

RESEARCH ARTICLE

Experimentally increased food availability allows for earlier departure in a long-distance migratory shorebird

Thomas K. Lameris^{1,2}  | Allert I. Bijleveld²  | Roeland A. Bom^{2,3}  |
 Julia Karagicheva^{4,5} | Hidde Kressin² | Eva M. A. Kok² | Sander Lagerveld⁵ |
 Luc G. G. de Monte² | Barbara Helm⁶ | Theunis Piersma^{1,2,3} 

¹Groningen Institute for Evolutionary Life Sciences (GELIFES), University of Groningen, Groningen, The Netherlands; ²Department of Coastal Systems, NIOZ Royal Netherlands Institute for Sea Research, Den Burg, The Netherlands; ³BirdEyes, Centre for Global Ecological Change at the Faculties of Science & Engineering and Campus Fryslân, University of Groningen, Leeuwarden, The Netherlands; ⁴Theoretical and Computational Ecology, Institute for Biodiversity and Ecosystem Dynamics, University of Amsterdam, Amsterdam, The Netherlands; ⁵Wageningen University & Research, Den Helder, The Netherlands and ⁶Swiss Ornithological Institute, Sempach, Switzerland

Correspondence

Thomas K. Lameris

Email: thomaslamers@gmail.com**Funding information**

Koninklijk Nederlands Instituut voor Onderzoek der Zee; Rijksuniversiteit Groningen; Exacte en Natuurwetenschappen, Grant/Award Number: VI.Veni.202.078

Handling Editor: Caroline Isaksson

Abstract

1. The timing of animal migrations is an interplay between migration programmes and physiological and environmental conditions. The rate of body store deposition underlies many timing options, with a key unresolved question being whether the rate of body store deposition and resource constraints limit advancements in migration departure.
2. To study limits of deposition on departure timing, we captured red knots (*Calidris canutus islandica*) wintering in the Wadden Sea and manipulated hours of food access per day during spring body store deposition and prenuptial moulting phases. These birds were then released and tracked until spring migration departure from the Wadden Sea.
3. When birds were allowed to feed more hours per day in captivity, they did not start body store deposition and plumage moult earlier, but gained stores faster, were heavier and had further progressed in prenuptial feather moult at the moment of release. After release, birds that had ad libitum access to food in captivity departed earliest from the Wadden Sea, and departure timing was explained by the rate of mass deposition in captivity.
4. We experimentally demonstrate flexibility in the timing of annual-cycle processes during spring migration. Red knots are flexible to adjust the rate of mass gain and moult to food availability, in turn allowing them flexibility in departure timing. This indicates that improvements in foraging conditions at staging sites will facilitate earlier departures, which will help migratory birds to keep pace with global warming.

KEYWORDS

Calidris canutus, fuelling, mass deposition, migration departure, prenuptial moult, red knot

This is an open access article under the terms of the [Creative Commons Attribution-NonCommercial-NoDerivs](https://creativecommons.org/licenses/by-nc-nd/4.0/) License, which permits use and distribution in any medium, provided the original work is properly cited, the use is non-commercial and no modifications or adaptations are made.

© 2025 The Author(s). *Functional Ecology* published by John Wiley & Sons Ltd on behalf of British Ecological Society.

1 | INTRODUCTION

Migratory animals annually travel long distances to make use of seasonal variation in resources across the globe (Alerstam, 1993; Holt & Fryxell, 2011). This spatio-temporal matching of movements with environmental conditions requires refined programming (Helm & Liedvogel, 2024) to govern complex series of physiological challenges (Lennox et al., 2016; Maggini et al., 2022). To fuel the sometimes-extreme distances between sites (Battley et al., 2012) animals first need to deposit ample body stores, in the form of fat and protein. This energy storage can be achieved by behavioural and physiological changes leading to hyperphagia, rapid increases in foraging intensity and activity (Mathot et al., 2020; Odum, 1960), anabolism (Guillemette et al., 2012; Schindler et al., 2024) or switches to more profitable resources (McWilliams et al., 2004; van Gils et al., 2005). In addition to building up body stores, many migrants undergo physiological changes such as a prenuptial moult of contour feathers in birds (Newton, 2009). This is an energetically costly process (Murphy, 1996), which may pose additional time constraints on migration phenology (e.g. Cristol et al., 2014). Birds depart on migration based on a combination of an endogenous migration programme (Bairlein & Gwinner, 1994; Coppack et al., 2008), indicative of the right time of year, as well as environmental and physiological factors including weather conditions (Dänhardt & Lindström, 2001; Deppe et al., 2015), behaviour of flock mates (Helm et al., 2006) and accumulated body stores (Aharon-Rotman et al., 2016; Bridge et al., 2010; Cooper et al., 2015; Stanley et al., 2022).

Late arrival on the breeding grounds can have strong negative repercussions for reproductive success (Drent et al., 2003; Kokko, 1999), which results in a trade-off between the need to depart on migration early yet only with ample body stores to cover the migratory travel. As departure with relatively limited body stores could impose a risk to survival (e.g. Rakhimberdiev et al., 2018), departing too early poses a risk to survival and future reproductive success (Karagicheva et al., 2018). Species with general low survivability may profit from taking the risk of departing with fewer body stores, if this allows a chance for successful reproduction. On the other hand, individuals of longer-lived species expecting to survive multiple years and having multiple chances for reproduction may take smaller risks (Karagicheva et al., 2018). As a result, they may only depart on migration when having enough body stores, or even forego migration for 1 year to enhance survival chances (Tavera et al., 2020).

This consideration becomes especially pressing in the context of rapid global change. In response to climate warming, many organisms advance the phenology of life-history events (Cleland et al., 2007; Thackeray et al., 2016), and advancements in the migration phenology of animals are also often documented, especially in birds (Jonzen et al., 2007; Knudsen et al., 2011). However, it is often considered that the rate at which birds are advancing their timing of arrival at breeding sites may not be enough to keep a match with the local phenology of prey (Visser & Gienapp, 2019). The potential for migrants to arrive earlier via faster migrations is ultimately limited by the rate at which body stores are deposited (Lindström et al., 2019). As such, a key question is

whether ecological constraints on body store deposition are currently preventing advancements in migration phenology. Given resource declines in multiple coastal habitats important for migratory birds (Frederiksen et al., 2004; Peng, Ma, et al., 2023; Zhang et al., 2018), this could have important implications for flexibility in migration timing.

Most of our understanding of the ecological constraints during migration comes from correlational field studies (Rakhimberdiev et al., 2018; Zhang et al., 2019) or laboratory experiments where actual migratory decisions are difficult to observe (Kvist & Lindström, 2003). While expected correlations between body stores and departure timing have been shown in several field studies (e.g. Cohen et al., 2014; Schmaljohann et al., 2013), this does not necessarily imply that body store deposition limits earlier departures (Schmaljohann & Eikenaar, 2017). To understand how constraints limit flexibility in migration timing, the integration of experiments and tracking studies is an essential step, with the potential to significantly further our understanding of migration ecology (Birnie-Gauvin et al., 2020).

Here, we combine experimental manipulation of resource availability in temporary confinement with tracking migration timing of individual birds released back in the wild, studying whether the rates of fuelling affected moulting and dates of migratory departure. We studied red knots (*Calidris canutus islandica*), a highly amenable study species for which much is known on migration ecology in the wild (Buehler & Piersma, 2008; Piersma, 2007) as well as annual rhythms in captivity (Karagicheva et al., 2016). After experimentally manipulating time access to food during the spring staging period in captive red knots, we subsequently released these birds tagged with radio transmitters to track their departure timing from the Wadden Sea. We expected that, given their high relative survival rates (Rakhimberdiev et al., 2015), red knots would prioritize survival over earlier migratory departure, resulting in a strong effect of manipulated food accessibility on migration timing.

2 | MATERIALS AND METHODS

2.1 | Ethics statement

Experimental work was conducted in accordance with the Dutch law on animal experiments under project AVD8020020171505 (study protocols NIOZ-2020-02 and NIOZ-2021-04) and AVD80200202215943 (study protocol NIOZ-2022-10).

2.2 | Study population

Red knots of the subspecies *islandica* spend the non-breeding period in north-west Europe, mostly in the Wadden Sea (Buehler & Piersma, 2008; Piersma et al., 2005). In late March, red knots undergo a prenuptial moult where they replace their body contour feathers, going from winter into summer plumage (Buehler & Piersma, 2008) (Figure 1). From mid-April onwards, birds start to store energy, gaining ~80 g (2/3 of their lean body mass) in just 2–3 weeks' time (Piersma

et al., 1996, 2005) (Figure 1). Between early and late May, birds depart from the Wadden Sea towards Iceland or northern Norway (Wilson et al., 2011) (Figure 1), from where they fly to their breeding grounds in Greenland and north-east Canada (Davidson & Wilson, 1992).

We conducted experiments in the spring seasons of 2021–2023, using red knots captured in the Wadden Sea. The experimental aim was to manipulate time access to food during the period of fuelling body stores and spring prenuptial moult, after which the birds were tagged and released in late April to study the timing of their migration departure from the Wadden Sea. In the first year (2021), the experiment was carried out as a pilot study where we kept individuals in captivity up to late May and the birds were not released with transmitters.

2.3 | Bird capture and housing

The 97 red knots used in this study were captured in mist nets at the island of Griend (53.15° N, 5.16° E) in the Wadden Sea in autumn and

winter (September–January) 2019, 2021 and 2023 (Table S1). We assumed that all birds belonged to the *C.c. islandica* subspecies as birds were caught in the Wadden Sea during winter, a period when birds of the *C.c. canutus* subspecies generally reside at wintering sites in west Africa (Kraan et al., 2010; Nebel et al., 2000). Note that in his samples, Conklin et al. (2022) identified a few wintering individuals with the genetic profiles of *C. c. canutus*. Upon capture, we took biometric measurements of birds, extracted a small blood sample (<75 µL) for molecular sexing (van der Velde et al., 2017) and aged birds as either '1st calendar-year', '2nd calendar-year' or 'adult' (older than 2nd calendar-year). We only selected adult birds for the experiment as younger birds over-summer in their non-breeding range rather than migrate (Martínez-Curci et al., 2020). Birds were housed in outdoor aviaries (7–8 birds per aviary; Figure S1) at the NIOZ Royal Netherlands Institute for Sea Research on the island of Texel, following the methods described in (Buehler & Piersma, 2008; Vézina et al., 2009); see supplemental material for details.

2.4 | Treatments

The experiments started in winter/early spring after capture, except for 2021, where birds had already been in captivity since October 2019 (Table S1). Birds were randomly divided in three treatment groups, which differed in the time that food was accessible: 6, 12 or 24 h per day. Per treatment, we used either 1 aviary (2021) or 2 aviaries (2022 and 2023). Birds and treatments were assigned randomly to each aviary. The 12-h treatment represents the foraging time that red knots experience in the wild (Bulla et al., 2017; Piersma et al., 1994). The 6- and 24-h treatments can therefore be considered as constrained and increased accessibility to food, respectively. Accessibility of food (Trout pellets, Produits Trouw, Vervins, France) was controlled by using automated cat feeders (Cat Mate C300, closerpets.eu) that open and close at set times. To avoid overlap between feeding times and biweekly bird measurements, food in the 6- and 12-h treatments was accessible at night between 00:00 and 06:00 and 18:00–06:00 (times in UTC), respectively. Like most shorebirds, red knots forage by day and night (Thomas et al., 2006; van Gils & Piersma, 1999). To reduce competition between birds, we placed three feeding units in every aviary. Treatments lasted until release (late May in 2021, late April in 2022 and 2023, Table S1).

2.5 | Measurements in captivity

During the experiment, birds were captured from aviaries twice a week (Tuesdays and Fridays) for measurements. In addition, we measured the birds on 29 April, the last day of the experiment before the birds were released in 2022 and 2023. We measured body mass by weighing the birds on an electronic scale with 0.1 g precision. Plumage status was scored as the fraction of summer plumage (red-brown feathers) relative to winter plumage (grey feathers) on

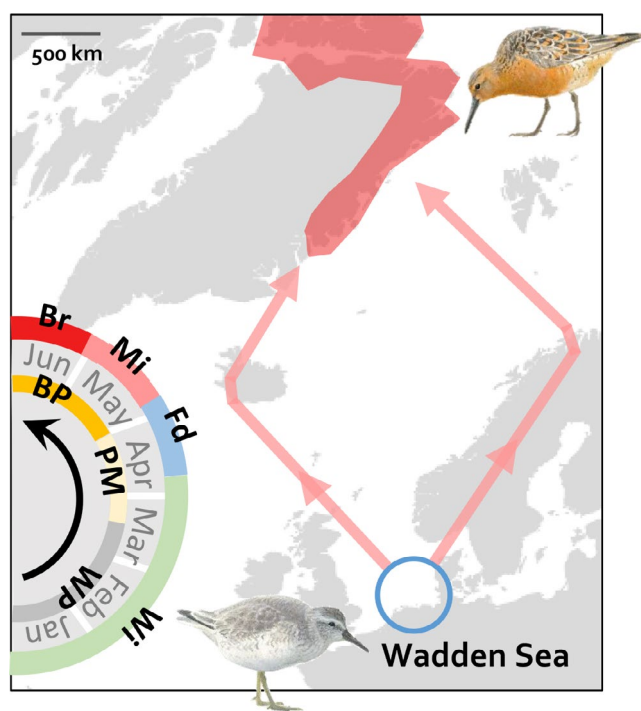


FIGURE 1 Migration routes and annual cycle of red knots *ssp. islandica* staging in the Wadden Sea. The blue circle shows the Wadden Sea, with the two main migration routes (red arrows and lines, Bauer et al., 2010) towards the breeding grounds in Greenland and the Canadian Arctic (red area, Baker et al., 2020). The half circle shows the annual cycle of red knots between January (bottom) and June (top), where after wintering (Wi) birds start fuel deposition (Fd, blue) in early April, depart on migration (Mi, pink) in early May and arrive on the breeding grounds (Br, red) in June. Birds are in winter plumage (WP, grey) up to mid-March when they start prenuptial moult (PM, yellow), which is finished around early May when birds are in full breeding plumage (BP, orange). Red knot illustrations by Elwin van der Kolk.

both the belly and back, and scored in percentage categories of 0%, ~5%, ~25%, ~50%, ~75%, ~75%, ~95% and 100% summer plumage.

2.6 | Body mass and plumage change

To determine the onset and rate of body mass deposition and plumage moult, we compiled trajectories of body mass (Figures S3–S5) and plumage status for every individual bird over the course of the experiment. From these trajectories, we determined the start and end of body mass deposition and plumage status increase, as well as the rates of change in this period. To determine the start of body mass deposition, a breakpoint analysis was conducted on body mass trajectories from 1 March up to the end of the experiment using the function 'selgmented' in the R-package 'segmented' (Muggeo, 2024), which compares models with different numbers of breakpoints (with a maximum of 3). We chose the number of breakpoints in the best-performing model and then determined the start of body mass deposition as the first breakpoint after which the slope coefficient was greater than 0.5 g/day. When none of the slope coefficients were greater than 0.5 g/day, we did not determine a start of body mass increase (27 out of 94 birds). These were typically birds that did not initiate body mass increase and kept a low body mass throughout the experiment. The maximum rate of body mass deposition was determined as the strongest slope coefficient between the breakpoints.

The start of plumage change was determined as the first measurement date at which plumage status reached 25% summer plumage or higher. For one bird which started the experiment with 25% summer plumage, we did not determine this. We determined the end of prenuptial moult as the first date on which the maximum plumage status was reached. The rate of plumage status increase was determined as the difference between the maximum and minimum fraction of summer plumage divided by the days between the start and end date. The rate of change of birds for which no start or end date could be determined, as they did not increase their plumage status, was set to 0 (47 out of 93 birds). For every bird, we also extracted the body mass (divided by length of the tarsus to correct for variation in body size) and plumage status measured on the day closest to the release day, that is 29 or 30 April. Individual plots of mass trajectories can be found in the supplements (Figures S3–S5).

2.7 | Departure timing

On 29 April 2022 and 2023, we released respectively 27 and 32 birds in the Wadden Sea (from the north-east side of the island Texel, 52.12°N, 04.90°E). In order to detect birds departing from both the western and eastern Wadden Sea, each bird was equipped with two radio transmitters: (1) a WATLAS transmitter (4.4 g), which emits signals to a network of receiver stations to determine tracks by reverse-GPS, currently operating in the western Wadden Sea, with detection ranges of up to 34 km for birds in flight (Bijleveld et al., 2022); (2)

a Lotek NTQB2-3-2 VHF nanotag (0.7 g) which can be picked up by the MOTUS network (Taylor et al., 2017), which covers most of the Wadden Sea except the central and eastern Dutch Wadden Sea (Figure 2a) where birds can be detected in flight up to 10–15 km (Taylor et al., 2017). WATLAS transmitters were attached to the skin of the birds' rump with cyanoacrylate glue after cutting away the vanes of feathers in a small circle, the same size as the transmitter. Thereafter, MOTUS transmitters were glued on top of the WATLAS transmitter (Figure S2). A MOTUS receiver was present at the release location (see above) to ensure tags were picked up in this network. Birds were released in flocks of 9–11 birds, each flock consisting of a mix of birds from every treatment.

We determined the date of departure from the Wadden Sea using both tracks received within the WATLAS network (Figure 2b) and detections received from the MOTUS network in the Wadden Sea region (Figure 2a). To improve data quality, both WATLAS and MOTUS data were filtered and smoothed (see supplemental materials). For the analyses, we only included birds that had left the Wadden Sea before 15 June, as we considered later departures might no longer represent spring migration flights but rather movement between summer staging areas. Of the 59 released birds, 44 birds (19 in 2022 and 25 in 2023) yielded recorded signals that showed departure movements out of the Wadden Sea. When birds were last detected by the WATLAS network on a northward movement out of the Wadden Sea (often moving northward over the Wadden Sea, Figure 2b), we set the date of this movement as the departure date. When birds were last detected in the WATLAS network moving in another direction (mostly towards the eastern Wadden Sea), we checked the MOTUS network for detections outside of the WATLAS network. For tags that were last detected by a MOTUS receiver, we visually inspected the series of bursts received on the last day of detection. We only included detections that showed a typical pattern of a 'departure event', with a peak in signal strength followed by a gradual decrease in signal strength (Müller et al., 2018). For one bird (Z101007), we excluded the last series of 4 consecutive bursts because they did not correspond to the typical departure pattern. Instead, we used the previous series of detections (that did show this pattern) as the departure event. Further details on birds for which we could not determine departure events, as well as individual plots and maps of MOTUS detections and WATLAS tracks, can be found in the Supporting Information (Figures S6 and S7).

2.8 | Statistical analyses

We tested how treatment affected (i) body mass deposition and (ii) plumage moult in captivity, and how (iii) treatment affected the date of departure from the Wadden Sea, as well as how (iv) departure was affected by body mass deposition and plumage moult.

(i, ii) We used generalized linear models (GLMs) to test the effects of treatment on (1) the start and (2) rate of body mass deposition, (3) body mass at release (reached on 29/30 April), as well as start (4) and rate (5) of plumage status change of each individual, and (6) plumage

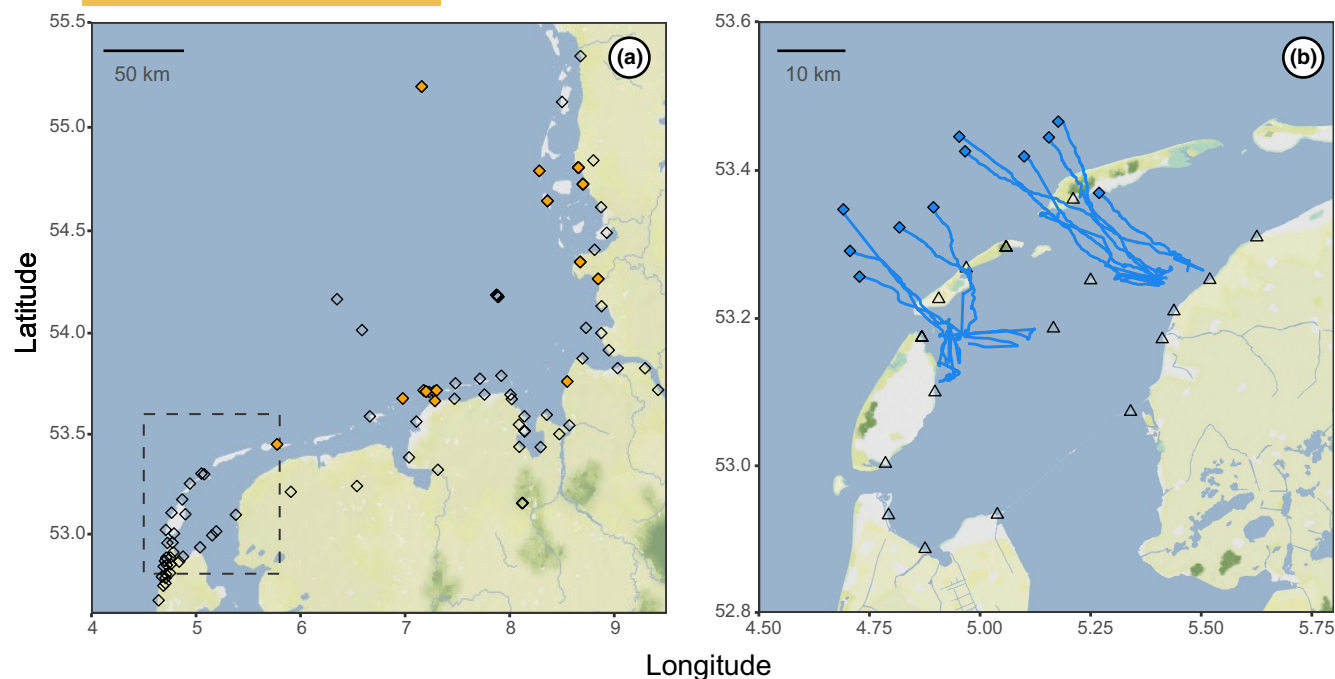


FIGURE 2 Departure locations of individual birds as detected by MOTUS receivers (a) and by WATLAS receivers (b). (a) Empty diamonds show all MOTUS receiver stations in the Wadden Sea region, while orange diamonds show the departure locations (last detections) of tagged birds. The dashed rectangle shows the area covered by WATLAS receiver stations as depicted in (b). (b) Empty triangles show all permanent WATLAS receiver stations. Blue diamonds show the last detected location of individually departing birds, with blue lines showing the track up to 2.5 h prior to the last detection.

status at release (on 29/30 April). As independent variables, we included treatment as an ordered factor ($6 < 12 < 24$ h of food accessible), sex as a factor (female/male) and year as a factor (2021, 2022, and 2023). For models 1, 3 and 4, we fitted GLMs with Gaussian errors. For models 2 and 5, we fitted Tweedie compound Poisson GLMs with a log link, and for model 6, we fitted Beta regression GLMs. We explored the data following the protocol described in Zuur et al. (2010). We checked for outliers using Cook's distance test in the 'check_outliers' function in the package 'performance' (Lüdtke et al., 2021). We explored collinearity by testing whether variance inflation factors (estimated from function 'vif' in the 'car' R-package (Fox et al., 2012)) were below 3.0. Models were validated by visual inspection of the square root of the absolute standardized residuals plotted over the fitted values, and fitted over co-variables within the model (treatment, sex and year) and co-variables not in the model (cage number). Within each model, we tested for significance of linear and quadratic trends of treatment, as well as significance of sex and year, using the *t*-statistic, or Wald's *z*-statistic for the Beta regression GLM.

(iii) We used Cox regression models to test how the date of departure from the Wadden Sea (expressed as days between release and departure) was affected by either treatment or individual body mass deposition and the extent of plumage development at release. We included data for 44 individuals with departure dates as well as 3 individuals that did not depart from the Wadden Sea, censoring the individuals from the latter group. We explored the data as described above. First, we tested the effects of treatment, including treatment

as an ordered factor, sex as a factor and year as a factor as independent variables. Within the model, we tested for the significance of linear and quadratic trends of treatment, as well as the significance of sex and year using the Wald's *z*-statistic. Due to the high variability of individual onset of mass increase, not all individuals started mass increase during the experiment. To explore how this affected our results, we also repeated the above analysis using a dataset of only the individuals that did start mass increase while in captivity ($n=30$).

(iv) Thereafter we tested the effects of body mass deposition and extent of plumage development on departure date using mixed effect Cox regression models. We included data from the 47 individuals as described above, after which we omitted 3 individuals for which the start of body mass increase could not be determined. We included (centred and scaled) start and rate of body mass deposition, body mass at release, rate of plumage status change, plumage status at release, sex and year as independent variables. We did not include start of plumage status change as more than half of the individuals did not show plumage changes. As rates and scores at release for body mass and plumage status were correlated (variance inflation factors >3.0), we did not include rates and scores at release in the same model. As these models included parameters affected by the experimental treatment rather than the treatment itself, we used AICc model selection to determine the best model, which was the model with the lowest AICc, or the model with the least amount of parameters within $2 \Delta AICc$ of this model (Arnold, 2010). A list of models is included in Table S2.

3 | RESULTS

3.1 | Body mass increase in captivity

The starting date of body mass deposition was not affected by treatment (linear trend: $t_{83}=0.70$, $p=0.48$, quadratic trend: $t_{83}=0.44$, $p=0.66$, Figure 3; Figure S6) yet birds started earlier in 2022 (2021: 12 April ± 3.6 days, 2022: 2 April ± 2.2 , 2023: 11 April ± 1.9 , $t_{87}=-2.25$, $p=0.027$). Birds that had longer access to food increased body mass faster (6-h access: 0.09 ± 0.16 g/day, estimated marginal mean $\pm$ standard error, 12-h: 0.25 ± 0.14 , 24-h: 0.90 ± 0.13 , linear trend: $t_{87}=5.17$, $p<0.001$, quadratic trend: $t_{87}=0.95$, $p=0.34$, Figure 3; Figure S7), with a slower body mass increase in 2022 (2021: 0.55 ± 0.20 , 2022: 0.07 ± 0.14 , 2023: 0.44 ± 0.11 , $t_{87}=-2.00$, $p=0.049$). In addition, birds that had longer access to food reached a higher body mass at release (6-h: 141 ± 4 g, 12-h: 154 ± 3 , 24-h: 162 ± 3 , linear trend: $t_{60}=4.34$, $p<0.001$, quadratic trend: $t_{60}=-0.69$, $p=0.50$, Figure 3; Figure S8) with no difference between years. There was no difference between sexes for the start and rate of body mass deposition, and neither for body mass at release.

3.2 | Plumage change in captivity

The start of plumage status change was not affected by treatment (linear trend: $t_{39}=-0.68$, $p=0.50$, quadratic trend: $t_{39}=1.37$, $p=0.18$, Figure S8); the rate of plumage change did not differ between treatments (linear trend: $t_{86}=1.78$, $p=0.08$, quadratic trend: $t_{86}=1.15$, $p=0.25$, Figure 3; Figure S7), while birds that had longer access to food developed a more complete summer plumage before release (6-h: $26.8\% \pm 2.8\%$, 12-h: $31.0\% \pm 3.2\%$, 24-h: $41.4\% \pm 3.8\%$, linear trend: $z=3.61$, $p<0.001$, quadratic trend: $z=0.80$, $p=0.43$, Figure 3; Figure S10). Development of plumage differed between years, with birds in 2023 having developed less into summer plumage (2021: $44.6\% \pm 5.9\%$, 2022: $37.3\% \pm 3.1\%$, 2023: $17.3\% \pm 1.8\%$, $z=-5.052$, $p<0.001$) as well as between males and females, with males having changed further into summer plumage upon release (females: $24.6\% \pm 2.8\%$, males: $41.6\% \pm 3.1\%$, $z=5.04$, $p<0.001$, Figure S10).

3.3 | Treatment effect on departure date

The treatment effect was not significant ($n=44$, $z=1.25$, $p=0.21$), yet birds that had longer access to food in captivity appeared to

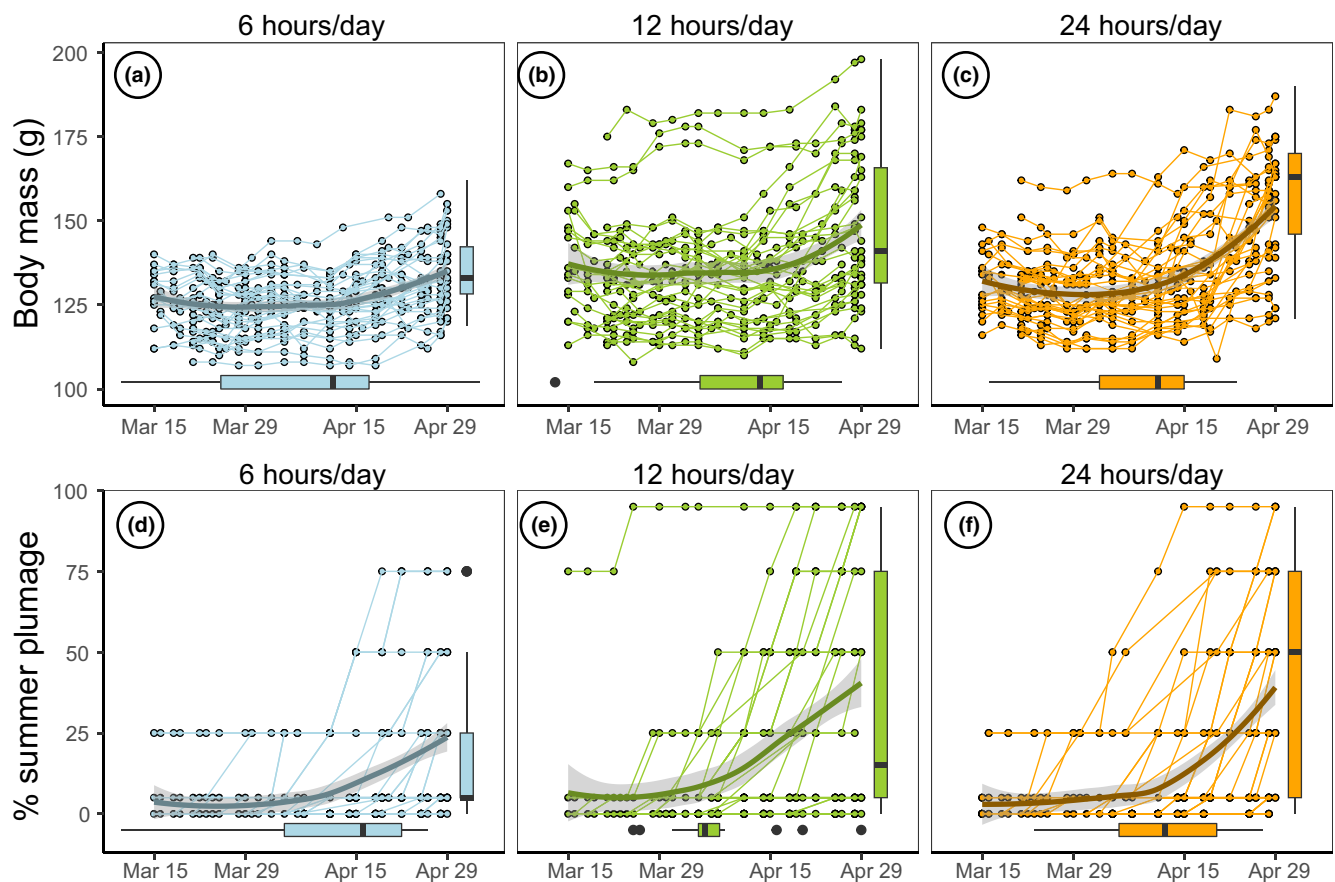


FIGURE 3 Trajectories of body mass (a–c) and plumage scores (d–f) from the years 2021–2023 combined and shown per treatment. Points and thin lines show data from individual birds, thick lines show loess regressions for all birds with grey areas showing 95% confidence intervals. Horizontal boxplots show the start date of increase in body mass and plumage status, vertical boxplots show the body mass and plumage status at release. Colours of dots and boxplots denote treatment, including 6-h (blue), 12-h (green) and 24-h food access (orange).

depart earlier from the Wadden Sea (mean departure date of 6h-group: 22 May ± 10 days, 12h-group: 23 May ± 11 , 24h-group: 13 May ± 12 , Figure 4a). When including only individuals that started mass increase while in captivity instead of all individual birds, the treatment effect was significant, with birds that had longer access to food departing earlier (linear trend: $n=30$, $z=1.99$, $p=0.046$), and departure also being earlier for males than for females (mean departure date males ($n=16$): 13 May ± 11 days, females ($n=14$): 21 May ± 7 days, $z=2.58$, $p=0.010$).

3.4 | Body mass and plumage development effects on departure date

Analysing departure date in relation to body mass deposition and extent of plumage development revealed that only the rate of body mass deposition was retained in the best model (8.78 lower AICc compared to the null model, Table S2). Birds that had gained body mass faster departed earlier (Hazard ratio 0.52 ± 0.15 , equals 5.3 ± 1.6 days earlier departure per gram/day faster body mass deposition).

4 | DISCUSSION

We showed how migratory shorebirds responded to altered food accessibility, increasing the rate of body mass deposition and

developing a more complete summer plumage when food was longer accessible, with no changes in the timing of the start of either process. When released back onto the spring staging site in the Wadden Sea, individuals that had deposited body mass faster also departed earlier. In addition, individuals that had longer access to food departed earlier, although this trend was only significant when excluding individual birds that did not start depositing body mass in captivity.

4.1 | Flexibility in mass deposition and feather moult

Effects of food accessibility on mass deposition of fuelling migratory birds are known from earlier experimental studies, showing increases in mass deposition under supplemental food (Kvist & Lindström, 2000; Ouwehand et al., 2023), or reduced intake rates under restricted food access (Reneerkens et al., 2007; Vézina et al., 2009). We show that mass deposition rates during spring body store deposition are regulated by food accessibility, with the comparison of three treatment levels reinforcing the idea that this stringency applies within individuals.

In addition to the effect of food accessibility on body mass deposition rates, we show an effect of food access on moult from winter to summer plumage. While the effect of treatment on the rate of pre-nuptial moult was not significant, treatment did affect differences in

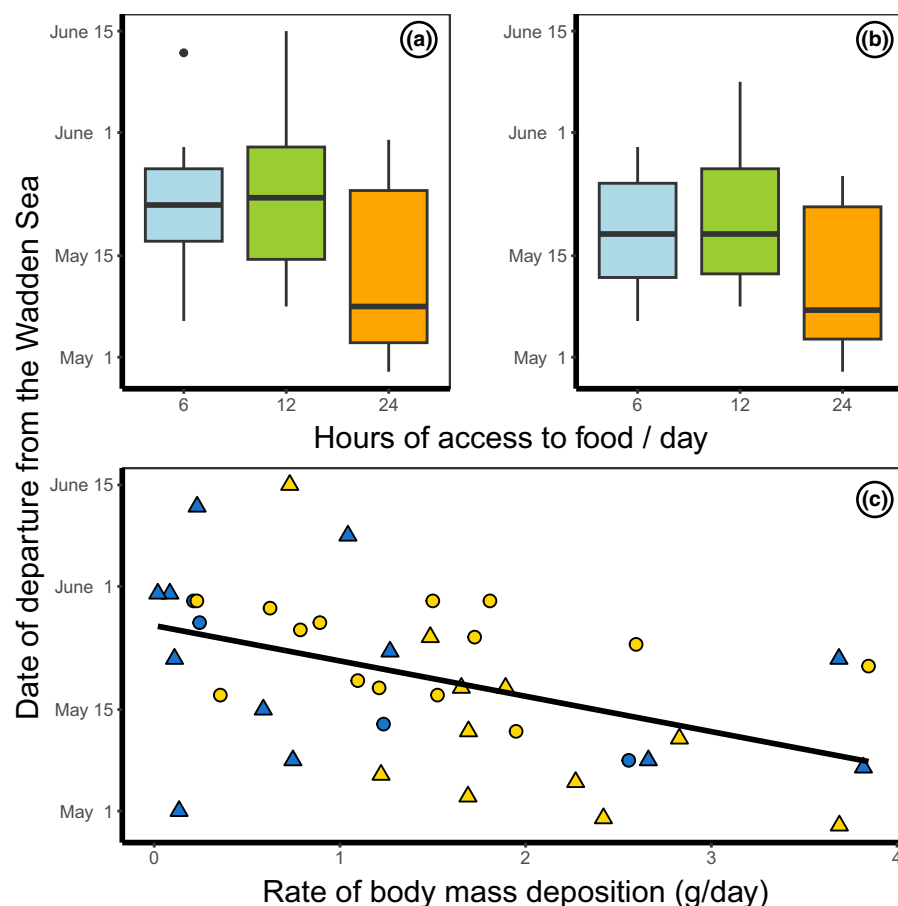


FIGURE 4 (a) Date of departure from the Wadden Sea as affected by the treatment (hours of access to food per day) for all individuals combined and (b) only for individuals that started depositing mass in captivity. Colours of boxplots denote treatment, including 6-h (blue), 12-h (green) and 24-h food access (orange). (c) Date of departure as affected by rate of body mass deposition (in g/day), with blue points show data from 2022 and yellow points show data from 2023, data from males as triangles and data from females as dots. The black line shows the linear regression as extracted from the best-performing Cox regression model.

developed summer plumage in late April. Birds like red knots are capable of gaining resources at rates sufficient to invest simultaneously in both mass deposition and moulting (Verhoeven et al., 2016), yet our experiments suggest that birds face a challenge once resources become restricted. In the trade-off between body mass deposition and moult to breeding plumage, the latter seems less critical at least at the early stages of migration. Red knots can arrest and resume the moult in the course of the migration (Piersma et al., 1992), and also in our experiment, many birds skipped prenuptial moult at least for the period of stay in the captivity. Together, this suggests that under limited foraging conditions, red knots prioritize body mass gain over plumage moult.

4.2 | Timing of migratory departure

We found an effect of body mass deposition rate on departure timing, with birds depositing body mass faster during the experiment also departing earlier after release. This suggests that departure timing from the Wadden Sea is constrained by the rate at which individual birds have been able to deposit body mass. Past evidence of individuals with more body stores departing earlier (e.g. Cohen et al., 2014; Schmaljohann et al., 2013) has been disputed (Schmaljohann & Eikenaar, 2017), as this is typically based on correlational data, with departure often being measured as disappearance from local study sites which could also be movements to alternative staging sites. Ouwehand et al. (2023) were the first to overcome the hurdle of correlational data by experimentally provide supplemental food to overwintering pied flycatchers *Ficedula hypoleuca* and observed that such individuals would disappear from the study site earlier in spring compared to individuals which were not fed. We take an additional step by measuring departure from two large regional radio-tracking networks covering the entire Wadden Sea, thereby also overcoming the limitation of measuring departure as disappearance from the study site. As such, we provide strong evidence of mass deposition rate as an important constraint for departure timing, and a prioritization of sufficient body stores over earlier departure, at least for red knots.

Even though birds from the 24-h treatment departed 10 days earlier on average compared to the 12-h and 6-h treatment, this effect of treatment was only significant when excluding individuals that did not start depositing body mass in captivity. This reflects an important role of variation in the onset of body mass deposition on the effect of the treatment. In all treatments, some birds did not start depositing body mass before 29 April. This fraction of birds was larger with less access to food (24h: 7 out of 33 birds; 12h: 10 out of 32; 6h: 13 out of 32, Figures S3–S5). While variation in the start of body mass deposition could be caused by individually consistent differences in phenology (Burnside et al., 2021), we consider it likely that especially in restricted treatments, access to food was monopolized by certain individuals that showed body mass deposition rates in accordance to the treatment (Bijleveld et al., 2012).

Our experiment forms an analogy to staging sites undergoing resource declines, yet an unchanging number of competing individuals.

When resources are plentiful, many individuals can quickly deposit body mass and depart early, yet when resources become restricted, competition increases (Peng, Choi, et al., 2023) and only some individuals may be successful in timely body mass deposition and departure. For species prioritizing survival, resource restrictions will likely result in more individuals skipping migration and over-summering on non-breeding grounds (Tavera et al., 2020). Alternatively, for species prioritizing reproduction, such resource limitations may impose mortality of individuals departing with small body stores. Strikingly, such imposed mortality is also found in bar-tailed godwits (*Limosa lapponica*), a species prioritizing survival (Rakhimberdiev et al., 2018). This suggests that there are more factors in play determining how birds choose in the trade-off between departure timing and survival, perhaps also related to individual variation (Ersoy et al., 2024).

A factor potentially complicating our results is the recent finding of a few individuals with the genetic make-up of the subspecies *C. c. canutus* overwintering in the Wadden Sea (Conklin et al., 2022). It is possible that some of the red knots in our experiment belonged to the *canutus* subspecies rather than *islandica*. Red knots ssp. *canutus* migrate to breeding grounds in the central Russian Arctic, and as such will differ in timing of migratory departure as well as fuel stores with which they depart (Dick et al., 1976, 1987). While red knots ssp. *islandica* are considered to depart earlier and with smaller body stores (Buehler & Piersma, 2008; Piersma et al., 2005), all previous work on how these aspects potentially differ between subspecies rests on the assumption that subspecies can be identified (Nebel et al., 2000), and unambiguously so based on wintering grounds (Conklin et al., 2022). The presence of both subspecies in our experiment seems rather unlikely and in the worst case will have increased the variation between individuals (e.g. in the onset of mass deposition and plumage change).

4.3 | Comparing experimental and free-living birds

Mass deposition rates of red knots are flexible and likely dependent on food availability, given a large range of rates observed in the wild (0.6 g/d to 3.0 g/d, Piersma et al., 2005) and even extreme rates in captivity (18.7 g/d, Kvist & Lindström, 2003). The aim of our experiment was to simulate both increased and reduced mass deposition rates relative to a control treatment that is equal to deposition rates of birds in the wild. However, mass deposition of birds held under the increased treatment of 24-h food accessibility (2.2 ± 1.7 g/d) was similar or even slightly lower compared to mass deposition rates found for red knots ssp. *islandica* in the Wadden Sea (2.8 g/d, Prokosch, 1988). It is possible that conditions in captivity were not optimal for fuelling, or that mass deposition rates in the Wadden Sea have declined in the last 30 years, yet recent measurements on fuelling rates in this area are missing. Interestingly, an advance in departure timing was mostly visible in the 24-h treatment, where departure timing of birds in the 12- and 6-h treatments was largely similar, suggesting that only the 24-h treatment allowed for an advance in migration timing. When comparing departure timing of experimental birds leaving towards the north-west as measured from WATLAS transmitters (Figure 2b) with

similar data from wild birds tagged in 2021 (supplemental materials), the departure date of wild birds (9 May ± 3 days, $n=9$) was roughly similar to birds from the 6- and 12-h treatment groups (6h: 12 May ± 6 days, $n=5$; 12h: 11 May ± 5 days, $n=3$), whereas birds from the 24-h treatment departed earlier (3 May ± 5 days, $n=3$). This suggests that the 24-h treatment indeed reflected favourable resource conditions and that current conditions in the Wadden Sea constrain earlier departures of red knots. This is perhaps not surprising, given the reported low efficiency of conservation efforts in the Wadden Sea (Meijer et al., 2025) and current declines in populations of molluscivorous species (Kleefstra et al., 2022). Lifting resource constraints on fuelling (for a practical example, see Zhang et al., 2021) could advance departure dates beyond what is currently observed in the population, perhaps better allowing birds to keep pace with global warming.

5 | CONCLUSIONS

Here, we experimentally demonstrated flexibility in the timing of annual-cycle processes during spring migration. Under reduced food availability, shorebirds like red knots can respond by (1) slowing down or even postponing prenuptial moult to invest into body mass gain, and (2) delaying departure on migration to allow for longer mass gain. By such responses, birds may risk timely arrival on the breeding grounds and thus successful reproduction, but secure survival (Grandmont et al., 2023; Legagneux et al., 2012; Norris et al., 2004). This strategy can be expected for a long-lived bird species (Karagicheva et al., 2018). Flexibility to adjust the rate of mass gain and moult, but not the onset of these processes, is supported by the previously shown cue responses in red knots, where the importance of environmental factors (other than photoperiod) increases in the course of the annual cycle (Karagicheva et al., 2016). Phenological events have been shown to advance under currently changing spring conditions (Helm et al., 2019), even in shorebirds (Conklin et al., 2021; Rakhimberdiev et al., 2018) despite reported high consistency in their movements (Conklin et al., 2013). Our results suggest that once birds start to prepare for migration, improvement of foraging conditions at staging sites could facilitate earlier departures of individual birds, likely in turn supporting fitness. This underlines the importance of refuelling hubs such as the Wadden Sea to support long-distance migrations, which makes maintenance of its ecosystem health a conservation priority.

AUTHOR CONTRIBUTIONS

Thomas K. Lameris, Julia Karagicheva, Barbara Helm and Theunis Piersma conceived the idea for this study; Thomas K. Lameris designed the experiments with help from Luc G. G. de Monte and Allert I. Bijleveld. Luc G. G. de Monte, Allert I. Bijleveld and Thomas K. Lameris captured birds. Thomas K. Lameris, Hidde Kressin and Luc G. G. de Monte collected data from birds in captivity. Thomas K. Lameris, Allert I. Bijleveld, Roeland A. Bom and Sander Lagerveld designed and conducted the tracking study of birds. Thomas K. Lameris analysed the data with help from Allert I. Bijleveld, Roeland A. Bom,

Eva M. A. Kok and Sander Lagerveld. Thomas K. Lameris wrote the initial draft of the manuscript, and all authors made significant contributions to the revisions.

ACKNOWLEDGEMENTS

We thank Anne Dekinga, Job ten Horn, Symen Deuzeman, Constanza Rivas, Morrison Pot, Rahel Weisser, Chiel Boom and other volunteers and students for their help during long nights of catching red knots. Wim-Jan Boon, Anne Dekinga and Anita Koolhaas have been indispensable for the transportation of people and birds from catching sites. We thank the many students and volunteers who have helped with the care of captive red knots, where we specifically want to express our thanks to Rahel Weisser and Kasper van Kraaij. We owe sincere thanks to colleagues operating MOTUS receiver stations along the Wadden Sea coast, in particular, Heiko Schmaljohann and his group. The work described in this manuscript has been financially supported by a NWO Veni grant (VI.Veni.202.078) awarded to Thomas K. Lameris, structural funding from the Royal Netherlands Institute for Sea Research and the Groningen University.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data and code are openly available at Figshare under <https://doi.org/10.6084/m9.figshare.28660718> (Lameris et al., 2025).

ORCID

Thomas K. Lameris  <https://orcid.org/0000-0001-7023-3406>

Allert I. Bijleveld  <https://orcid.org/0000-0002-3159-8944>

Roeland A. Bom  <https://orcid.org/0000-0001-8180-1958>

Theunis Piersma  <https://orcid.org/0000-0001-9668-466X>

REFERENCES

- Aharon-Rotman, Y., Gosbell, K., Minton, C., & Klaassen, M. (2016). Why fly the extra mile? Latitudinal trend in migratory fuel deposition rate as driver of trans-equatorial long-distance migration. *Ecology and Evolution*, 6, 6616–6624.
- Alerstam, T. (1993). *Bird migration*. Cambridge University Press.
- Arnold, T. W. (2010). Uninformative parameters and model selection using Akaike's Information Criterion. *The Journal of Wildlife Management*, 74, 1175–1178.
- Bairlein, F., & Gwinner, E. (1994). Nutritional mechanisms and temporal control of migratory energy accumulation in birds. *Annual Review of Nutrition*, 14, 187–215.
- Baker, A., Gonzalez, P., Morrison, R. I. G., & Harrington, B. A. (2020). Red Knot (*Calidris canutus*), version 1.0. In S. M. Billerman (Ed.), *Birds of the World*. Cornell Lab of Ornithology. <https://doi.org/10.2173/bow.redkno.01>
- Battley, P. F., Warnock, N., Tibbitts, T. L., Gill, R. E., Piersma, T., Hassell, C. J., Douglas, D. C., Mulcahy, D. M., Gartrell, B. D., Schuckard, R., Melville, D. S., & Riegen, A. C. (2012). Contrasting extreme long-distance migration patterns in bar-tailed godwits *Limosa lapponica*. *Journal of Avian Biology*, 43, 21–32.
- Bauer, S., Ens, B. J., & Klaassen, M. (2010). Many routes lead to Rome: Potential causes for the multi-route migration system of Red Knots, *Calidris canutus islandica*. *Ecology*, 91, 1822–1831.

- Bijleveld, A. I., Folmer, E. O., & Piersma, T. (2012). Experimental evidence for cryptic interference among socially foraging shorebirds. *Behavioral Ecology*, 23, 806–814.
- Bijleveld, A. I., Van Maarseveen, F., Denissen, B., Dekinga, A., Penning, E., Ersoy, S., Gupte, P. R., de Monte, L., ten Horn, J., Bom, R. A., & Toledo, S. (2022). WATLAS: High-throughput and real-time tracking of many small birds in the Dutch Wadden Sea. *Animal Biotelemetry*, 10, 36.
- Birnie-Gauvin, K., Lennox, R. J., Guglielmo, C. G., Teffer, A. K., Crossin, G. T., Norris, D. R., Aarestrup, K., & Cooke, S. J. (2020). The value of experimental approaches in migration biology. *Physiological and Biochemical Zoology*, 93, 210–226.
- Bridge, E. S., Kelly, J. F., Bjornen, P. E., Curry, C. M., Crawford, P. H. C., & Paritte, J. M. (2010). Effects of nutritional condition on spring migration: Do migrants use resource availability to keep pace with a changing world? *Journal of Experimental Biology*, 213, 2424–2429.
- Buehler, D. M., & Piersma, T. (2008). Travelling on a budget: Predictions and ecological evidence for bottlenecks in the annual cycle of long-distance migrants. *Philosophical Transactions of the Royal Society, B: Biological Sciences*, 363, 247–266.
- Bulla, M., Oudman, T., Bijleveld, A. I., Piersma, T., & Kyriacou, C. P. (2017). Marine biorhythms: Bridging chronobiology and ecology. *Philosophical Transactions of the Royal Society, B: Biological Sciences*, 372, 20160253.
- Burnside, R. J., Salliss, D., Collar, N. J., & Dolman, P. M. (2021). Birds use individually consistent temperature cues to time their migration departure. *Proceedings of the National Academy of Sciences of the United States of America*, 118, e2026378118.
- Cleland, E. E., Chuine, I., Menzel, A., Mooney, H. A., & Schwartz, M. D. (2007). Shifting plant phenology in response to global change. *Trends in Ecology & Evolution*, 22, 357–365.
- Cohen, E. B., Moore, F. R., & Fischer, R. A. (2014). Fuel stores, time of spring, and movement behavior influence stopover duration of red-eyed vireo *Vireo olivaceus*. *Journal of Ornithology*, 155, 785–792.
- Conklin, J. R., Battley, P. F., & Potter, M. A. (2013). Absolute consistency: Individual versus population variation in annual-cycle schedules of a long-distance migrant bird. *PLoS One*, 8, e54535.
- Conklin, J. R., Lisovski, S., & Battley, P. F. (2021). Advancement in long-distance bird migration through individual plasticity in departure. *Nature Communications*, 12, 4780.
- Conklin, J. R., Verkuil, Y. I., Battley, P. F., Hassell, C. J., Ten Horn, J., Johnson, J. A., Tomkovich, P. S., Baker, A. J., Piersma, T., & Fontaine, M. C. (2022). Global flyway evolution in red knots *Calidris canutus* and genetic evidence for a Nearctic refugium. *Molecular Ecology*, 31, 2124–2139.
- Cooper, N. W., Sherry, T. W., Marra, P. P., & Inouye, B. D. (2015). Experimental reduction of winter food decreases body condition and delays migration in a long-distance migratory bird. *Ecology*, 96, 1933–1942.
- Coppack, T., Tindemans, I., Czisch, M., Van der Linden, A., Berthold, P., & Pulido, F. (2008). Can long-distance migratory birds adjust to the advancement of spring by shortening migration distance? The response of the pied flycatcher to latitudinal photoperiodic variation. *Global Change Biology*, 14, 2516–2522.
- Cristol, D. A., Johnson, K. M., Jenkins, K. D., & Hawley, D. M. (2014). Timing of feather molt related to date of spring migration in male white-throated sparrows, *Zonotrichia albicollis*. *Journal of Experimental Zoology*, 321, 586–594.
- Dänhardt, J., & Lindström, Å. (2001). Optimal departure decisions of songbirds from an experimental stopover site and the significance of weather. *Animal Behaviour*, 62, 235–243.
- Davidson, N., & Wilson, J. (1992). The migration system of European-wintering knots *Calidris canutus islandica*. *Wader Study Group Bulletin*, 64, 39–51.
- Deppe, J. L., Ward, M. P., Bolus, R. T., Diehl, R. H., Celis-Murillo, A., Zenal, T. J., Moore, F. R., Benson, T. J., Smolinsky, J. A., Schofield, L. N., & Enstrom, D. A. (2015). Fat, weather, and date affect migratory songbirds' departure decisions, routes, and time it takes to cross the Gulf of Mexico. *Proceedings of the National Academy of Sciences of the United States of America*, 112, E6331–E6338.
- Dick, W. J., Piersma, T., & Prokosch, P. (1987). Spring migration of the Siberian knots *Calidris canutus canutus*: Results of a co-operative wader study group project. *Ornis Scandinavica*, 18, 5–16.
- Dick, W. J. A., Pienkowski, M. W., Walter, M., & Minton, C. D. T. (1976). Distribution and geographical origins of knot *Calidris canutus* wintering in Europe and Africa. *Ardea*, 64, 22–47.
- Drent, R., Both, C., Green, M., Madsen, J., & Piersma, T. (2003). Pay-offs and penalties of competing migratory schedules. *Oikos*, 103, 274–292.
- Ersoy, S., Groothuis, T. G. G., Piersma, T., & Bijleveld, A. I. (2024). When slow explorers are fast: Personality-related differences in timing of migration in red knots (*Calidris canutus*). *Ibis*, 166, 1146–1156.
- Fox, J., Weisberg, S., Adler, D., Bates, D., Baud-Bovy, G., Ellison, S., Firth, D., Friendly, M., Gorjanc, G., & Graves, S. (2012). *Package 'car'*, 16. R Foundation for Statistical Computing.
- Frederiksen, M., Wanless, S., Harris, M. P., Rothery, P., & Wilson, L. J. (2004). The role of industrial fisheries and oceanographic change in the decline of North Sea black-legged kittiwakes. *Journal of Applied Ecology*, 41, 1129–1139.
- Grandmont, T., Fast, P., Grentzmann, I., Gauthier, G., Bêty, J., & Legagneux, P. (2023). Should I breed or should I go? Manipulating individual state during migration influences breeding decisions in a long-lived bird species. *Functional Ecology*, 37, 602–613.
- Guillemette, M., Richman, S. E., Portugal, S. J., & Butler, P. J. (2012). Behavioural compensation reduces energy expenditure during migration hyperphagia in a large bird. *Functional Ecology*, 26, 876–883.
- Helm, B., & Liedvogel, M. (2024). Avian migration clocks in a changing world. *Journal of Comparative Physiology A*, 210, 691–716.
- Helm, B., Piersma, T., & van der Jeugd, H. (2006). Sociable schedules: Interplay between avian seasonal and social behaviour. *Animal Behaviour*, 72, 245–262.
- Helm, B., Van Doren, B. M., Hoffmann, D., & Hoffmann, U. (2019). Evolutionary response to climate change in migratory pied flycatchers. *Current Biology*, 29, 3714–3719.
- Holt, R. D., & Fryxell, J. M. (2011). Theoretical reflections on the evolution of migration. In *Animal migration: A synthesis* (pp. 17–31). Oxford University Press.
- Jonzen, N., Hedenström, A., & Lundberg, P. (2007). Climate change and the optimal arrival of migratory birds. *Proceedings of the Royal Society B: Biological Sciences*, 274, 269–274.
- Karagicheva, J., Rakhimberdiev, E., Dekinga, A., Brugge, M., Koolhaas, A., Ten Horn, J., & Piersma, T. (2016). Seasonal time keeping in a long-distance migrating shorebird. *Journal of Biological Rhythms*, 31, 509–521.
- Karagicheva, J., Rakhimberdiev, E., Saveliev, A., & Piersma, T. (2018). Annual chronotypes functionally link life histories and life cycles in birds. *Functional Ecology*, 32, 2369–2379.
- Kleefstra, R., Bregnballe, T., Frikke, J., Günther, K., Hälterlein, B., Hansen, M. B., Hornman, M., Meyer, J., & Scheiffarth, G. (2022). Wadden sea quality status report: Migratory BIRDS. In *Wadden Sea Quality Status Report*. Common Wadden Sea Secretariat (CWSS).
- Knudsen, E., Lindén, A., Both, C., Jonzén, N., Pulido, F., Saino, N., Sutherland, W. J., Bach, L. A., Coppack, T., Ergon, T., Gienapp, P., Gill, J. A., Gordo, O., Hedenström, A., Lehtikoinen, E., Marra, P. P., Möller, A. P., Nilsson, A. L. K., Péron, G., ... Stenseth, N. C. (2011). Challenging claims in the study of migratory birds and climate change. *Biological Reviews*, 86, 928–946.
- Kokko, H. (1999). Competition for early arrival birds in migratory birds. *Journal of Animal Ecology*, 68, 940–950.
- Kraan, C., van Gils, J. A., Spaans, B., Dekinga, A., & Piersma, T. (2010). Why afro-Siberian red knots *Calidris canutus canutus* have stopped staging in the western Dutch Wadden Sea during southward migration. *Ardea*, 98, 155–160.

- Kvist, A., & Lindström, Å. (2000). Maximum daily energy intake: It takes time to lift the metabolic ceiling. *Physiological and Biochemical Zoology*, 73, 30–36.
- Kvist, A., & Lindström, Å. (2003). Gluttony in migratory waders—Unprecedented energy assimilation rates in vertebrates. *Oikos*, 103, 397–402.
- Lameris, T. K., Bijleveld, A. I., Bom, R. A., Karagicheva, J., Kressin, H., Kok, E. M. A., Lagerveld, S., de Monte, L. G. G., Helm, B., & Piersma, T. (2025). Data from: Experimentally increased food availability allows for earlier departure in a long-distance migratory shorebird. Figshare <https://doi.org/10.6084/m9.figshare.28660718>
- Legagneux, P., Fast, P. L. F., Gauthier, G., & Bêty, J. (2012). Manipulating individual state during migration provides evidence for carry-over effects modulated by environmental conditions. *Proceedings of the Royal Society B: Biological Sciences*, 279, 876–883.
- Lennox, R. J., Chapman, J. M., Souliere, C. M., Tudorache, C., Wikelski, M., Metcalfe, J. D., & Cooke, S. J. (2016). Conservation physiology of animal migration. *Conservation Physiology*, 4, cov072.
- Lindström, Å., Ålerstam, T., & Hedenström, A. (2019). Faster fuelling is the key to faster migration. *Nature Climate Change*, 9, 288–289.
- Lüdecke, D., Makowski, D., Ben-Shachar, M. S., Patil, I., Waggoner, P., Wiernik, B. M., Arel-Bundock, V., & Jullum, M. (2021). Package “performance.” Version 0.7.2. <https://easystats.github.io/performance/>
- Maggini, I., Noakes, M. J., Hawkes, L. A., & Hegemann, A. (2022). Editorial: Ecophysiological adaptations associated with animal migration. *Frontiers in Ecology and Evolution*, 10, 1022173.
- Martínez-Curci, N. S., Isacch, J. P., D’Amico, V. L., Rojas, P., & Castresana, G. J. (2020). To migrate or not: Drivers of over-summering in a long-distance migratory shorebird. *Journal of Avian Biology*, 51, jav.02401.
- Mathot, K. J., Kok, E. M. A., van den Hout, P., Dekinga, A., & Piersma, T. (2020). Red knots (*Calidris canutus islandica*) manage body mass with dieting and activity. *Journal of Experimental Biology*, 223, jeb.231993.
- McWilliams, S. R., Guglielmo, C., Pierce, B., & Klaassen, M. (2004). Flying, fasting, and feeding in birds during migration: A nutritional and physiological ecology perspective. *Journal of Avian Biology*, 35, 377–393.
- Meijer, K. J., Franken, O., Witte, S., Holthuijsen, S. J., Van Der Heide, T., Govers, L. L., & Olff, H. (2025). Hotspots in peril: Misalignment of conservation efforts and ecological values in a shallow coastal sea. *People and Nature*, 7, 160–179.
- Muggeo, V. M. (2024). Package ‘segmented’.
- Müller, F., Eikenaar, C., Crysler, Z. J., Taylor, P. D., & Schmaljohann, H. (2018). Nocturnal departure timing in songbirds facing distinct migratory challenges. *Journal of Animal Ecology*, 87, 1102–1115.
- Murphy, M. E. (1996). Energetics and nutrition of molt. In C. Carey (Ed.), *Avian energetics and nutritional ecology* (pp. 158–198). Springer US.
- Nebel, S., Piersma, T., van Gils, J. A., Dekinga, A., & Spaans, B. (2000). Length of stopover, fuel storage and a sex-bias in the occurrence of red knots *Calidris c. canutus* and *C. c. islandica* in the Wadden Sea during southward migration. *Ardea*, 88, 165–176.
- Newton, I. (2009). Molt and plumage. *Ringed & Migration*, 24, 220–226.
- Norris, D. R., Marra, P. P., Kyser, T. K., Sherry, T. W., & Ratcliffe, L. M. (2004). Tropical winter habitat limits reproductive success on the temperate breeding grounds in a migratory bird. *Proceedings of the Royal Society B: Biological Sciences*, 271, 59–64.
- Odum, E. P. (1960). Premigratory hyperphagia in birds. *American Journal of Clinical Nutrition*, 8, 621–629.
- Ouwehand, J., Asso, A. A., Johnston, B., Bot, S., Bil, W., Groenewoud, F., & Both, C. (2023). Experimental food supplementation at African wintering sites allows for earlier and faster fuelling and reveals large flexibility in spring migration departure in pied flycatchers. *Ardea*, 111, 343–370.
- Peng, H., Ma, Z., Rakhimberdiev, E., van Gils, J. A., Battley, P. F., Rogers, D. I., Choi, C. Y., Wu, W., Feng, X., Ma, Q., & Hua, N. (2023). Arriving late and lean at a stopover site is selected against in a declining migratory bird population. *Journal of Animal Ecology*, 92, 2109–2118.
- Peng, H.-B., Choi, C.-Y., Ma, Z., Bijleveld, A. I., Melville, D. S., & Piersma, T. (2023). Individuals of a group-living shorebird show smaller home range overlap when food availability is low. *Movement Ecology*, 11, 70.
- Piersma, T. (2007). Using the power of comparison to explain habitat use and migration strategies of shorebirds worldwide. *Journal of Ornithology*, 148, S45–S59.
- Piersma, T., Bruinzeel, L., Drent, R., Kersten, M., Van Der Meer, J., & Wiersma, P. (1996). Variability in basal metabolic rate of a long-distance migrant shorebird (red knot, *Calidris canutus*) reflects shifts in organ sizes. *Physiological Zoology*, 69, 191–217.
- Piersma, T., Prokosh, P., & Bredin, D. (1992). The migration system of afro-Siberian knots *Calidris canutus canutus*. *Wader Study Group Bulletin*, 64, 52–63.
- Piersma, T., Rogers, D. I., González, P. M., Zwarts, L., Niles, L. J., de Lima Serrano do Nascimento, I., Minton, C. D., & Baker, A. J. (2005). Fuel storage rates before northward flights in red knots worldwide. Facing the severest ecological constraints in tropical intertidal environments? In R. Greenberg & P. P. Marra (Eds.), *Birds of two worlds: Ecology and evolution of migration* (pp. 262–273). Johns Hopkins University Press.
- Piersma, T., Verkuil, Y., & Tulp, I. (1994). Resources for long-distance migration of knots *Calidris canutus islandica* and *C. c. canutus*: How broad is the temporal exploitation window of benthic prey in the western and eastern Wadden Sea? *Oikos*, 71, 393–407.
- Prokosh, P. (1988). Das Schleswig-Holsteinische Wattenmeer als Frühjahrs-Aufenthaltsgebiet arktischer Watvogel-Populationen am Beispiel von Kiebitzregenpfeifer (*Pluvialis squatarola*, L. 1758), Knutt (*Calidris canutus*, L. 1758) und Pfuhschnepfe (*Limosa lapponica*, L. 1758). *Corax*, 12, 273–442.
- Rakhimberdiev, E., Duijns, S., Camphuysen, C. J., Dekinga, A., Dekker, R., Gavrilov, A., Ten Horn, J., Jukema, J., & Saveliev, A. (2018). Fuelling conditions at staging sites can mitigate Arctic warming effects in a migratory bird. *Nature Communications*, 9, 4263.
- Rakhimberdiev, E., van den Hout, P. J., Brugge, M., Spaans, B., & Piersma, T. (2015). Seasonal mortality and sequential density dependence in a migratory bird. *Journal of Avian Biology*, 46, 332–341.
- Reneerkens, J., Piersma, T., & Sinninghe Damsté, J. S. (2007). Expression of annual cycles in preen wax composition in red knots: Constraints on the changing phenotype. *Journal of Experimental Biology*, 139, 127–139.
- Schindler, A. R., Fox, A. D., Winkle, C. K., Ballard, B. M., Walsh, A. J., Kelly, S. B. A., Cao, L., Griffin, L. R., & Weegman, M. D. (2024). Energetic trade-offs in migration decision-making, reproductive effort and subsequent parental care in a long-distance migratory bird. *Proceedings of the Royal Society B: Biological Sciences*, 291, 20232016.
- Schmaljohann, H., & Eikenaar, C. (2017). How do energy stores and changes in these affect departure decisions by migratory birds? A critical view on stopover ecology studies and some future perspectives. *Journal of Comparative Physiology A*, 203, 411–429.
- Schmaljohann, H., Korner-Nievergelt, F., Naef-Daenzer, B., Nagel, R., Maggini, I., Bulte, M., & Bairlein, F. (2013). Stopover optimization in a long-distance migrant: The role of fuel load and nocturnal take-off time in Alaskan northern wheatears (*Oenanthe oenanthe*). *Frontiers in Zoology*, 10, 26.
- Stanley, C. Q., Hallager, S. H., Dudash, M. R., & Marra, P. P. (2022). Food limitation modulates the endogenous control of spring migratory behavior in a captive long-distance migratory bird population. *Behavioral Ecology and Sociobiology*, 76, 1–13.
- Tavera, E. A., Stauffer, G. E., Lank, D. B., & Ydenberg, R. C. (2020). Oversummering juvenile and adult semipalmated sandpipers in Perú gain enough survival to compensate for foregone breeding opportunity. *Movement Ecology*, 8, 42.

- Taylor, P. D., Crewe, T. L., Mackenzie, S. A., Lepage, D., Aubry, Y., Cryslar, Z., Finney, G., Francis, C. M., Guglielmo, C. G., Hamilton, D. J., Holberton, R. L., Loring, P. H., Mitchell, G. W., Norris, D. R., Paquet, J., Ronconi, R. A., Smetzer, J. R., Smith, P. A., Welch, L. J., & Woodworth, B. K. (2017). The Motus wildlife tracking system: A collaborative research network to enhance the understanding of wildlife movement. *Avian Conservation and Ecology*, 12, 8.
- Thackeray, S. J., Henrys, P. A., Hemming, D., Bell, J. R., Botham, M. S., Burthe, S., Helaouet, P., Johns, D. G., Jones, I. D., Leech, D. I., Mackay, E. B., Massimino, D., Atkinson, S., Bacon, P. J., Brereton, T. M., Carvalho, L., Clutton-Brock, T. H., Duck, C., Edwards, M., ... Wanless, S. (2016). Phenological sensitivity to climate across taxa and trophic levels. *Nature*, 535, 241–245.
- Thomas, A. R. J., Székely, T., Powell, R. F., & Cuthill, I. C. (2006). Eye size, foraging methods and the timing of foraging in shorebirds. *Functional Ecology*, 20, 157–165.
- van der Velde, M., Haddrath, O., Verkuil, Y. I., Baker, A. J., & Piersma, T. (2017). New primers for molecular sex identification of waders. *Wader Study*, 124, 147–151.
- van Gils, J. A., Battley, P. F., Piersma, T., & Drent, R. (2005). Reinterpretation of gizzard sizes of red knots world-wide emphasises overriding importance of prey quality at migratory stopover sites. *Proceedings of the Royal Society B: Biological Sciences*, 272, 2609–2618.
- van Gils, J. A., & Piersma, T. (1999). Day and nighttime movements of radiomarked red knots staging in the western Wadden Sea in July–August 1995. *Bulletin - Wader Study Group*, 89, 36–44.
- Verhoeven, M. A., Van Eerbeek, J., Hassell, C. J., & Piersma, T. (2016). Fuelling and moult in red knots before northward departure: A visual evaluation of differences between ages, sexes and subspecies. *Emu—Austral Ornithology*, 116, 158–167.
- Vézina, F., Petit, M., Buehler, D. M., Dekinga, A., & Piersma, T. (2009). Limited access to food and physiological trade-offs in a long-distance migrant shorebird. I. Energy metabolism, behavior, and body-mass regulation. *Physiological and Biochemical Zoology*, 82, 549–560.
- Visser, M. E., & Gienapp, P. (2019). Evolutionary and demographic consequences of phenological mismatches. *Nature Ecology & Evolution*, 3, 879–885.
- Wilson, J., Benediktsson, G. Ö., Croger, R., Dick, W., Hooper, K., Morrison, G., & Potts, P. (2011). Red knots marked in N Norway switch spring staging area to Iceland. *Wader Study Group Bulletin*, 118, 175–180.
- Zhang, S., Bai, Q., Melville, D. S., Feng, C., Piersma, T., & Ma, Z. (2021). Food supplementation as a conservation intervention: A framework and a case of helping threatened shorebirds at a refuelling site. *Biological Conservation*, 264, 109394.
- Zhang, S.-D., Ma, Z., Choi, C.-Y., Peng, H.-B., Bai, Q.-Q., Liu, W.-L., Melville, D. S., He, P., Chan, Y.-C., van Gils, J. A., & Piersma, T. (2018). Persistent use of a shorebird staging site in the Yellow Sea despite severe declines in food resources implies a lack of alternatives. *Bird Conservation International*, 28, 534–548.
- Zhang, S.-D., Ma, Z., Choi, C.-Y., Peng, H.-B., Melville, D. S., Zhao, T.-T., Bai, Q.-Q., Liu, W.-L., Chan, Y.-C., van Gils, J. A., & Piersma, T. (2019). Morphological and digestive adjustments buffer performance: How staging shorebirds cope with severe food declines. *Ecology and Evolution*, 9, 3868–3878.
- Zuur, A. F., Ieno, E. N., & Elphick, C. S. (2010). A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution*, 1, 3–14.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1. Aviary with 7 red knots, including two automated feeding trays (white round, in front, third one not visible), a tray for fresh water which is constantly refreshed (left) and a basin filled with salt water, including fountains (right).

Figure S2. Radio-transmitters and release of red knots.

Figure S3–S5. Body mass trajectories of all experimental birds in 2021 (S1), 2022 (S2) and 2023 (S3), dots showing individual (bi weekly) measurements of mass, black lines showing the trajectories, coloured lines showing the predicted mass trajectories from segmented regression analyses (colours in accordance with treatment, orange = 24 h access to food, green 12 h access, blue 6 h access). Grey vertical lines show onset of mass increase, grey dotted vertical lines show offset of mass increase.

Figure S6. For each individual bird released in 2022, a top panel showing WATLAS and MOTUS detections over time and a bottom panel showing detections on a map.

Figure S7. For each individual bird released in 2023, a top panel showing WATLAS and MOTUS detections over time and a bottom panel showing detections on a map.

Figure S8. Effect of treatment (hours of access to food/day) on the start of body mass increase and plumage status increase. Blue bars show data for males, yellow bars show data for females.

Figure S9. Effect of treatment (hours of access to food/day) on slope of body mass increase and plumage status increase. Blue bars show data for males, yellow bars show data for females.

Figure S10. Effect of treatment (hours of access to food/day) on final body mass and final plumage status (expressed as % summer plumage) at release. Blue bars show data for males, yellow bars show data for females.

Table S1. Sample sizes and metadata of birds used in the experiments, including date and location of capture, dates of the experimental manipulation, and the number of aviaries and birds used in the experiments.

Table S2. The top-20 mixed effect Cox regression models of departure date (DD) including independent variables start (Sbm) and rate (Rbm) of body mass deposition and final body mass (Fbm), rate of plumage status change (Rpl) and final plumage status (Fpl), sex (S) and year (Y).

How to cite this article: Lameris, T. K., Bijleveld, A. I., Bom, R. A., Karagicheva, J., Kressin, H., Kok, E. M. A., Lagerveld, S., de Monte, L. G. G., Helm, B., & Piersma, T. (2025). Experimentally increased food availability allows for earlier departure in a long-distance migratory shorebird. *Functional Ecology*, 39, 3434–3445. <https://doi.org/10.1111/1365-2435.70183>