NATURE COMMUNICATIONS

Corrected: Author correction

ARTICLE

https://doi.org/10.1038/s41467-019-09971-8 OPEN

Stochastic simulations reveal few green wave surfing populations among spring migrating herbivorous waterfowl

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Tracking seasonally changing resources is regarded as a widespread proximate mechanism underpinning animal migration. Migrating herbivores, for example, are hypothesized to track seasonal foliage dynamics over large spatial scales. Previous investigations of this green wave hypothesis involved few species and limited geographical extent, and used conventional correlation that cannot disentangle alternative correlated effects. Here, we introduce stochastic simulations to test this hypothesis using 222 individual spring migration episodes of 14 populations of ten species of geese, swans and dabbling ducks throughout Europe, East Asia, and North America. We find that the green wave cannot be considered a ubiquitous driver of herbivorous waterfowl spring migration, as it explains observed migration patterns of only a few grazing populations in specific regions. We suggest that ecological barriers and particularly human disturbance likely constrain the capacity of herbivorous waterfowl to track the green wave in some regions, highlighting key challenges in conserving migratory birds.

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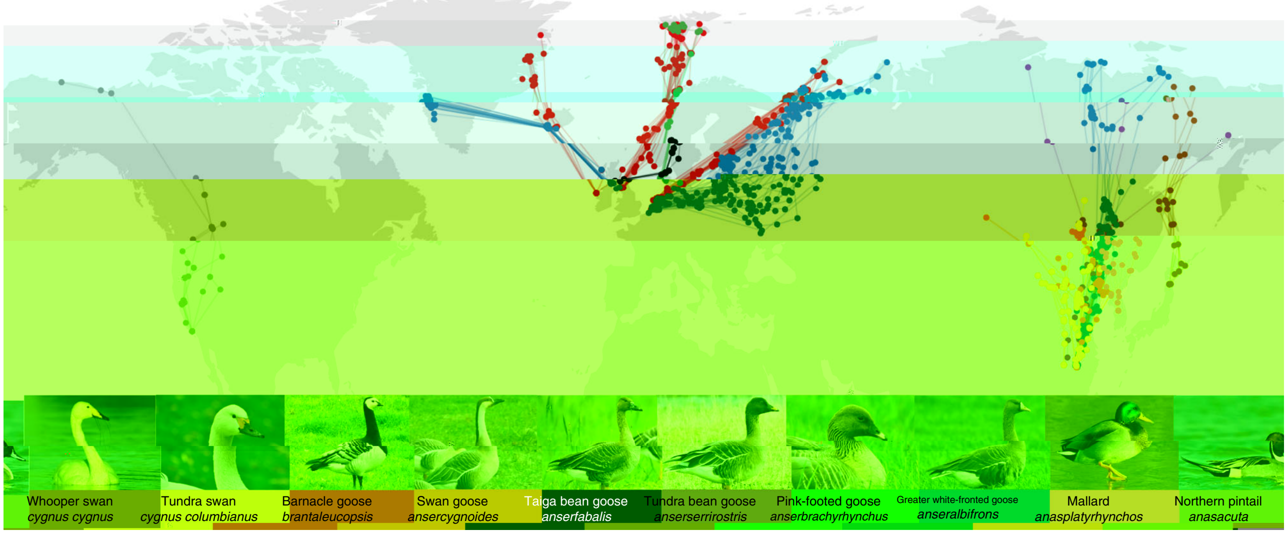

Fig. 1 Overview of spring migration and stopover site dataset for Anatidae. The dataset includes 222 spring migrations from 193 individuals belonging to 14 populations (five grazers, seven facultative8(rs)ean te-999878(usie[(populations)-680175514.10.527139eWn1Tf24.756700510TD()T/F91Tf.5-/F103t)14.5(ric99.3999

Results

Dataset

Branta leucopsis, *Anser albifrons*, *Cygnus cygnus*, *Cygnus columbianus*, *Anser cygnoides*, *Anser fabalis*, *Anser serrirostris*, *Anser brachyrhynchus*, *Anser albifrons flavirostris*, *Anas platyrhynchos*, *Anas acuta*

Method evaluation

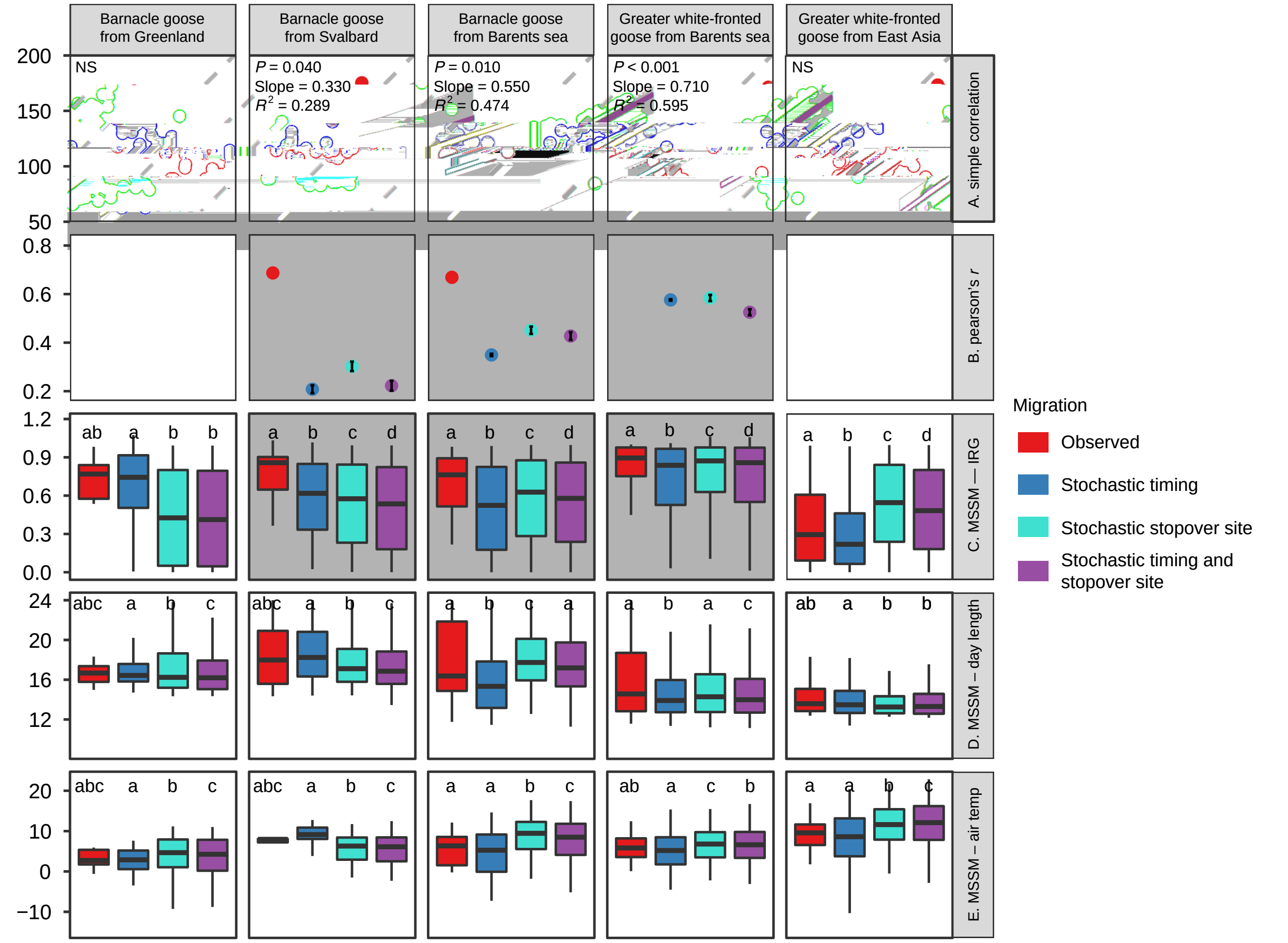

Fig. 2 Testing the green wave hypothesis for grazers by three different methods. We present the results of the Simple Conventional Correlation (a, upper row), Correlation method evaluated by stochastic migrations (b, second row) and the Metric Selection approach based on Stochastic Migrations (MSSMs) (c–e, three lower rows). Red, blue, turquoise and purple dots/boxes denote observed, stochastic timing, stochastic stopover site and stochastic timing and stopover site migrations, respectively. **a** The *x* and *y* axes denote the expected arrival day of the year at stopover sites (the day with peak instantaneous rate of green-up [IRG] value) and the observed arrival day of the year by birds, respectively. The grey pecked lines with slope = 1 and intercept = 0 indicate perfect match of migration and green wave. N.S. denotes insignificant slope; otherwise the *p*-value and coefficient of the slope, and marginal R^2 are provided. Blue lines show the significant positive slope of the green wave in models of green wave surfers, and grey bands are the prediction intervals of the models. **b** Pearson's correlation coefficient r and 95% CI (*y* axis) of observed and stochastic migrations (*x* axis). For populations without available migration tracks, only stochastic timing simulations were performed, compared and plotted. Blank panels denote not applicable because this method only applies to green wave surfers or weak surfers identified by Simple Conventional Correlation. **c**–**e** Three metrics compared for observed versus stochastic migrations: IRG (instantaneous rate of green-up), day length and air temperature. Lower case letters indicate significantly different groups using Kruskal–Wallis test followed by Dunn's test of multiple comparisons. Boxplots show median, first and third quartiles with whiskers reaching to the last data point within 1.5 × interquartile range. For clear presentation, outliers out of 10 and 90% quantiles were excluded from the plots but kept in all analyses. All grey shaded plots in all panels denote significant migration–green wave associations. Source data are provided as a Source Data file

[illegible]

Methods

Migration data

Stopover/migration information

Remote-sensing data and green wave metrics

$$(t) = \alpha + (\beta - \alpha) \cdot \left(\frac{}{+ \; ^{-\gamma \cdot (t-\delta)}} + \frac{}{+ \; ^{\varepsilon \cdot (t-\theta)}} - \right) \qquad (\;)$$

α β γ ε δ θ t

$$(t) = \frac{(t) - \alpha}{\beta - \alpha} \times \; \% \qquad (\;)$$

Simple Conventional Correlation

Correlation method evaluated by Stochastic Migrations

(*sensu*

MSSM

Variation in the migration–green wave associations

$R =$, $N =$

Data availability

Code availability

Published online: 16 May 2019

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Acknowledgements

[illegible]

Author contributions

[illegible]

Additional information

Supplementary Information [illegible]

Competing interests: [illegible]

Reprints and permission [illegible]

Journal peer review information *Nature Communications* [illegible]

Publisher's note: [illegible]