to minimize the time spent in that area. The strong increase in predator numbers such as White-tailed eagles in the Baltic; a fourfold increase in Estonia (from 40 to 150–170 [49]), Latvia and Finland and expansion into Gotland, Sweden [50], indicates that the Baltic has indeed become a more dangerous place for Barnacle geese compared to the Netherlands. For example, on the island of Saaremaa (2,672km²), Estonia, which is a major stopover site in the Baltic, there are 28 known White-tailed eagle territories (pers. comm. V. Volke). Contrastingly, there is currently only a single breeding pair in the Netherlands (41,528km²). For this breeding pair it has been confirmed that it preys on Greylag geese Anser anser [51].

Additionally, predation danger caused birds to not take full advantage of available resources, as they take the danger into account in their decision of where to forage [32]. These non-lethal effects of predation can potentially be larger than the lethal effects [24]. Hence, increased predation danger can reinforce the already existing effects of decreased intake rates. The influence of density-dependent effects on this trade-off are not immediately clear. Potentially, danger can cause many geese to shift to safer areas, thereby decreasing the competition for food in the dangerous areas. However, it is known that Barnacle geese facilitate each other while grazing [33]. Consequently, a dangerous and less grazed area does not necessarily lead to better feeding conditions. Our model did not take these density-dependent effects into account.

In conclusion, predation danger, in addition to food availability, can be a key factor in explaining the observed changes in migratory behavior of Barnacle geese. This study only approached the problem from a theoretical point of view, but identified critical factors to be studied empirically in the field. These new insights...

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**Figure 5. Predicted delay in danger scenario.** The delay in departure (in days since April 12, which was the median departure date in the 1970's) from the wintering site in the Netherlands as a function of predation danger at the Baltic stopover site. Above a predation danger of 3·10⁻⁵, the geese adjusted their migration by abruptly delaying their departure date from the wintering site by up to 28 days.

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also suggest that challenging geese with natural predators in the Netherlands, e.g. by creating suitable nesting places for White-tailed Eagles, may improve management of the agricultural conflict. Future empirical research needs to test our predictions by measuring the direct and indirect effects of predator activities on goose behavior. Although this study focused on the case of the Barnacle goose, its conclusions are not limited to goose migration. It is often assumed that timing of migration is synchronized with the phenology of resources [11], resulting in potential mismatches and associated population declines as a result of climate change [54]. These two studies state respectively that looking at predation in addition to resources as explanatory factor is very difficult or do not even mention predation at all as potential explanatory factor. We want to emphasize that in addition to currently well studied factors such as food availability and climatic change, predation danger should be considered in the suite of potential explanatory variables for changes in the migratory behavior of birds.

References

1. Sutherland WJ (1998) Evidence for flexibility and constraint in migration systems. Journal of Avian Biology 29: 441–446.
2. Jonzén N, Linden A, Ergon T, Knudsen E, Vik JO, et al. (2006) Rapid advance of spring arrival dates in long-distance migratory birds. Science 312: 1959–1961.
3. Both C (2007) Comment on “Rapid advance of spring arrival dates in long-distance migratory birds”. Science 315.
4. Gill JA, Norris K, Potts PM, Gunnarsson TG, Atkinson PW, et al. (2001) The buffer effect and large-scale population regulation in migratory birds. Nature 412: 436–438.
5. Klaassen M, Bauer S, Madsen J, Ingum T (2006) Modelling behavioural and fitness consequences of disturbance for geese along their spring flyway. Journal Of Applied Ecology 43: 92–100.

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Author Contributions

Conceived and designed the experiments: RMJ GE FVL SB. Performed the experiments: RMJ. Analyzed the data: RMJ FVL. Contributed reagents/materials/analysis tools: SB. Wrote the paper: RMJ GE FVL SB. Provided guidance during the whole study: FVL SB.

Figure 6. Predicted use of Baltic stopover site in danger scenario. The predicted response to increased predation danger, described as the proportion of the geese that make use of the Baltic as a stopover site. With low predation danger all geese are predicted to use the Baltic stopover site (solid line), i.e. no skipping of the Baltic (broken line). However, with increasing predation danger the majority (+/−75%) of the geese skip the site while some geese with (very) low body reserves continue to use the Baltic stopover site for a few days to build up extra reserves. doi:10.1371/journal.pone.0011369.g006

6. Alerstam T, Lindström A (1990) Optimal bird migration: the relative importance of time, energy and safety. In: Gwinner E, ed. Bird migration, physiology and eco-physiology. Berlin: Springer-Verlag. pp 331–350.
7. Eichhorn G, Drent RH, Stuhl J, Leito A, Alerstam T (2009) Skipping the Baltic: the emergence of a dichotomy of alternative spring migration strategies in Russian barnacle geese. Journal of Animal Ecology 78: 63–72.
8. Eichhorn G, Afanasiev V, Drent RJ, van der Jeugd HP (2006) Spring stopover routines in Russian Barnacle geese Branta leucopsis tracked by resightings and geolocation. Ardea 94.
9. Marra PP, Francis CM, Mulvihill RS, Moore FR (2005) The influence of climate on the timing and rate of spring bird migration. Oecologia 142: 307–315.
10. Stervander M, Lindström Å, Jonzén N, Andersson A (2005) Timing of spring migration in birds: long-term trends, North Atlantic Oscillation and
the significance of different migration routes. Journal of Avian Biology 36: 210–221.
11. Visser ME, Both C (2005) Shifts in phenology due to global climate change: the need for a yardstick. Proceedings of the Royal Society B-Biological Sciences 272: 2561–2569.
12. Faunafonds (2009) Dordrecht: Agricultural damage by Barnacle geese in the months April and May. (In Dutch: Faunaschade door brandganzen in de maanden april en mei).
13. Lank DB, Ydenberg RC (2003) Death and danger at migratory stopovers: problems with “predation risk”. Journal of Avian Biology 34: 225–229.
14. Crick HQP, Dudley C, Glue DE, Thomson DL (1997) UK birds are laying eggs earlier. Nature 388: 526–528.
15. Gordo O (2007) Why do birds migrate earlier? A review of weather and climate effects on avian migratory phenology. Climate Research 35: 57–68.
16. Van der Graaf AJ, Stahl J, Klimentiw A, Bakker JP, Drent RH (2006) Surfing on a green wave - how plant growth drives spring migration in the Barnacle Goose. Ardea 94: 567–577.
17. Beekman JH, Nolet BA, Klaassen M (2002) Skipping swans: Fuelling rates and wind conditions determine differential use of migratory stopover sites of Bewick’s Swans Cygnus bewickii. Ardea 90: 437–460.
18. Van der Graaf AJ, Stahl J, Veen GF, Haviinga RM, Drent RH (2007) Patch choice of avian herbivores along a migration trajectory - From Temperate to Arctic. Basic and Applied Ecology 8: 354–363.
19. Van der Graaf AJ (2006) Geese on a green wave: Flexible migrants in a changing world. [PhD Thesis]. Groningen: Rijksuniversiteit Groningen. 224 p.
20. Van der Jeugd HP, Okhond P, Larsson K, et al. (2009) Keeping up with early springs: Rapid range expansion in an avian herbivore incurs a mismatch between reproductive timing and food supply. Global Change Biology 15: 1057–1071.
21. Fordson P, Larsson K (1991) Breeding Range Expansion Of The Barnacle Goose Branta leucopsis In The Baltic Area. Ardea 79: 342–346.
22. Prins HHT, Gordon IJ (2008) Introduction: Grazer and Browsers in a Changing World. In: Gordon IJ, Prins HHT, eds. The Ecology of Browsing and Grazing Berlin Heidelberg: Springer. pp 5–9.
23. Ydenberg RC, Dill LM (1986) The Economics of Fleeing from Predators. Princeton University Press. 288 p.
24. Cresswell W (2008) Non-lethal effects of predation in birds. Ibis 150: 3–17.
25. Alerstam T, Hedenstro¨m A, A ´kesson S (2003) Long-distance migration: evolution and determinants. Oikos 103: 247–260.
26. Houston AI, McNamara JM (1999) Models of Adaptive Behaviour - An evolutionary ecology of routing, timing and molt by long-distance migrants. Oikos 103: 247–260.
27. Prins HHT, Gordon IJ (2008) Introduction: Grazer and Browsers in a Changing World. In: Gordon IJ, Prins HHT, eds. The Ecology of Browsing and Grazing Berlin Heidelberg: Springer. pp 5–9.
28. Lank DB, Butler RW, Ireland J, Ydenberg RC (2003) Death and danger at migratory stopovers: problems with “predation risk”. Journal of Avian Biology 34: 225–229.
29. Crick HQP, Dudley C, Glue DE, Thomson DL (1997) UK birds are laying eggs earlier. Nature 388: 526–528.
30. Dierschke V (2003) Predation hazard during migratory stopover: are light or color-related factors important? Oikos 103: 303–319.
31. Clark CW, Mangel M (2000) Dynamic state variable models in Ecology; Methods and applications. May RM, Pagel MD, eds. Oxford, New York: Oxford University Press. 295 p.
32. Houston AI, McNamara JM (1999) Models of Adaptive Behaviour - An evolutionary ecology of routing, timing and molt by long-distance migrants. Oikos 103: 247–260.
33. Peterman AC, Dudley C, Glue DE, Thomson DL (1997) UK birds are laying eggs earlier. Nature 388: 526–528.
34. Jones T, Cresswell W (2010) The phenology mismatch hypothesis: are declines of migrant birds linked to uneven global climate change? Journal of Animal Ecology 79: 98–108.