Unravelling processes between phenotypic plasticity and population dynamics in migratory birds

Jin Liu[1, 2], Weipan Lei[1], Xunqiang Mo[3], Chris J. Hassell[4], Zhengwang Zhang[1*], Tim Coulson[2]

1. Key Laboratory for Biodiversity Science and Ecological Engineering, College of Life Sciences, Beijing Normal University, Beijing, 100875, China.
2. Department of Zoology, University of Oxford, Oxford, OX1 3SZ, UK
3. School of Geographic and Environmental Sciences, Tianjin Normal University, Tianjin, 300387, China
4. Global Flyway Network, PO Box 3089, Broome, WA 6725, Australia

*Corresponding author: zzw@bnu.edu.cn

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Data will be archived from the Dryad Digital Repository if the paper is accepted for publication.

Abstract

Populations can rapidly respond to environmental change via adaptive phenotypic plasticity, which can also modify interactions between individuals and their environment, affecting population dynamics. Bird migration is a highly plastic resource-tracking strategy in seasonal environments. Investigating the link between migration strategy plasticity and population dynamics can help to understand the regulation of migrant populations under environmental change. We first estimated population trends of migratory waterbirds in the face of the loss of staging habitat by using census data. We found increasing trends both in abundance and species richness in the remaining staging area, which we hypothesised was a consequence of behavioural plasticity generated by the loss of the historical suitable staging habitat. To test whether our hypothesis could explain observed trends, we constructed and analysed a full-annual-cycle individual-based model where each individual follows the same set of rules in the course of migration under a range of different staging habitat scenarios. Our empirical and theoretical results align well: the loss of staging habitat generates plasticity in migration strategies, with individuals remaining on the staging habitat for longer to obtain food due to a reduction in per capita food availability. The subsequent increasing population density on the staging habitat has knock on effects on population dynamics in the breeding and overwintering stage. Our results demonstrate how environmental change that impacts one energetically costly life history stage in migratory birds can have population dynamics impacts across the entire annual cycle via phenotypic plasticity.

Key words: annual cycle, carrying capacity, density-dependent, individual-based model, life history stage, population regulation, staging area

Introduction

Populations can rapidly respond to environmental change via adaptive phenotypic plasticity, and this allows them to cope with profound environmental impacts (Pigliucci 2001, Piersma and Drent 2003, Coulson et al. 2017). Plasticity modifies interactions between individuals and their environment, ultimately affecting population dynamics (Miner et al. 2005). Migration can be an adaptive plastic strategy in seasonal environments (Lack 1968), that allows individuals to increase reproductive output by avoiding unsuitable ecological conditions (Hedenström 2008, Winkler et al. 2014). Plasticity of migration strategies enables migratory species to respond to environmental changes in multiple ways, such as by altering migratory routes (Sutherland and Crockford 1993, Dolman and Sutherland 1995), timing of migration (Gienapp et al. 2007, Balbontín et al. 2009), and through diet (Parrish 2000). However, the link between the population dynamics of migratory species and migration strategy plasticity is not well understood.

Bird migration is a resource-tracking strategy that aims to optimize a bird's energy budget in the face of fluctuating resources in seasonal environments, and in the face of strong competition (Cox 1968, Alerstam et al. 2003, Somveille et al. 2018, Winger et al. 2019). Migration is energetically costly, so birds build up fat reserves. However, carrying a large energy reserve increases flight costs and can also attract predators (Alerstam and Lindström 1990). One

strategy to minimise such costs is to stop over several times during the journeys between breeding and wintering sites to refuel (Piersma 1987). For individuals to remain in favourable environments across their migration route, they must carefully manage the timing of departure and arrival (Alerstam and Lindström 1990, Alerstam et al. 2003, Winkler et al. 2014). In general, individuals that arrive at breeding grounds earlier have higher reproductive success than those that arrive later (Marra et al. 1998, Norris et al. 2004), and selection favours individuals that minimize the time spent travelling between the wintering and breeding grounds (Lindstrom and Alerstam 1992). Migratory birds usually spend much longer accumulating energy reserves in staging areas than in flying (Hedenström and Alerstam 1997). Therefore, the total time spent on migration is consequently strongly influenced by the quality of, and an individual's behaviour at, staging areas (Hedenström and Alerstam 1997, Erni et al. 2002).

For migratory species, all stages of the annual cycle are closely linked at both the individual- and population-level, through carry-over and density-dependent effects (Newton 2010, Harrison et al. 2011). The individual state in one stage can influence individual performance in subsequent stages, and the change in population size in one stage can influence per capita rates and consequently regulate population size in later stages (Marra et al. 1998, Studds and Marra 2005, Ryan Norris and Marra 2007, Ratikainen et al. 2008). The strategy an individual follows while at the staging area can consequently affect breeding and overwintering performance, and impact population dynamics.

Staging habitat for migratory waterbirds in the Yellow Sea is being lost in significant

quantities, primarily due to land reclamation for infrastructure development and aquaculture (Bi et al. 2012, Murray et al. 2014, Wang et al. 2014). It has been suggested as the main contribution to population declines of migratory birds along the East Asian Australasian Flyway (EAAF) (Amano et al. 2012, Ma et al. 2014, Piersma et al. 2016, Studds et al. 2017), presumably because staging habitat in this system is the stage of the annual cycle where density-dependence is strongest (Sutherland 1996b). Habitat loss in staging habitats can reduce food resources, decrease foraging and fat-accumulation rates of migrants (Baker et al. 2004, Morrision 2006, Verkuil et al. 2012), increase competition and interference in the population, and can have significant consequences for population regulation (Sutherland 1996b, Newton 2010). However, the way in which individuals respond to such changes, as well as the processes and mechanisms that cause population declines, are yet to be generally established. Migratory waterbirds along the EAAF provides a unique system to explore how individuals respond to changes in one life history stage, and how this response would influence their population.

In this study, we first examine trends in the number of waterbirds staging during the boreal spring in response to habitat loss in the Yellow Sea, based on 13 years of census data. Results from our empirical analysis led us to hypothesize that the loss of alternative staging areas around the Yellow Sea has led to an increase in the number of individuals using the small amount of suitable area that remains. The increased number of birds results in an increase in competition for food such that individuals may have to remain longer in the staging habitat in order to acquire sufficient energy to continue their journey. If the average length of time each bird remains within

the staging area has increased, this will be reflected in an apparent increase in numbers observed during surveys.

To investigate the dynamics our hypothesis would generate, we conducted an individual-based modelling (IBM) exercise. IBMs are a powerful tool to address population dynamics questions by simulating individual strategies and interactions (DeAngelis and Grimm 2014, Railsback and Grimm 2019). We built a full annual-cycle model with a stylized migratory population in which individuals follow the same migrating rules in a range of different staging habitat scenarios to (a) identify processes that led to population density changes in the staging habitat, (b) investigate how individual stopover duration changes and how energy accumulation rate changes in the staging habitat, and (c) estimate the influences of per capita rate and the consequences on population dynamics.

Our theoretical results supported our hypothesis constructed from our empirical analyses. We found the loss of staging habitat generates plasticity in migration strategy, with individuals remaining in the staging habitat for longer to obtain food due to a reduction in per capita food availability. The subsequent increasing population density in the staging habitat has knock on effects on breeding and overwintering stage that impact the population dynamics, via modified survival and recruitment rates. We conclude that environmental change effects on one life history stage in migratory birds can consequently have population dynamics impacts across the entire annual cycle via phenotypic plasticity.

Materials and Methods

Empirical data

Our empirical study was conducted in the wetlands in the north of Bohai Bay, between 38°36'-39°13'N and 117°11'-118.22'E, located in the north-west of the Yellow Sea (details of the study area are provided in Appendix S2, Supporting information). Census data of waterbirds were collected at boreal spring between 2004 and 2018 (details of data collection are provided in Appendix S2, Supporting information). All waterbirds were identified to species when possible within each survey. The number of waterbirds by species was recorded, while unidentifiable species that were partially obscured by vegetation or distance from observers were recorded as "unidentified". Those "unidentified" species were included in analyses when examining the total abundance of waterbirds but were not used in other analyses. In addition, the date, the survey site name, and the number of observers for each survey were also recorded in the dataset.

Statistical analyses for bird number trends

The abundance of all waterbirds, the abundance of the ten most common species, and waterbird species richness were analyzed in this study. Survey sites that were surveyed on less than 30% of survey dates were excluded from the analysis.

To estimate total waterbird abundance, we summed the counts of all species i (including unidentified species) observed from all of the survey sites k in each day j, denoting it as N_a.

To pick out the ten most common species, we used two methods: the first one (Frequency Based Method) focused on the frequency of each species i, (f_i) , by using the relative abundance

(Preston 1948, Magurran and Henderson 2011). We calculated the frequency of each species within the whole community each day, and obtained the average value for each species over all the survey days as:

$$f_i = \frac{\sum_j^J \frac{n_{i,j}}{N_j}}{J} \quad (1)$$

Where i is species, J is the total number of observation days, $n_{i,j}$ is the population size of species i on day j, and N_j is the total number of waterbirds counted on day j. Using this approach, the ten most common species were Red Knot *(Calidris canutus),* Black-tailed Godwit (*Limosa limosa*), Kentish Plover (*Charadrius alexandrinus*), Relict Gull (*Larus relictus*), Tundra Swan (*Cygnus columbianus*), Dunlin *(Calidris alpina*), Black-headed Gull (*Larus ridibundus*), Curlew Sandpiper (*Calidris ferruginea*), Pied Avocet (*Recurvirostra avosetta*) and Falcated Duck (*Mareca falcata*). We summed the counts of these ten species observed on each day j and survey site k, denoting it as N_b.

The second approach (Distribution Based Method) to identify common species focused on the species distribution. We used the number of occupied sites to define commonness (Pearman & Weber 2007) and ranked waterbirds by averaging the number of sites occupied by each species each year. The ten most common species were Kentish Plover, Black-headed Gull, Pied Avocet, Black-winged Stilt (*Himantopus himantopus*), Common Shelduck *(Tadorna tadorna*), Eurasian Curlew (*Numenius arquata*), Dunlin, Black-tailed Godwit, Common Tern (*Sterna hirundo*) and Relict Gull. We summed the counts of these ten species observed in each day j on each site k, denoting it as N_c.

To estimate waterbird richness, we calculated the number of species observed each day j and survey site k, excluding unidentified species, denoting it as M.

We calculated effort as the number of observers each day at each site as $E_{j,k}$. We transformed date to Julian date t, and calculated t^2 as visual examination of the data revealed a quadratic relationship. We treated 'year' as a continuous variable in our models, denoting it as T, and we treated 'survey site' as a categorical variable, denoting it as A_j.

Waterbird abundance and richness (including N_a, N_b, N_c *and* M) were used as response variables, $E_{j,k}$, A_j, t, t^2 and T were explanatory variables. The distribution of N_a, N_b, N_c and M was well described as an over-dispersed Poisson (variance greater than mean), so we fitted Generalized Linear model (GLM) with a "quasi-Poisson" error structure in program R. The regression equations were of the form:

$$Y = \exp\left(\alpha_1 + \beta_1 (T) + \beta_2 (E_{j,k}) + \beta_3 (T \times E_{j,k}) + \beta_4 (A_j) + \beta_5 (T \times A_j) + \beta_6 (t) + \beta_7 (t^2) + \varepsilon_1\right), \quad (Y = N_a, N_b, N_c \text{ and } M) \qquad (2)$$

We used the ANOVA command in R to assess the significance of each variable, only retaining variables that remained significant at $p<0.05$.

Model description: Individual based model

The IBM we constructed is a full-annual-cycle model to test how migration strategies would be changed in a range of different staging habitat scenarios. We provide details of the model description in Appendix S3 (supporting information). Our IBM includes three types of habitats in the model landscape, which are wintering habitat, breeding habitat and staging habitat. The

staging habitat split into two habitat types – S1 and S2 area which is equivalent to the relationship between the Bohai Bay and other staging areas in the Yellow Sea. In order to simulate the process of habitat loss in the staging habitat, the size of S1 remained constant across all simulations, while the habitat size of S2 was adjusted (Fig.1). Each grid cell within those three types of habitats contained renewing food resources, while the rest of the landscape did not. Each time step in this model represented one day such that one year was comprised of 365 steps.

We only considered the female component of the population and characterised each individual by identity, age, reproductive status, and energy reserve. The behaviours of each individual included: fly, search for food, eat, orient, mature, reproduce and die (Fig. S2, supporting information). Birds moved one grid cell per time step between the three habitat types, and they lost energy through movement. Birds searched for food by following a random movement rule, towards the grid cell with the highest food value, ate and increased their energy reserves when food was available. When the energy reserve of an individual reached the energy threshold for departure, or the time reached for the latest possible departure arrived, the individual oriented towards the next destination habitat. Individuals whose energy reserves reached the threshold for reproduction can reproduce once each year. Reproduction also consumed individuals' energy reserves. Newborns were set as an initial value of age, reproduction status, and energy reserves. Individuals aged 15, or with zero energy reserves, died and were removed from the population.

The energy reserve of each individual was assumed to be dependent on their initial energy,

energy gained, and energy expended. The expected energy gained from food relied on both population density and food density (Goss-Custard et al. 2002), and there was no randomness of food acquisition in this model. The stopover duration of a bird in the staging habitat was related to the energy requirement for migration, and the rate of energy acquisition (Hedenström and Alerstam 1997). In our model, the conditions for leaving the staging habitat were either the energy reserves exceeded the energy threshold or time passed the time threshold. Details of individual energy reserves and stopover duration are provided in Appendix S3 (supporting information). Parameters and their values are provided in the Table S1, Appendix S1 (supporting information).

Model implementation

The effect of change in habitat size on population size, the number of individuals, individual stopover duration, individual energy reserve and energy accumulation rate during stopover, were examined by comparing the mean value of simulation results from staging habitats of different sizes. Eight scenarios were tested by modifying the size of S2 (Table S2, Appendix S1 in supporting information). The model was run 10 times for each scenario, and for 30 years in each simulation, which was sufficient to converge to stationary dynamics. Results were obtained from year five to year 30 of the simulation (Fig S3, Appendix S1 in supporting information).

Population size during stopover was recorded at equilibrium, and it was the average of daily number of individuals in the staging habitat, during the time started when the first individual arrives and ended when the last individual leaves the staging habitat. The number of individuals

was the number of unique individuals who visited each habitat each year; the number of individuals was recorded in addition to the age and maturity status (juvenile, mature adult, immature adult) of each individual.

Per capita rates of recruitment, reproduction, and survival were calculated. Recruitment rate was the ratio of the number of surviving juveniles to the number of adults in the overwintering stage; reproduction rate was the ratio of the number of juveniles and the number of adults in the breeding stage; survival rate was split into two periods, one including the northward migration (the ratio between the number of adults in the breeding ground and the number of individuals on the first day of each year), and the survival rate during the southward migration (the ratio between the number of individuals on the overwintering ground and the number of individuals on the breeding ground).

Mean individual stopover duration in the S1 area was recorded each year. Individual departure energy was recorded for three types of habitat respectively, as the energy reserves at the last day before the individual left the habitat range. Individual stopover energy reserves was recorded at each time step when the individual stayed in the staging habitat. The energy accumulation rate during stopover was estimated with linear regression (Table S6).

Sensitivity analysis

To examine which parameters had the greatest impact on model outputs and to test the robustness of the model results were to variation in parameter values, we conducted a local sensitivity analysis (methods and results see Appendix S4 in the supporting information).

Results

Trends of bird numbers based on empirical data

A total of 148 waterbird species were recorded and analysed from 811 observation days between 2004 and 2018. Nineteen survey sites were included in the analysis, with four survey sites excluded because they had <30% time coverage.

Waterbird abundance

Analysis of the abundance of all recorded species revealed a significant increase (Fig.2a) in numbers of waterbirds at a rate of 10.96% per year ($F_{1, 809} = 13.08$, $p < 0.001$). Although effort significantly affected abundance estimates ($F_{1, 808} = 10.62$, $p = 0.0012$) with more birds counted as effort increased; there was no interaction between year and effort ($F_{1, 787} = 0.091$, $p = 0.76$). There was a positive relationship between waterbird abundance and Julian date, initially at a rate of 2.7% per day ($F_{1, 789} = 5.75$, $p = 0.017$). This slowed, and became negative with time, as the quadric term of date ($F_{1, 788} = 9.94$, $p = 0.0017$) indicated a parabola of waterbird abundance within the migration season. The average waterbird abundance ($F_{18, 790} = 29.63$, $p < 0.001$), and the annual trend ($F_{18, 769} = 3.45$, $p < 0.001$) differed between survey sites (Fig.3a).

The abundance of ten most common species

In the analysis of the ten most common species identified from the Frequency Based Method, bird numbers (Fig.2b) increased at a rate of 18.49% per year ($F_{1, 803} = 32.29$, $p < 0.001$). Bird numbers were associated with effort ($F_{1, 802} = 7.22$, $p = 0.0073$), but there was no interaction between year and effort ($F_{1, 781}=1.30$, $p=0.26$). There was a quadratic association between Julian

date and the number of birds (linear term, $F_{1, 783} = 16.94$, $p < 0.001$; quadratic term $F_{1, 782} = 21.03$, $p < 0.001$). The bird numbers ($F_{18, 784} = 18.82$, $p < 0.001$) and the annual trend ($F_{18, 763} = 2.64$, $p < 0.001$) differed between survey sites (Fig.3b).

In the analysis of ten most common species identified by the Distribution Based Method, there was also an increasing trend in bird numbers (Fig.2c) at the rate of 9.55% per year ($F_{1, 804} = 74.96$, $p < 0.001$). Bird numbers varied with the level of effort ($F_{1, 803} = 4.03$, $p = 0.045$), but there was no evidence of an interaction between year and effort ($F_{1, 782} = 0.018$, $p = 0.89$). There was also a quadratic association between Julian date and the number of birds (linear term, $F_{1, 784} = 37.52$, $p < 0.001$; quadratic term, $F_{1, 783} = 53.95$, $p < 0.001$). The average number of birds ($F_{18, 785} = 12.09$, $p < 0.001$) and the annual trend ($F_{18, 764} = 3.70$, $p < 0.001$) differed between survey sites (Fig.3c).

Waterbird richness

Waterbird richness significantly increased with time ($F_{1, 805} = 28.20$, $p < 0.001$) having corrected for effort (Fig.2d), with a rate of 7.93% per year. Although effort was not statistically significant on richness ($F_{1, 804} = 0.26$, $p = 0.61$), but a weak interaction between year and effort was observed ($F_{1, 783} = 4.69$, $p = 0.031$). The relationship between richness and Julian date within a year was positive, with an initial rate of increase of 3.76% per day ($F_{1, 785} = 34.50$, $p < 0.001$). This rate slowed as Julian date increased, as the relationship between richness and the quadric term of Julian date was negative ($F_{1, 784} = 63.55$, $p < 0.001$), indicating an arched parabola in each migration season. The waterbird richness ($F_{18, 786} = 29.16$, $p < 0.001$) and yearly trend ($F_{18, 765} =$

4.69, $p < 0.001$) differed among survey sites (Fig.3d).

Population dynamics based on the IBM

As the size of S2 area decreased through eight scenarios in our simulation, there was a significant reduction in the number of individuals staging, and a significant increase in population size in the S1 area. The number of individuals staging decreased from 123.24 (± 0.471) to 82.71 (± 0.623), while the population size in the S1 area increased from 16.45 (± 0.056) to 65.35 (± 0.103) (Fig 4a, Table S3). In each annual cycle stage, the number of mature adults decreased, the number of new-born juveniles in the breeding stage also decreased, while the number of immature adults increased significantly through the eight scenarios (Fig 4b, Table S4). The reproduction rate and the survival rate in the northward migration decreased, the recruitment rate and the survival rate in the southward migration increased (Fig 4c).

Individual stopover duration based on the IBM

Individual's annual stopover duration in the S1 area of the staging habitat increased as the size of S2 decreased. The average stopover duration of individuals staging in the S1 area increased from 45.00 (SE = 0.255) days to 143.70 (SE = 0.190) days in the simulation (Fig 5a, Table S5).

Individual energy reserve based on the IBM

As the size of S2 area decreased, the individual energy accumulation rate when birds remained in the staging habitat decreased from 0.99 (linear regression, SE = 0.0003, $R^2 = 0.50$) to 0.57 (linear regression, SE = 0.0006, $R^2 = 0.50$). Although the energy reserve on the first day

that individuals arrived in the staging habitat increased from 49.38 (SE = 0.036) to 63.66 (SE = 0.060), the departure energy reserve from the staging habitat also decreased from 199.00 (SE = 0.054) to 170.94 (SE = 0.277) (Fig 6b-6c, Table S5-S6). The distribution shifted towards lower energy reserves with fewer individuals having reached the energy threshold for departure from the staging habitat. The energy reserves when individuals left the breeding habitat and wintering habitat increased, both in adults and juveniles (Fig 5d, Table S6).

Discussion

By building an IBM where each individual in the stylized population follows the same set of rules, we provide evidence to support the mechanisms we hypothesized following analysis of empirical data. Specifically, our results are consistent with the loss of staging habitat generating plasticity in migration strategy via increased intraspecific competition during migration stopovers. As the size of the staging area is reduced, individuals need to remain in the staging area for longer to obtain sufficient food to continue on their way due to an increase in the density of competitors. A consequence of this is individuals depart later, and often in poor condition, and fewer individuals make it to the breeding area. However, those that do make it fare well. The dynamics at the staging area can consequently have knock on effects on populations in the overwintering and breeding areas that impact the population dynamics across the annual cycle, by altering the component of the life history where population dynamics are regulated.

Our theoretical and empirical results align well, and are consistent with, patterns reported in the existing literature on the EAAF migration flyway (Wilson et al. 2011, Yang et al. 2011,

Clemens et al. 2016, Piersma et al. 2016, Studds et al. 2017). Habitat loss in the staging habitat reduces the carrying capacity of the flyway, leading to population declines along it. As a consequence, the part of the annual cycle that determines the carrying capacity has been switched from the breeding ground and wintering ground to the staging habitat, as the spatial extent of staging habitat decreases. The staging habitat in the course of northward migration becomes the stage where the strongest density-dependence operates, and the population becomes regulated by the carrying capacity of staging habitat (Fig.6). In contrast, competition on the breeding or wintering habitat is reduced, with processes operating in these areas no longer playing a major role in regulating the population dynamics. As the seasonal compensation as previous studies have suggested (Fretwell 1972, Åström et al. 1996, Boyce et al. 1999, Norris 2005, Ratikainen et al. 2008). The contributions of different life history stages to the population dynamics can consequently vary with the spatial extent of the staging area. Such changes have the potential to alter selection on traits associated with competition for resources, and the entire life history.

In our simulations, population size changes spatio-temporally following habitat loss in the staging habitat. This contrasts the “buffer effect” hypothesis, which proposes that population density changes only in space (Brown 1969, Sutherland 1996a, Gill et al. 2001). Our model shows that in addition to birds becoming more concentrated in the remaining area, a decrease in the extent of the staging area can result in an increase in time spent there, and this can alter the strength of population regulation in either the wintering or breeding areas. How do we reach this conclusions? First, our sensitivity analyses shows that the average time a bird spends in the

staging habitat has a negative effects on population size in the S1 area, and on individual stopover duration (Fig. S4, Appendix S1, supporting information). This indicates that a time threshold in the staging habitat can determine the intensity of competition during stopover determined by a reduction in food resources during this part of the life cycle. Therefore, during the time-limited northward migration, the reduced staging area not only leads to a higher population density in the staging habitat as individual birds stay longer, but also that the high population density is maintained for a longer period of time during this part of the life cycle (Fig.6).

These changes can alter what happens elsewhere in the life cycle. In our model, individuals shift their migration strategy from maximizing migration speed when energy in staging areas is abundant, to maximizing energy reserves when energy becomes scarce. As a consequence, individuals often arrive at the breeding ground late and with low energy reserves, or they fail to reach the breeding grounds. This results in fewer adults arriving in the breeding ground, fewer adults reproducing, and a decline in total reproductive output. However, those individuals that do arrive experience less competition, and have higher per capita recruitment rates. Reproductive status was determined by the level of energy reserves before individuals leave the staging habitat. Individuals with the status of “ready to reproduce” produce offspring immediately when they arrive at the breeding ground before accumulating energy there. The decreased reproductive rate in our results reflects the consequence of increased competition and reduced energy reserves accumulated during stopover, and the increased recruitment rate reflects the consequence of

decreased competition and increased energy reserves accumulated in the breeding and overwintering grounds. Previous studies have reported evidence that support parts of the processes we describe here including: longer staging duration is related to scarce food or high density of competitors (Moore and Yong 1991, Kelly et al. 2002), decreased refuelling rate causes poor departure body mass in the staging area (Baker et al. 2004), limited refuelling time reducing survival rates in the northward migration (Rakhimberdiev et al. 2018), and reductions in total population-level reproductive output but increased per capita reproductive performance (Newton 2006, Desprez et al. 2018).

All of this is due to increased competition in the staging habitat, which reduces per capita food availability, and generates behavioural plasticity in migratory strategy. As individual behaviour changes, so to do the population dynamics. The altered population dynamics, in turn, affect individual behaviour (Miner et al. 2005). This process continues until an equilibrium is reached, when the behaviour settles down to equilibrium, as do the population dynamics. The connection between individual phenotypic plasticity and population dynamics is the result of feedback process across the annual cycle that can result in eco-evolutionary feedbacks are argued by Coulson (2020).

If the part of the annual cycle that determines carrying capacity is not altered by the reduction in size of the staging area, we would expect individual stopover duration to be prolonged as habitat is lost, but the impacts on other stages of the life cycle would be small or non-existence. Evidence from such cases has been reported by Norris et al. (2004), who reported

a decrease in per capita reproductive output, (Holmes et al. 1996) who observed reduced survival rates, and (Marra and Holmes 2001, Tomotani et al. 2018) who reported a period of shortened offspring development and poor physical condition of young. Such processes might explain the non-linearity in our results. It is presumably because, as staging habitat is lost, the system underwent a change in the part of the life cycle where the population is regulated. Therefore, whether the changes to the extent of the staging habitat alters the part of the life cycle where carrying capacity is determined will determine the direction of change in vital rates.

Our study reveals the underlying mechanisms behind a seemingly positive phenomena observed in migratory birds, while also highlighting the crucial role of one life history stage to population dynamics across the whole annual cycle. Migratory birds need to be studied in depth at their breeding, wintering and staging areas to allow us to fully understand their dynamics. Focusing on a single area in detail, with limited data elsewhere, makes dynamical inference challenging, and may also lead researchers to reach erroneous conclusions. In addition, migratory species play a key role for a number of other ecological processes by transporting energy and nutrients between spatially distinct areas, or via their impacts on the ecological networks they form with other species in geographically separated areas (Bauer and Hoye 2014), understanding their dynamics is also important to further extend our knowledge on their roles in ecosystem stability. Although logistically difficult, and costly, our work suggests that studies of migratory species across the entire annual cycle are necessary if we are going to understand the dynamics of species that exhibit one of the most remarkable behaviours in the animal kingdom.

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Author contributions

JL, TC and ZZ conceived the idea, ZZ established the empirical study, JL and TC developed the theoretical framework. JL, WL, XM, and CJH carried out the fieldwork. JL analysed the data, built the model and wrote the manuscript with significant contributions from TC. All authors gave valuable comments to the manuscript.

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Figure legends

Figure 1. Different scenarios for a landscape in which the size of the staging habitat differed along the migration route. B represents the breeding habitat, W represents the wintering habitat, S1 and S2 represent two areas of the staging habitat, and the grey dashed line is the outline of the maximum possible staging habitat area. S1 remained constant in size, but S2 changed. a) S2 was larger than S1, b) S2 was equal in size to S1, c) S2 was smaller than S1, and d) S2 disappeared. The wintering and breeding habitats were the same size in each scenario (more details are provided in the Appendix S3, supporting information).

Figure 2. Waterbird abundance (a), the abundance of ten most common species estimated using the Frequency Based Method (b), the abundance of ten most common species estimated using the Distribution Based Method (c), waterbird richness (d) as a function of year from 2004 to 2018. The bold lines are regression lines between year and waterbird numbers, the filled areas are 95% confidence intervals.

Figure 3. Temporal trends in waterbird abundance (a), the abundance of ten most common species estimated using the Frequency Based Mothed (b), the abundance of ten most common species estimated using the Distribution Based Method (c), waterbird richness (d) in different survey sites. The location of survey sites are shown in Fig.S1, Appendix S1 (supporting information).

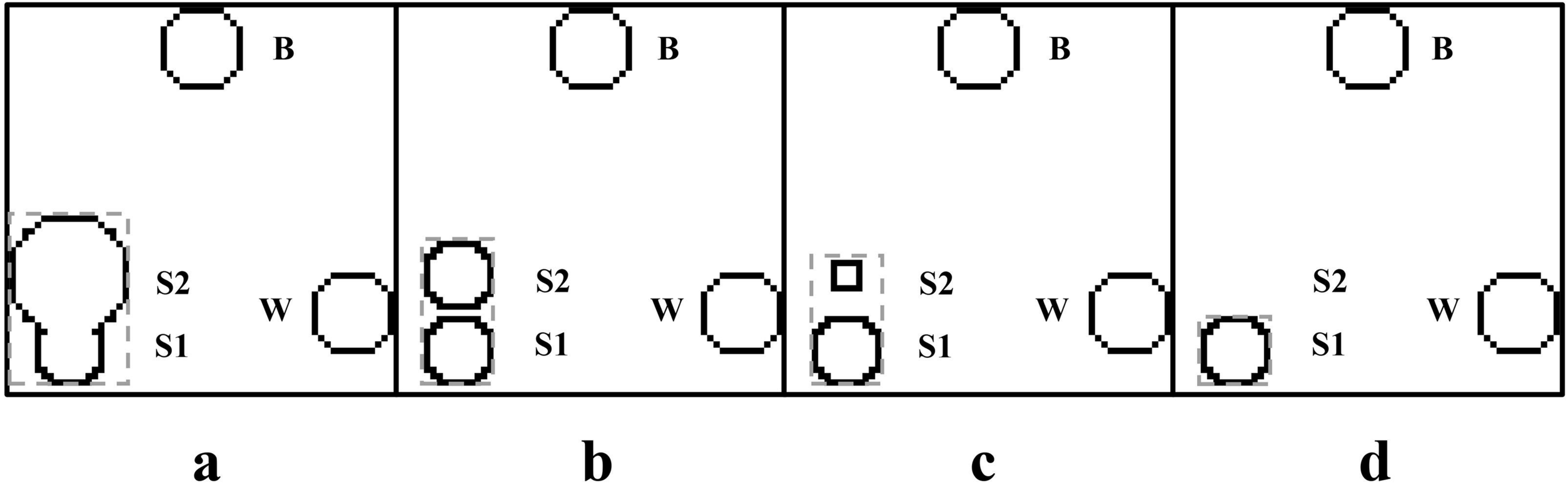
Figure 4. Population dynamics as the size of the staging habitat decreased across the eight scenarios. a) The relationship between population size in S1 area and the number of individuals

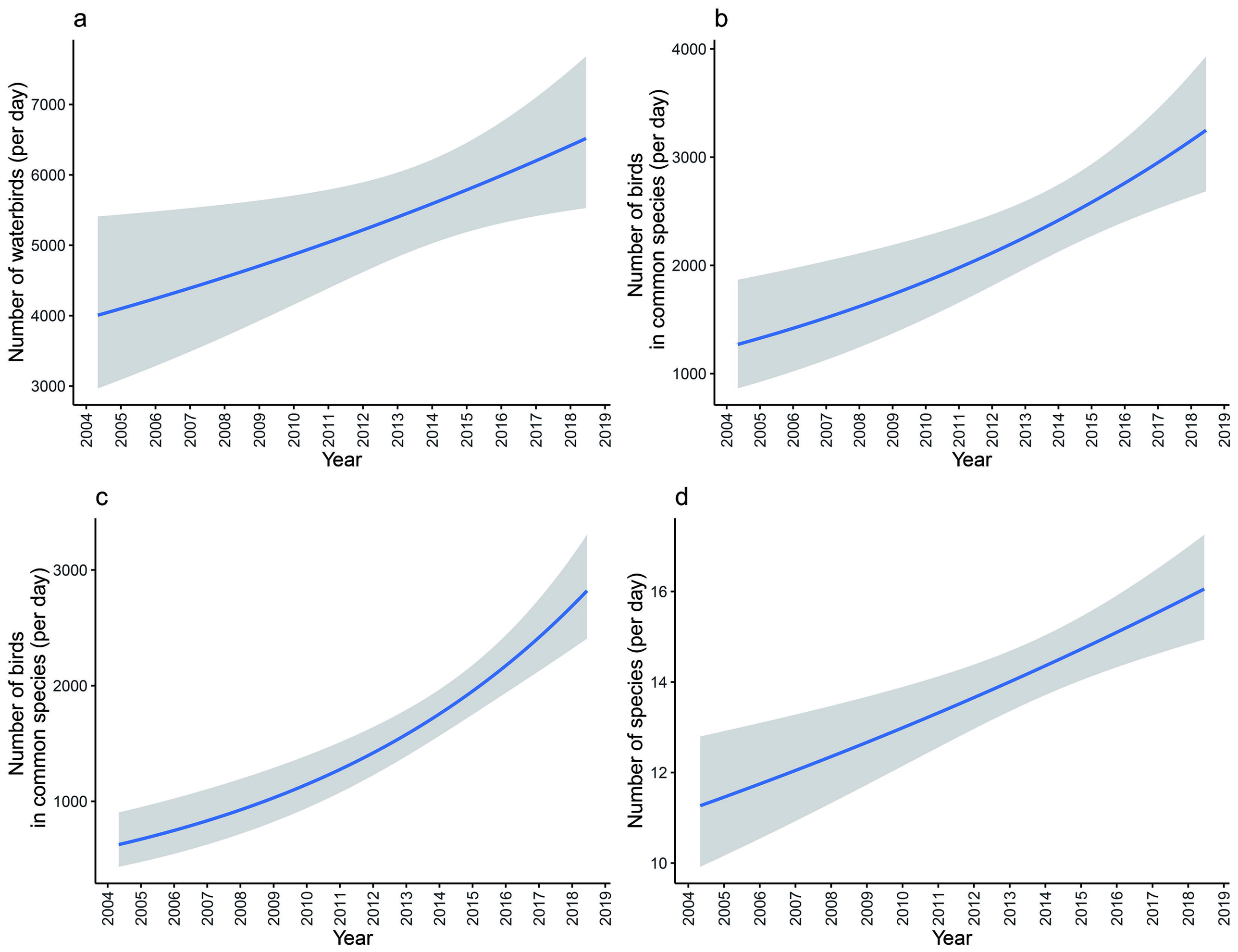
in the staging habitat; b) Number of individuals in different age groups and maturity status in three stages of the annual cycle. (Juveniles are individuals aged zero; mature adults are individuals aged above zero, with high energy reserves before leaving the staging habitat, and can reproduce in the current year; immature adults are individuals aged above zero, with a relatively low level of energy reserves before leaving the staging habitat, and cannot reproduce in the current year.); c) Per capita rates of recruitment, reproduction and survival.

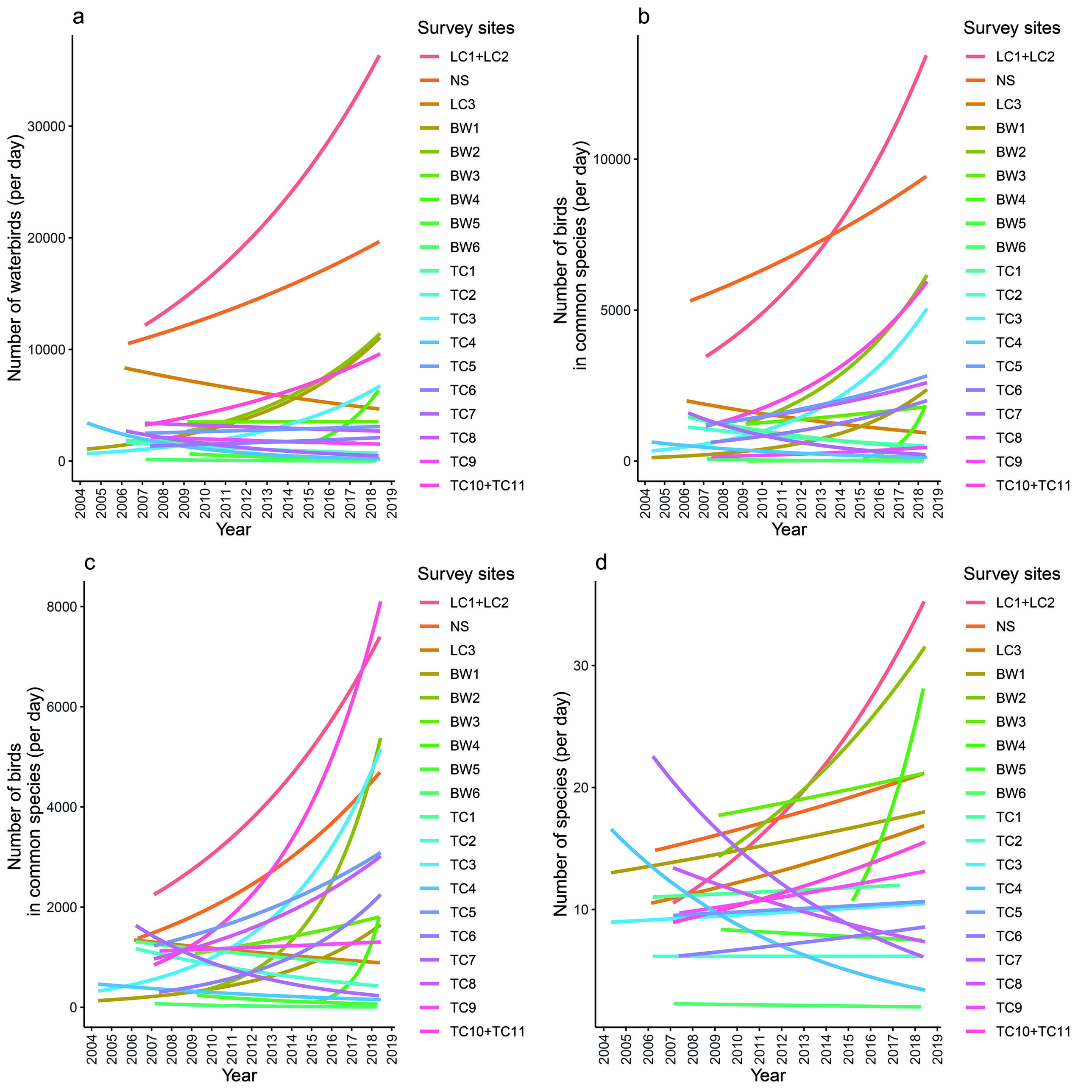
Figure 5. Individual stopover duration and energy reserves. a) Individual annual stopover duration in the S1 area in eight habitat scenarios. Mean values and standard errors are shown. b) The energy accumulation rate when individuals stayed in the staging habitat, calculated from the day the individual arrived, to the last day before the individual departed. c) The individual energy reserve when individuals left the staging habitat. The points and lines show the mean and variance of the population, respectively. The violin plot shows the distribution of the individual energy reserve in the population. Colours represent the eight habitat scenarios, the darker the shade of blue, the smaller the S2 area. d) The adult energy reserve and juvenile energy reserve when individuals left the breeding habitat and wintering habitat. Circles represent the energy reserves when individuals left the breeding habitat, triangles represent energy reserves when individuals left the wintering habitat, yellow represents adults, and grey represents juveniles.

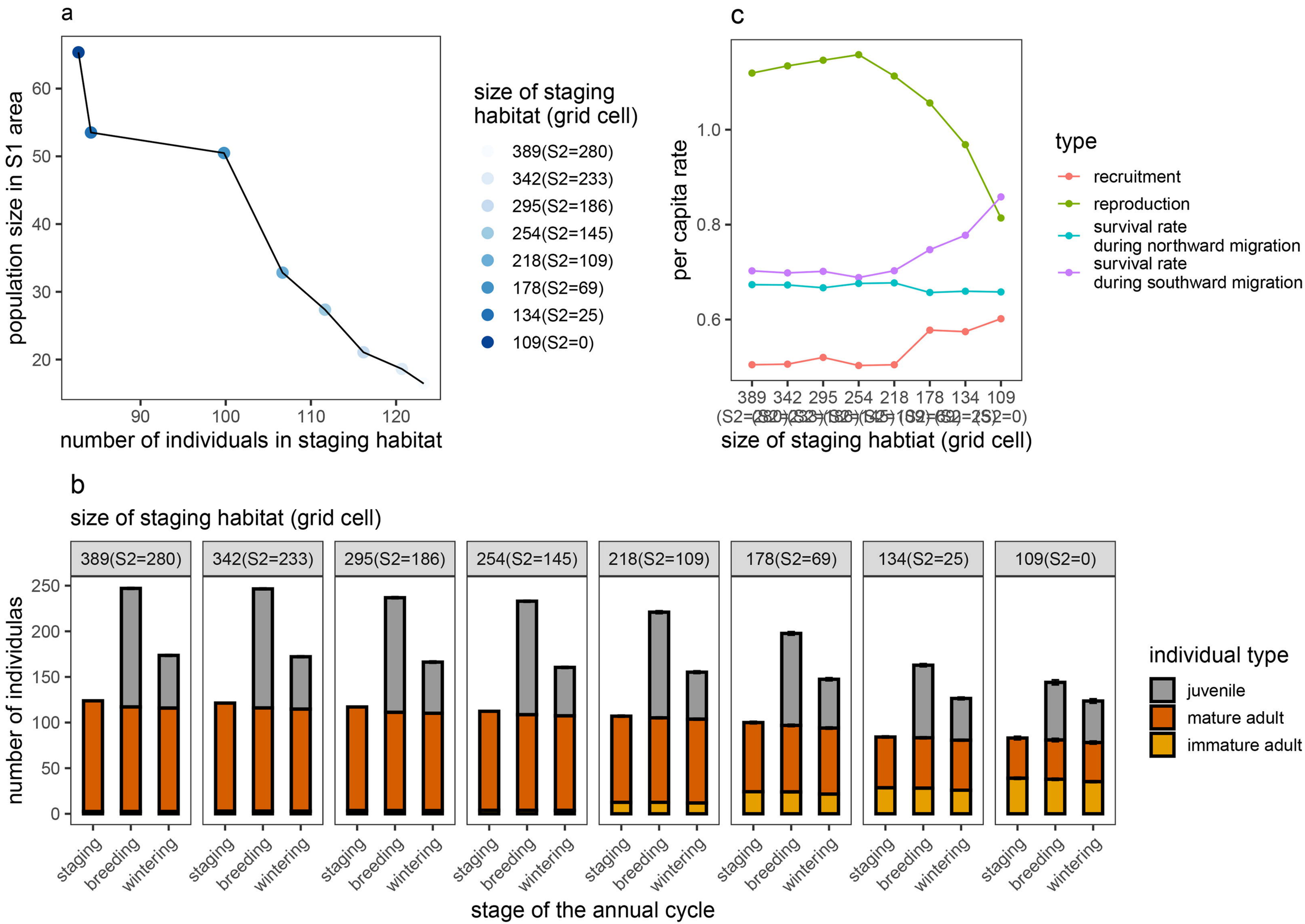
Figure 6. Changes in carrying capacity, vital rates, and population density as a function of the size of the staging habitat. S1 and S2 represents the two areas of the staging habitat, B represents the breeding habitat, and W represents the wintering habitat. The circle sizes represent the

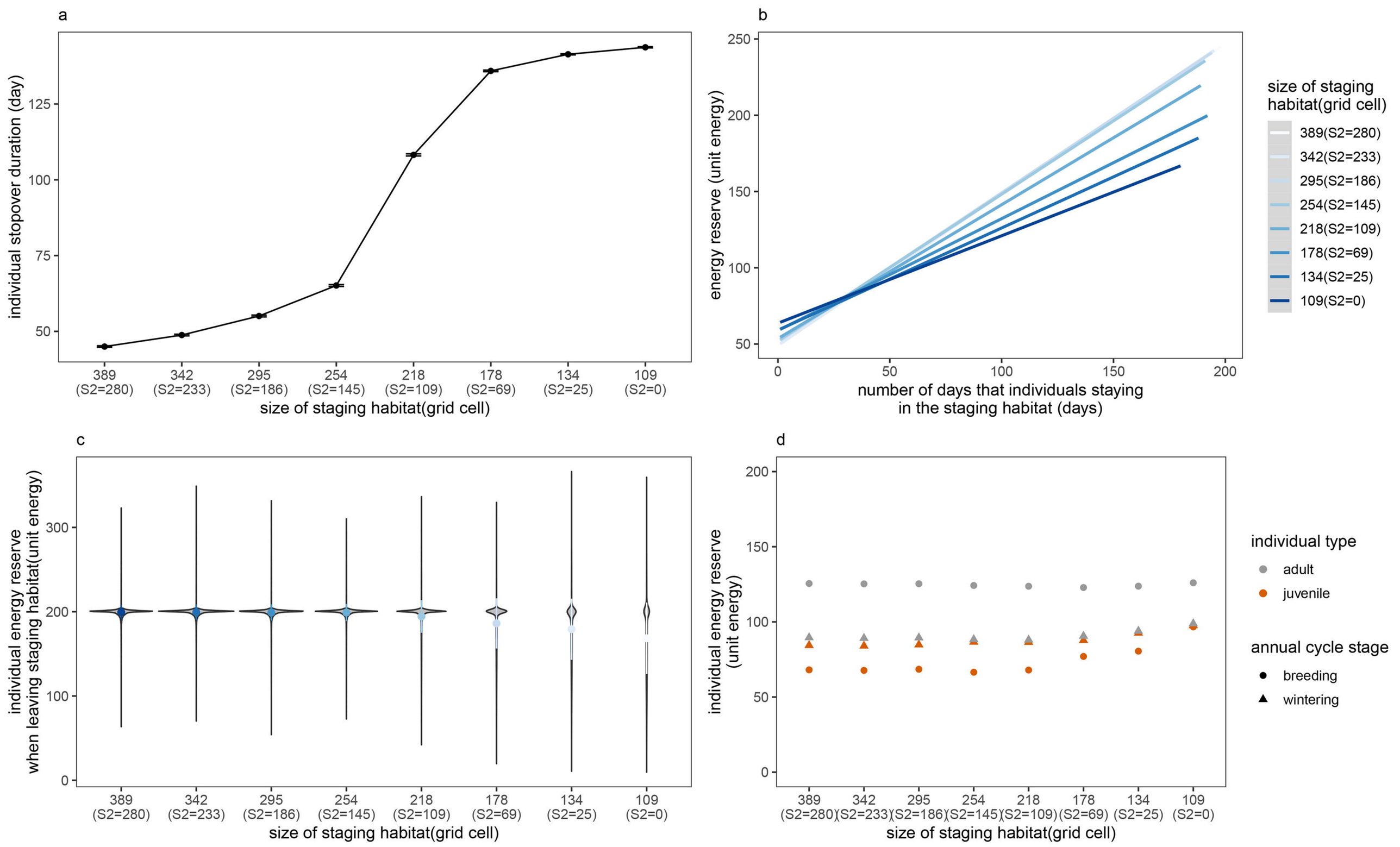
carrying capacity of each habitat, with the gray rectangles representing maximum population size across the annual cycle. In (a) the size of the wintering and breeding habitats determine carrying capacity, while in (b) the size of the staging habitat determines it. In (c) and (d), the line charts shows how population density in the staging areas changes during the period of migration stopover for scenarios (a) and (b) respectively.

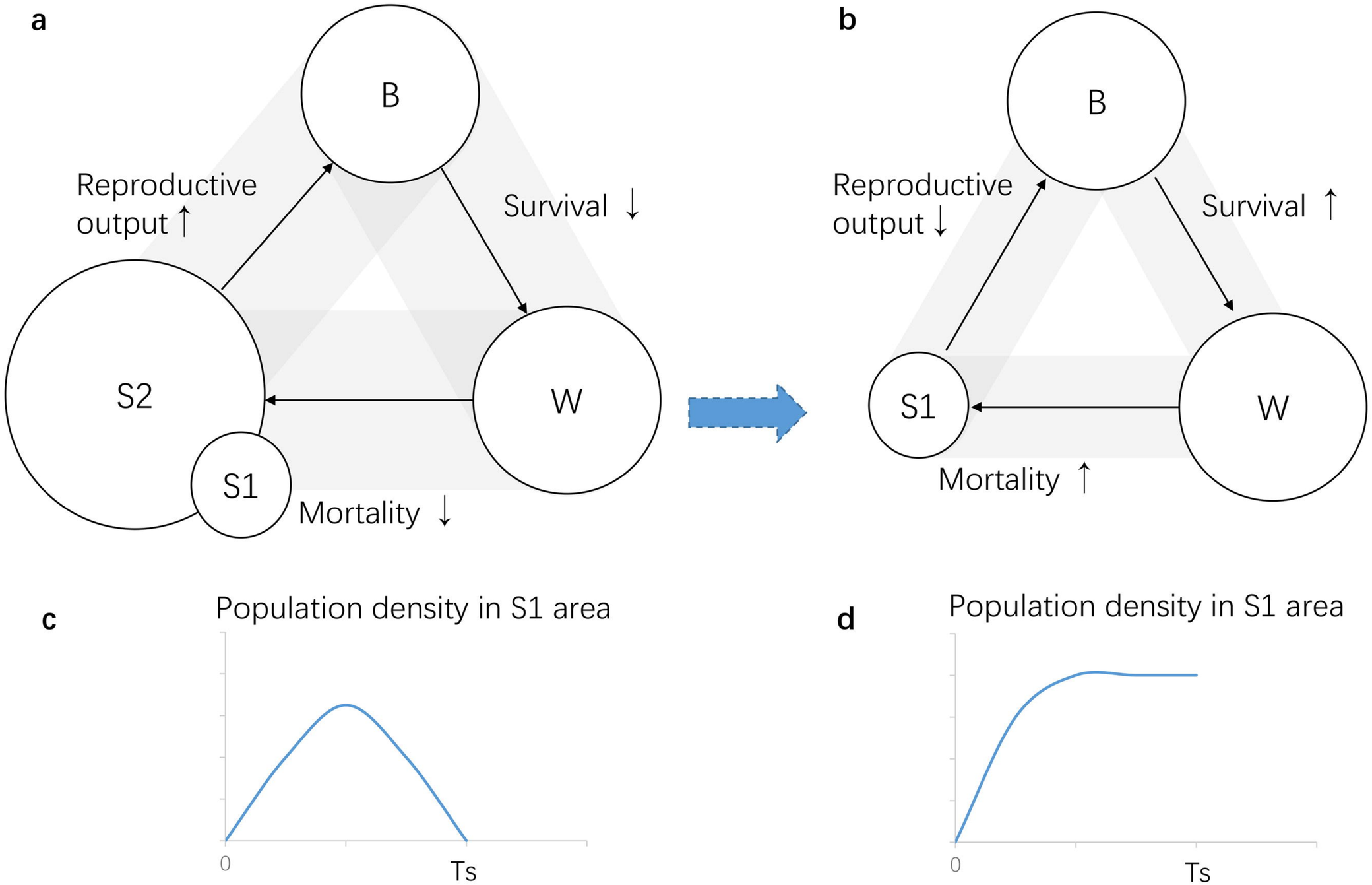

B
S2
S1
W
B
S2
S1
W
B
S2
S1
W
B
S2
S1
W
a
b
c
d


a
Number of waterbirds (per day)
7000
6000
5000
4000
3000
2004
2005
2006
2007
2008
2009
2010
2011
2012
2013
2014
2015
2016
2017
2018
2019
Year
b
Number of birds
in common species (per day)
4000
3000
2000
1000
2004
2005
2006
2007
2008
2009
2010
2011
2012
2013
2014
2015
2016
2017
2018
2019
Year
c
Number of birds
in common species (per day)
3000
2000
1000
2004
2005
2006
2007
2008
2009
2010
2011
2012
2013
2014
2015
2016
2017
2018
2019
Year
d
Number of species (per day)
16
14
12
10
2004
2005
2006
2007
2008
2009
2010
2011
2012
2013
2014
2015
2016
2017
2018
2019
Year


a
Number of waterbirds (per day)
0
10000
20000
30000
Year
2004
2005
2006
2007
2008
2009
2010
2011
2012
2013
2014
2015
2016
2017
2018
2019
Survey sites
LC1+LC2
NS
LC3
BW1
BW2
BW3
BW4
BW5
BW6
TC1
TC2
TC3
TC4
TC5
TC6
TC7
TC8
TC9
TC10+TC11
b
Number of birds
in common species (per day)
0
5000
10000
Year
c
Number of birds
in common species (per day)
0
2000
4000
6000
8000
Year
d
Number of species (per day)
10
20
30
Year


a
population size in S1 area
60
50
40
30
20
90
100
110
120
number of individuals in staging habitat
size of staging habitat (grid cell)
389(S2=280)
342(S2=233)
295(S2=186)
254(S2=145)
218(S2=109)
178(S2=69)
134(S2=25)
109(S2=0)
c
per capita rate
1.0
0.8
0.6
389 342 295 254 218 178 134 109
size of staging habtiat (grid cell)
type
recruitment
reproduction
survival rate during northward migration
survival rate during southward migration
b
size of staging habitat (grid cell)
389(S2=280)
342(S2=233)
295(S2=186)
254(S2=145)
218(S2=109)
178(S2=69)
134(S2=25)
109(S2=0)
number of individulas
250
200
150
100
50
0
staging
breeding
wintering
stage of the annual cycle
individual type
juvenile
mature adult
immature adult


a
individual stopover duration (day)
125
100
75
50
389 (S2=280)
342 (S2=233)
295 (S2=186)
254 (S2=145)
218 (S2=109)
178 (S2=69)
134 (S2=25)
109 (S2=0)
size of staging habitat(grid cell)
b
energy reserve (unit energy)
250
200
150
100
50
0
50
100
150
200
number of days that individuals staying in the staging habitat (days)
size of staging habitat(grid cell)
389(S2=280)
342(S2=233)
295(S2=186)
254(S2=145)
218(S2=109)
178(S2=69)
134(S2=25)
109(S2=0)
c
individual energy reserve when leaving staging habitat(unit energy)
300
200
100
0
389 (S2=280)
342 (S2=233)
295 (S2=186)
254 (S2=145)
218 (S2=109)
178 (S2=69)
134 (S2=25)
109 (S2=0)
size of staging habitat(grid cell)
d
individual energy reserve (unit energy)
200
150
100
50
0
389 (S2=280)
342 (S2=233)
295 (S2=186)
254 (S2=145)
218 (S2=109)
178 (S2=69)
134 (S2=25)
109 (S2=0)
size of staging habitat(grid cell)
individual type
adult
juvenile
annual cycle stage
breeding
wintering


a
B
Reproductive output ↑
Survival ↓
S2
W
S1
Mortality ↓
b
B
Reproductive output ↓
Survival ↑
S1
W
Mortality ↑
c
Population density in S1 area
0
Ts
d
Population density in S1 area
0
Ts