

Research



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Carry-over effects, sequential density dependence and the dynamics of populations in a seasonal environment

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Most animal populations have distinct breeding and non-breeding periods, yet the implications of seasonality on population dynamics are not well understood. Here, we introduce an experimental model system to study the population dynamics of two important consequences of seasonality: sequential density dependence and carry-over effects (COEs). Using a replicated seasonal population of *Drosophila*, we placed individuals at four densities in the non-breeding season and then, among those that survived, placed them to breed at three different densities. We show that COEs arising from variation in non-breeding density negatively impacts individual performance by reducing *per capita* breeding output by 29–77%, implying that non-lethal COEs can have a strong influence on population abundance. We then parametrized a bi-seasonal population model from the experimental results, and show that both sequential density dependence and COEs can stabilize long-term population dynamics and that COEs can reduce population size at low intrinsic rates of growth. Our results have important implications for predicting the successful colonization of new habitats, and for understanding the long-term persistence of seasonal populations in a wide range of taxa, including migratory organisms.

1. Introduction

One of the central problems in population biology, ecology and conservation is to understand temporal fluctuations in population abundance. In seasonal environments, where species have distinct breeding and non-breeding periods, the dynamics of populations can be influenced by density-dependent mechanisms at multiple stages of the annual cycle. Such ‘sequential (or seasonal) density dependence’ occurs when changes in population abundance in one season influence vital rates the following season via density-dependent compensation [1–4]. Although traditional population models often ignore seasonality [5,6], theoretical and empirical work suggest that seasonality can have important consequences for the dynamics of populations, e.g. by either stabilizing or destabilizing population fluctuation [3,7–10].

Another mechanism that could arise from seasonality is a ‘carry-over effect’ (COE), which is an event or process that affects an individual in one season and that continues to affect an individual’s success the following season [11,12]. For example, observational and experimental evidence in both resident and migratory animals suggest that events that induce individual variation in physiological condition during the non-breeding period can explain a significant amount of individual variation in the timing and success of reproduction the following breeding period [13–17]. Despite the fact that several studies on both resident and migratory animals provide evidence that COEs can shape individual fitness [13,15–18], and that theoretical models suggest that they can interact with sequential density dependence to influence population dynamics [4,11,19], there is no empirical evidence that COEs influence *per capita* rates or have an effect at the population level.

Although COEs have been traditionally linked to changes in habitat quality, intraspecific density could also be a mechanism that drives COEs, whereby

individuals that survive at high densities in one season could be in poor physiological condition and have low success the following season [4,12]. With sequential density dependence, high density in the non-breeding season may result in low density the following breeding season, and, consequently, high *per capita* breeding output. If individuals are also experiencing a COE (i.e. are in poor physiological condition as a result of being in high density the previous season), then *per capita* breeding output could be even lower than expected based on sequential density dependence. The interaction between sequential density dependence and COEs can have important consequences on the long-term dynamics of populations, because a delay in the response to density is usually thought to destabilize dynamics [3,6], but if a COE interacts with sequential density dependence to lower *per capita* breeding output, then it is possible that dynamics would become more stable because individuals would not achieve high *per capita* breeding output. Thus, it is critical to separate the effects of sequential density dependence from COE if we want to understand the dynamics of populations in seasonal environments [12].

Here, we develop a model system to investigate the role of both sequential density dependence and COEs in a seasonal population. We simulated seasonality in a non-overlapping population of the common fruitfly (*Drosophila melanogaster*) by manipulating the food medium to prevent females from laying eggs during part of their life cycle and, thus, creating a 'non-breeding season'. Previous research on *Drosophila* has shown that conspecific crowding can affect survival [20] and may reduce energy reserves [21], which could reduce fecundity. Therefore, to test if COEs could be caused by density and influence vital rates the following season, we first placed individuals at low, medium and high densities during the non-breeding season, and then, among those that survived, placed them at low, medium and high densities during the breeding season. Thus, individuals that survived the non-breeding season, and could potentially experience negative COEs, were used to establish all four breeding densities. This full factorial design allowed us to control for sequential density-dependence effects to examine how the variation in non-breeding density produced individual-based, non-lethal residual effects on breeding output the following season, and how this might interact with density dependence during the breeding season. We then parametrized a Ricker model for each season (i.e. one density dependence function for the breeding and one for the non-breeding season) and then modified this model to include COEs, as determined from our experimental results. These models allowed us to investigate how sequential density dependence and COEs influenced long-term population fluctuations.

2. Material and methods

(a) Experimental system

We used *D. melanogaster* from an outbred population collected in Dahomey (now Benin) in 1970, which has since been maintained in cage culture at 25°C. To simulate seasonality in populations with non-overlapping generations, we changed food quality to generate two distinct 'seasons'. During the 'breeding season', flies were allowed to lay eggs for 24 h in a dead yeast–agar–sugar medium (1000 ml H₂O, 100 g sucrose, 50 g Fleischmann's

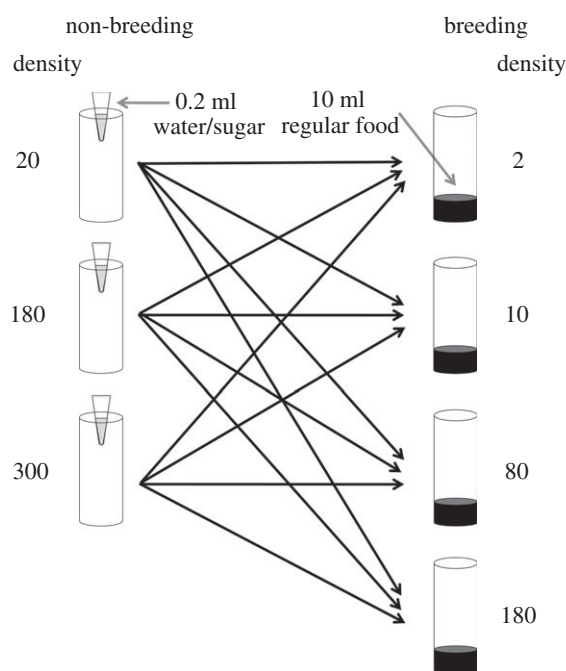


Figure 1. Schematic of the experimental setup to simulate seasonality in *D. melanogaster* populations. Flies spent 4 days in the non-breeding season at different densities (20, 180 and 300 flies per vial, respectively), and those that survived were transferred to vials with protein-rich food to lay eggs for 24 h at different breeding densities (2, 10, 80 and 180 flies per vial).

yeast, 16 g agar, 8 g C₄H₄KNaO₆, 1 g KH₂PO₄, 0.5 g NaCl, 0.5 g MgCl₂, 0.5 g CaCl₂, 0.5 g Fe₂(SO₄)₃), then adults were discarded, and larvae were allowed to mature to adults. During the 'non-breeding season', adults were placed in an empty vial with a pipette tip containing 0.200 ml of 5 per cent water–sugar solution per day, for 4 days, which prevented females from producing eggs [22,23]. Oviposition resumed within less than 12 h when flies were placed back on a protein-rich food [23]. During all experiments, flies were kept at 25°C, 12 L:12 D cycles, and humidity was between 30 and 50 per cent. The same sized vial (28 × 95 mm) was used for both seasons.

(b) Carry-over effect experiment

To separate COEs from sequential density dependence, we first placed flies in the non-breeding season in three different densities and then moved the survivors into four different breeding densities. For the non-breeding season, we used flies between 1 and 6 days old randomly selected from the stock population, lightly anaesthetized with CO₂, and placed them in vials at low, medium and high density (20, 180 and 300, respectively). After 4 days in the non-breeding season, we sexed and moved the remaining flies to vials with regular food to breed at low, medium and high densities (figure 1). For breeding density = 2, we used 20, 20 and 10 replicates for each of the three non-breeding densities (i.e. 20, 180 and 300, respectively). For breeding density = 10, samples sizes for replicates were 26, 20 and 28; for breeding density = 80, the replicates were 10, 10 and 8 and for breeding density = 180, 8, 10 and 10. It is important to note that, because all flies in the non-breeding season were sampled at random from the stock population and received the same amount of food, and because we controlled for breeding density, any potential effect of the non-breeding density on the *per capita* breeding output could only be attributable to non-lethal COEs related to individuals originating from different non-breeding densities.

Table 1. Parameters values estimated with experiment results and used in the breeding, non-breeding and the carry-over effect (COE) from the non-breeding season to the breeding season. Note that in the COE model, the intercept was forced to be 2.24. s.e. represents standard errors and R^2 is the adjusted R^2 .

model	estimate	s.e.	t-value	p-value	R^2
breeding					
intercept	2.24	0.11	21.19	<0.001	0.76
slope	-0.01	7.56×10^{-4}	-14.78	<0.001	
non-breeding					
intercept	-5.68×10^{-2}	1.19×10^{-2}	-4.76	<0.001	0.30
slope	-6.72×10^{-4}	9.17×10^{-5}	-7.33	<0.001	
COE					
slope	-3.10×10^{-3}	4.38×10^{-4}	-7.07	<0.001	0.50

(c) Sequential density dependence and carry-over effect models

To investigate how sequential density dependence and COE could potentially affect long-term population fluctuation, we used a simple Ricker model with season-specific parameters [6,8]. We chose the Ricker model because it has been used in the past to describe laboratory populations of *Drosophila* [24,25]. We let X_t be the population size at the end of the breeding season at generation t , and Y_t be the population size at the end of the non-breeding season at generation t . The population size at the end of the breeding season in generation $t + 1$ was predicted by the equation:

$$X_{t+1} = Y_t e^{r_b(1-Y_t/K_b)}, \quad (2.1)$$

and the population size at the end of the non-breeding season in generation $t + 1$ was predicted by:

$$Y_{t+1} = X_{t+1} e^{r_{nb}(1-X_{t+1}/K_{nb})}, \quad (2.2)$$

where r_b and K_b are the breeding season maximum growth of rate and carrying capacity, respectively, and r_{nb} and K_{nb} are the non-breeding season maximum growth of rate and carrying capacity, respectively. We estimated r_i and K_i ($i \in \{b, nb\}$) for both seasons with two input–output experiments. For the breeding season, flies between 1 and 6 days old from the stock population were sexed, counted and allowed to lay eggs for 24 h in a dead yeast–agar–sugar. Adults were then discarded, and larvae were allowed to mature to adults. Adults were sexed and counted daily until all individuals emerged. For this experiment, we used seven different breeding densities (2, 10, 20, 40, 80, 160 and 320, 50 : 50 sex ratio), with 10 replicates for each density. For the non-breeding season, flies from the stock population were placed in vials with the water and sugar concentration for 4 days at five different densities (20, 100, 180, 240 and 300). Number of replicates for the non-breeding season was 80, 10, 24, 9 and 9, respectively. To estimate $r_b - K_b$ and $r_{nb} - K_{nb}$ from our data, we fit a regression line to $\ln(X_{t+1}/Y_t)$ and $\ln(Y_{t+1}/X_{t+1})$, respectively, as a function of population density in the previous season. The y -intercept is r , and K is the negative intercept divided by the slope [6].

To examine the influence of a COE linked to density in the previous season, we let the *per capita* breeding output be a function of density at the beginning of the previous non-breeding season, which was determined with our COE experiment in a similar way we estimated the parameters for equations (2.1) and (2.2); we fit a regression line to the relationship between *per capita* breeding output $\ln(X_{t+1}/Y_t)$ and density at beginning of the non-breeding season X_t , only for flies that bred at density = 10, and spent the non-breeding density at three different densities (low, medium and high). We forced the intercept to be r_b (as estimated above, table 1), because we sought to isolate the effect of the COE. It is important to use density at the beginning of the non-breeding

season to estimate the strength of COE, because we hypothesized that high non-breeding densities would affect individual condition in the non-breeding season and carry-over to influence vital rates in the next season. We used breeding density = 10 to parameterize the COE model, because flies at this density were effectively released from density dependence effects. We then replaced r_b in (2.1) with the COE regression function (see below).

We used the sequential density-dependence model (equations (2.1) and (2.2)) to first examine the effects of seasonality on population dynamics in the absence of COEs. We projected the population to equilibrium over a range of r_b values using bifurcation plots, which represent a classical way in nonlinear analysis to investigate the emergence of cycles as a function of some parameter. We then used the COE function to understand if and how COE influenced the long-term population dynamics.

(d) Statistical analysis

We investigated the effect of density during the breeding and non-breeding season on the *per capita* breeding output from each treatment with a factorial ANOVA with the density during the breeding and non-breeding season, and their interaction, as explanatory variables. We then used a Tukey honest significance difference (HSD) test to investigate the differences between treatment pairs. All analyses were conducted in R [26].

3. Results

(a) Carry-over effect experiment

There was a significant interaction between non-breeding (which produced the non-lethal COE) and breeding density ($F_{6,158} = 3.47$, $p = 0.003$; figure 2): non-breeding density caused a decrease in *per capita* breeding output at breeding density 2 ($F_{2,53} = 6.81$, $p = 0.002$), 10 ($F_{2,47} = 22.18$, $p < 0.001$), 80 ($F_{2,33} = 20.51$, $p < 0.001$), but not at 180 ($F_{2,25} = 2.37$, $p = 0.11$, figure 2). For flies that bred at breeding density 2, the decrease in reproductive output caused by the non-breeding density was 39 per cent and 51 per cent for medium and high non-breeding density, respectively (figure 2). For breeding density 10, the decrease was 29 and 77 per cent, and for breeding density 80, it was 29 and 54 per cent (figure 2).

(b) Sequential density dependence and carry-over effect models

As expected, our input–output experiment suggested that density in the breeding season decreased *per capita* breeding

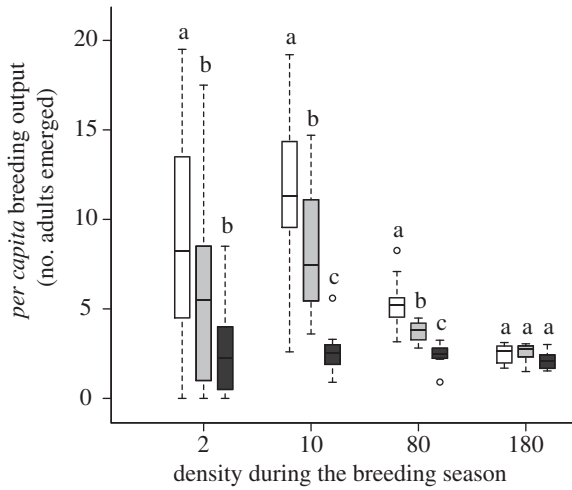


Figure 2. The effect of density during the non-breeding season (white bar, 20; light grey, 180; dark grey, 300) on *per capita* breeding output (number of adults emerged) in adult *D. melanogaster* that bred at different densities. The horizontal line within each box represents the median value, the edges are 25th and 75th percentiles, the whiskers extend to the most extreme data points, and points are potential outliers. Different letters indicate a significant difference between non-breeding densities treatments within a given breeding density according to Tukey HSD test ($p < 0.01$).

output (table 1 and figure 3*a*). In the non-breeding season, density significantly decreased survival (table 1 and figure 3*b*). Non-breeding density had a significant effect on *per capita* breeding output when flies bred at density 10 (table 1 and figure 3*c*). Furthermore, because *per capita* reproductive success was a linear function of non-breeding density (figure 3*c*), the COE can be described by the following function:

$$r_b - aX_t, \quad (2.3)$$

where a is the parameter to be estimated. aX_t represents the magnitude of the COE, and r_b is as defined before. In principle, equation (2.3) can be negative for large values of X_t , but for our analysis parameter estimates were such that this did not occur. In other systems, it may be necessary for equation (2.3) to be non-linear, such that it asymptotes at a minimum growth rate for large values of X_t . Replacing r_b in (2.1) for (2.3) introduces the COE into the Ricker model.

$$X_{t+1} = Y_t e^{(r_b - aX_t)(1 - Y_t/K_b)}. \quad (2.4)$$

Using this model, over one generation, the values predicted by equation (2.4) explained approximately 83 per cent of the variation of the observed values from the experiment ($\beta = 0.82$, s.e. = 0.11, $t = 7.45$, d.f. = 10, $p < 0.001$). To predict population dynamics under influence of COE, we replaced equation (2.1) for equation (2.4) and estimated the number of individuals at the end of the breeding season for several generations. The COE model qualitatively incorporates the interaction between non-breeding and breeding density, as observed in the experiment (figure 2), such that *per capita* rates converge across non-breeding densities as the density in the breeding season increases.

(c) Long-term effects of sequential density dependence and carry-over effect

The bi-seasonal model with only sequential density dependence (equations (2.1) and (2.2)) produced more stable

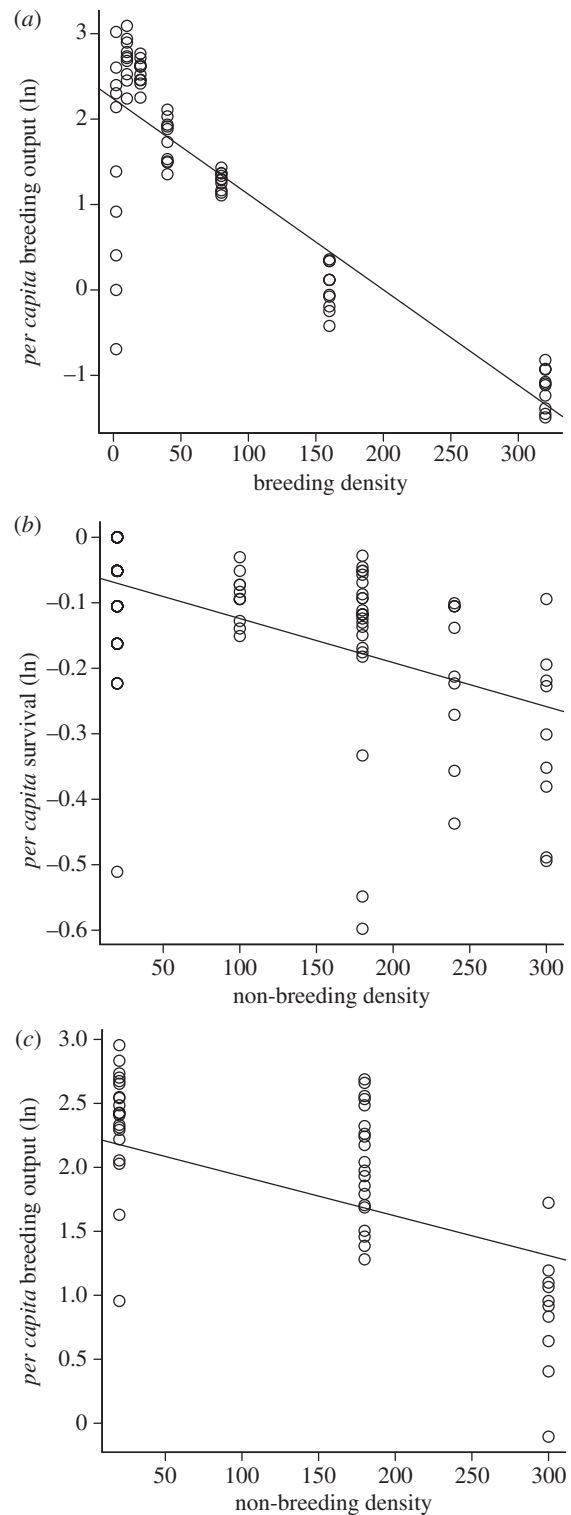


Figure 3. *Per capita* (a) breeding output (log-transformed) as a function of breeding density for *D. melanogaster* that bred at 2, 10, 20, 40, 80, 180 and 320 densities (50 : 50 sex ratio), (b) survival (fraction of adults that survived the non-breeding season) as a function of non-breeding density and (c) breeding output for flies that bred at density = 10, and spent the non-breeding season at 20, 180 and 300 flies per vial. The solid line represents the least square regression that was used to parametrize the bi-seasonal model (equations (2.1) and (2.2) in the text) and the carry-over effect model (equation (2.3)). Parameters are presented in table 1.

dynamics than the simple Ricker model without seasonality by displacing to a larger value the intrinsic growth rate (r_b) at which unstable dynamics are observed (figure 4*a,b*). COEs (equations (2.4) and (2.2)) further stabilized population

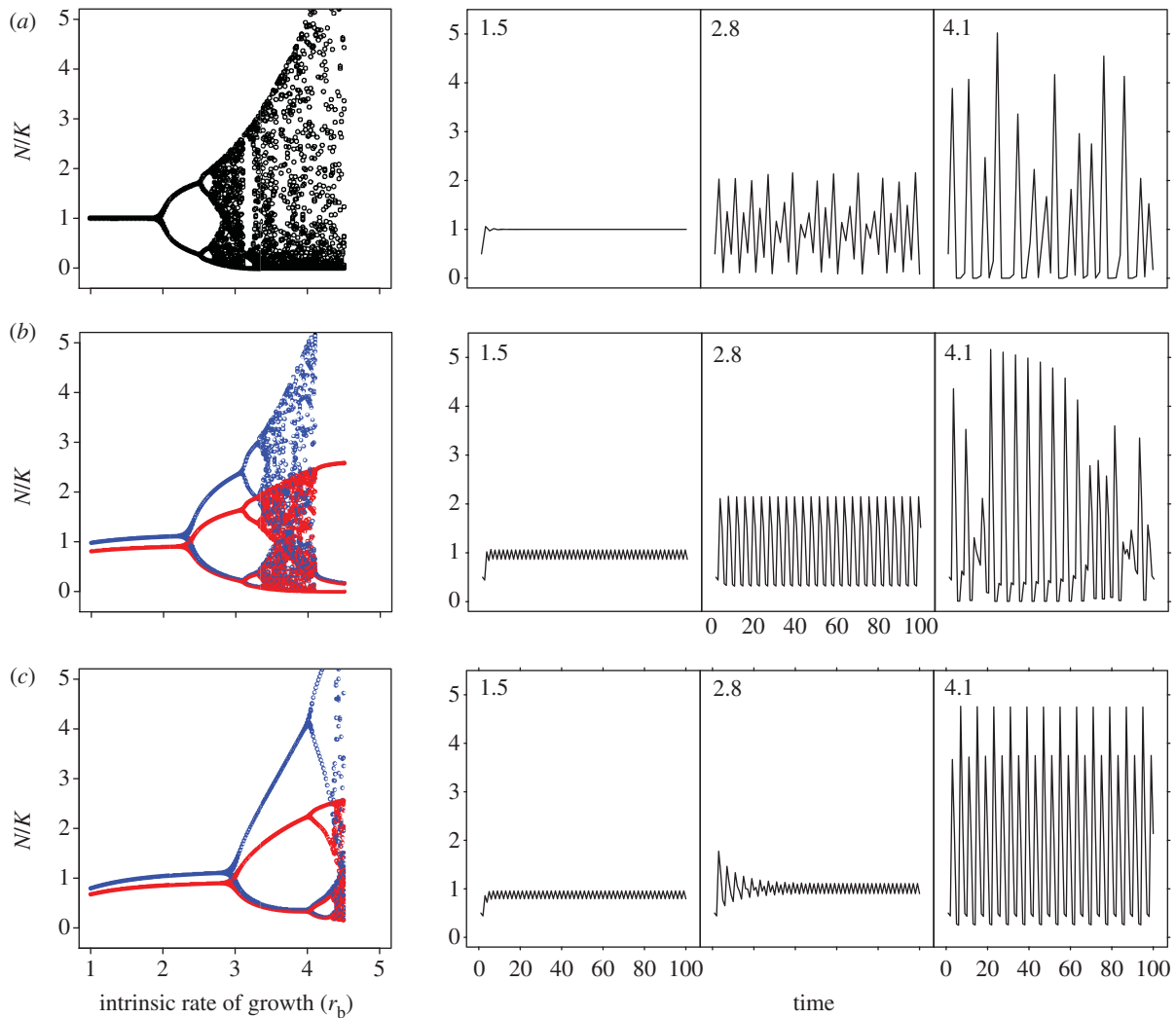


Figure 4. Dynamics of the (a) aseasonal Ricker, and the (b) bi-seasonal Ricker and (c) bi-seasonal with COE Ricker models for a range of r_b values. All three models were parametrized with our experiment results. Bifurcation plots are shown on the left, and the corresponding time series on the right, with r_b values on the top left of each time series. The dark grey (blue) and light grey (red) trajectories on the bifurcation plots indicate population size during the breeding and non-breeding seasons, respectively. n , population size; K , carrying capacity. (Online version in colour.)

dynamics (figure 4c) when compared with dynamics of a seasonal model without COEs (figure 4b).

4. Discussion

Although previous studies have shown that COEs can influence reproductive success at the individual level [14,15,18,27], we provide the first empirical evidence that COEs can have a significant effect on the *per capita* rates of population. In a recent study [17], greater snow geese (*Anser caerulescens atlanticus*) kept in captivity during the migratory period experienced a decrease in reproductive success between 45 and 71 per cent the following season and that this was likely caused by stress. We found that COEs caused by medium and high non-breeding density treatments resulted in a decrease in *per capita* reproductive output between 29 and 77 per cent relative to the low non-breeding density treatment. However, we also found a significant interaction between non-breeding season density and breeding density, suggesting that, as density during the breeding season approached carrying-capacity, decreases in *per capita* breeding output could be attributed almost exclusively to density dependence during the breeding season. Importantly, when

a linear COE term was incorporated into a simple bi-seasonal Ricker model, we also observed this interaction between non-breeding and breeding density. Previous studies have proposed that COE and sequential density dependence are likely to interact to affect population dynamics [12,19]. However, separating these phenomena in the field is extremely challenging. The model system we have developed here provides a key link between theory and empirical data for understanding the dynamics of seasonal populations.

Previous studies have linked COEs with variation in social status [27–30] and habitat quality [15,31]. We provide the first empirical evidence that COEs can be driven by variation in conspecific density during the previous season. Variation in density could be a common mechanism driving COEs in wild populations given that several studies have shown that the condition of individuals within a season may be compromised at high densities [32–35].

Flies that suffered strong COEs did not increase *per capita* breeding output at low breeding densities as expected under a pure sequential density-dependence model. Although density dependence is a fundamental concept in ecological theory, it is not clear why it is usually difficult to detect in natural populations [36–38]. Our results suggest that COEs caused by density in one season could change the relationship between

per capita breeding output and density in the following season, thus masking the positive effects of density dependence. Indeed, our COE model that incorporates the decrease in the maximum growth rate caused by high non-breeding densities showed that cyclic and/or chaotic dynamics that are driven by high intrinsic growth rates are not likely to happen. This stabilizing effect of COE caused by density is expected to be stronger in populations that experience large differences in population size between seasons. Thus, it would be interesting to investigate how processes that enhance population size asymmetries between seasons (such as migratory mortality and hunting) affect the stability of populations.

How can we reconcile our results that suggest stabilizing properties of COEs with the idea that delayed density-dependence mechanisms usually destabilize population dynamics [39–41]? Theoretical studies on maternal effects have shown that when fecundity is negatively affected by past generations, extreme values of population size are not likely to happen, resulting in a more stable system [42]. Similarly, we showed that COE caused by high density in the previous season results in low growth rates, which is likely to stabilize population dynamics. These results taken together suggest that even populations under strong effect of delayed density-dependence mechanism can be stable. It would be interesting to investigate if our results hold true for a wider range of situations, e.g. increasing model complexity and stochasticity [9,41,42]. Nevertheless, we provide evidence that COE can potentially change the long-term dynamic of populations, and this result seems to be a common property of COEs.

Our simulations indicate that population equilibrium size decreased up to 30 per cent at low intrinsic growth rates compared with the value obtained for populations with only sequential density dependence, suggesting that COEs linked to density can potentially reduce population size. Previous studies have also found that COEs can decrease population equilibrium size [4,11], which support the idea that failing to incorporate COEs into population models could potentially overestimate population size.

If COEs are linked to density the previous season, then individuals colonizing new areas may not be 'released' from density-dependent effects, because individual condition could carry-over to compromise performance. This might be particularly important when trying to understand dynamics of metapopulations where dispersal to 'sink' areas can occur more frequently from high density at 'source' areas [43]. Models that do not include COEs might overestimate colonization rates and lead to inaccurate predictions about the effects of dispersal on metapopulation dynamics.

COEs also have important implications for applied biological control. A common strategy to control pests or invasive species is to release potential predators in the field that were reared at high density in the laboratory [44]. COEs might decrease the probability of success of these programmes, because individuals reared at high densities could experience high levels of COEs and thus have lower breeding success even when density dependence is weak. We believe that rearing density should be included as a new variable in quality control of mass rearing.

The lack of positive density-dependent effects at low population size also has important implications for understanding the evolution of migration. Migratory species are generally thought of as arising from partially migratory populations, where migratory and resident individuals share a single site during one period of the annual cycle [45]. Models predict

that the evolution of migration is primarily driven by a release from density dependence [46,47], but COEs linked to density may dampen these positive effects and lower the likelihood of the development of a completely migratory system.

Although we show how density in one season can have non-lethal effects on individuals the following season, the model developed here can also be modified to include COE caused by any other mechanism. For example, if COE is caused by variation in habitat quality during the non-breeding season, then the maximum growth rate could be a function of the habitat quality in the non-breeding season. The relationship between habitat quality in one season and *per capita* breeding in the following season that is needed to parametrize the model could be established experimentally [12]. Thus, our model can be generalized and used for any kind of situation where changes in the growth rate between seasons are expected, although COE caused by habitat quality might not have the same stabilizing force compared with COE caused by density in the previous season.

Previous studies have found that sequential density dependence can have an either stabilizing or destabilizing effect on population dynamics [3,7–10], but our results suggest that sequential density dependence arising from seasonality will result in more stable dynamics compared with an aseasonal model. One possible reason for this might be the way seasonality has been simulated. Previous studies usually treated seasonality as a change in resource availability overtime [48], with individuals having the opportunity to breed in all seasons. By contrast, our experimental system was designed to have two distinct periods, one where individuals breed and the other when they can only die. Because mortality during the non-breeding period is density-dependent, the population by the end of each non-breeding season tends to be more similar across generations. As a consequence, the population at the beginning of each breeding season will also be more similar across generations, creating a more stable system than a system governed exclusively by breeding density dependence, where strong density-dependence feedbacks might dominate. This scenario might be comparable with the results in [3] and [8], where small amounts of seasonality in very productive environments stabilize dynamics. Nevertheless, distinct breeding and non-breeding periods are common in nature, particularly among vertebrates and in almost all temperate breeding species.

Given the importance of density-dependent processes regulating populations [5,6,37] and the role of individual condition mediating fitness within seasons [13], our results are applicable to a wide range of plants and animals. Our study suggests that it is critical to understand how events throughout the annual cycle interact to influence population dynamics, including how non-lethal, condition-mediated COEs that occur at the individual level affect population-level *per capita* rates. These results may help explain why density dependence is usually weak or difficult to detect in natural populations [37], and provide a new mechanism to help explain why populations do not show unstable dynamics that are predicted by simpler population models [5].

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References

- Fretwell SD. 1972 *Populations in a seasonal environment*. Princeton, NJ: Princeton University Press.
- Sutherland WJ. 1996 Predicting the consequences of habitat loss for migratory populations. *Proc. R. Soc. Lond. B* **263**, 1325–1327. (doi:10.1098/rspb.1996.0194)
- Stenseth NC, Viljuginen H, Saitoh T, Hansen TF, Kittilsen MO, Bølviken E, Glöckner F. 2003 Seasonality, density dependence, and population cycles in Hokkaido voles. *Proc. Natl Acad. Sci. USA* **100**, 11478–11483. (doi:10.1073/pnas.1935306100)
- Ratikainen I, Gill J, Gunnarsson T, Sutherland W, Kokko H. 2008 When density dependence is not instantaneous: theoretical developments and management implications. *Ecol. Lett.* **11**, 184–198. (doi:10.1111/j.1461-0248.2007.01122.x)
- May MR. 1974 Biological populations with nonoverlapping generations: stable points, stable cycles, and chaos. *Science* **186**, 645–647. (doi:10.1126/science.186.4164.645)
- Turchin P. 2003 *Complex population dynamics: a theoretical/empirical synthesis*. Princeton, NJ: Princeton University Press.
- Luckinbill L, Fenton M. 1978 Regulation and environmental variability in experimental populations of Protozoa. *Ecology* **59**, 1271–1276. (doi:10.2307/1938241)
- Kot M, Schaffer WM. 1984 The effects of seasonality on discrete models of population growth. *Theor. Popul. Biol.* **26**, 340–360. (doi:10.1016/0040-5809(84)90038-8)
- Aström P, Lundberg S, Lundberg P. 1996 Population dynamics with sequential density dependencies. *Oikos* **75**, 174–181. (doi:10.2307/3546241)
- Dugaw CJ, Hastings A, Preisser EL. 2004 Seasonally limited host supply generates microparasite population cycles. *Bull. Math. Biol.* **66**, 583–594. (doi:10.1016/j.bulm.2003.09.005)
- Norris DR. 2005 Carry-over effects and habitat quality in migratory populations. *Oikos* **109**, 178–186. (doi:10.1111/j.0030-1299.2005.13671.x)
- Harrison XA, Blount JD, Inger R, Norris DR, Bearhop S. 2011 Carry-over effects as drivers of fitness differences in animals. *J. Anim. Ecol.* **80**, 4–18. (doi:10.1111/j.1365-2656.2010.01740.x)
- Festa-Bianchet M. 1998 Condition-dependent reproductive success in big-horn ewes. *Ecol. Lett.* **1**, 91–94. (doi:10.1046/j.1461-0248.1998.00023.x)
- Bearhop S, Hilton GM, Votier SC, Waldron S. 2004 Stable isotope ratios indicate that body condition in migrating passerines is influenced by winter habitat. *Proc. R. Soc. Lond. B* **271**, S215–S218. (doi:10.1098/rsbl.2003.0129)
- Norris DR, Marra PP, Montgomerie R, Kyser TK, Ratcliffe LM. 2004 Reproductive effort molting latitude, and feather color in a migratory songbird. *Science* **306**, 2249–2250. (doi:10.1126/science.1103542)
- Kennedy J, Witthames PR, Nash RDM, Fox CJ. 2008 Is fecundity in plaice (*Pleuronectes platessa* L.) down-regulated in response to reduced food intake during autumn? *J. Fish Biol.* **72**, 78–92. (doi:10.1111/j.1095-8649.2007.01651.x)
- Legagneux P, Fast PLF, Gauthier G, Bêty J. 2012 Manipulating individual state during migration provides evidence for carry-over effects modulated by environmental conditions. *Proc. R. Soc. B* **279**, 876–883. (doi:10.1098/rspb.2011.1351)
- Gill JA, Norris K, Potts PM, Gunnarsson TG, Atkinson PW, Sutherland WJ. 2001 The buffer effect and large-scale population regulation in migratory birds. *Nature* **412**, 436–438. (doi:10.1038/35086568)
- Norris DR, Taylor CM. 2006 Predicting the consequences of carry-over effects for migratory populations. *Biol. Lett.* **2**, 148–151. (doi:10.1098/rsbl.2005.0397)
- Pearl R, Miner JR, Parker SL. 1927 Experimental studies on the duration of life. XI. Density of population and life duration in *Drosophila*. *Am. Nat.* **675**, 289–318. (doi:10.1086/280154)
- Joshi A, Mueller LD. 1997 Adult crowding effects on longevity in *Drosophila melanogaster*: increase in age-independent mortality. *Curr. Sci.* **72**, 255–260.
- Bownes M, Blair M. 1986 The effects of a sugar diet and hormones on the expression of the *Drosophila* yolk protein genes. *J. Insect Physiol.* **32**, 493–501. (doi:10.1016/0022-1910(86)90011-9)
- Terashima J, Takaki K, Sakurai S, Bownes M. 2005 Nutritional status affects 20-hydroxyecdysone concentration and progression of oogenesis in *Drosophila melanogaster*. *J. Endocrinol.* **187**, 69–79. (doi:10.1677/joe.1.06220)
- Mueller LD, Joshi A. 2000 *Stability in model populations*. Princeton, NJ: Princeton University Press.
- Dey S, Joshi A. 2006 Stability via asynchrony in *Drosophila* metapopulations with low migration rates. *Science* **312**, 434–436. (doi:10.1126/science.1125317)
- R Development Core Team. 2009 R: a language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing.
- Pusey A, Williams J, Goodall J. 1997 The influence of dominance rank on the reproductive success of female chimpanzees. *Science* **277**, 828–831. (doi:10.1126/science.277.5327.828)
- Marra PP, Hobson KA, Holmes RT. 1998 Linking winter and summer events in a migratory bird by using stable-carbon isotopes. *Science* **282**, 1884–1886. (doi:10.1126/science.282.5395.1884)
- Catry P, Campos A, Almada V, Cresswell W. 2004 Winter segregation of migrant European robins *Erithacus rubecula* in relation to sex, age and size. *J. Avian Biol.* **35**, 204–209. (doi:10.1111/j.0908-8857.2004.03266.x)
- Lu X, Zheng G. 2007 Dominance-dependent micro-roost use in flock living Tibetan Eared-pheasants. *Ardea* **95**, 225–234.
- Norris DR, Marra PP. 2007 Seasonal interactions, habitat quality and population dynamics in migratory birds. *Condor* **109**, 535–547. (doi:10.1650/8350.1)
- Sherry TW, Holmes RT. 1996 Winter habitat quality, population limitation, and conservation of Neotropical–Nearctic migrant birds. *Ecology* **77**, 36–48. (doi:10.2307/2265652)
- Jenkins TM, Diehl Jr S, Kratz KW, Cooper SD. 1999 Effects of population density on individual growth of brown trout in streams. *Ecology* **80**, 941–956. (doi:10.1890/0012-9658(1999)080[0941:EOPDOI]2.0.CO;2)
- Stewart KM, Bowyer RT, Dick BL, Johnson BK, Kie JG. 2005 Density-dependent effects on physical condition and reproduction in North American elk: an experimental test. *Oecologia* **143**, 85–93. (doi:10.1007/s00442-004-1785-y)
- Burton NHK, Rehlfisch MM, Clark NA, Dodd SG. 2006 Impacts of sudden winter habitat loss on the body condition and survival of redshank *Tringa totanus*. *J. Appl. Ecol.* **43**, 464–473. (doi:10.1111/j.1365-2664.2006.01156.x)
- Brook BW, Bradshaw CJA. 2006 Strength of evidence for density dependence in abundance time series of 1198 species. *Ecology* **87**, 1445–1451. (doi:10.1890/0012-9658(2006)87[1445:SOEFDJ]2.0.CO;2)
- Knape J, de Valpine P. 2012 Are patterns of density dependence in the global population dynamics database driven by uncertainty about population abundance? *Ecol. Lett.* **15**, 17–23. (doi:10.1111/j.1461-0248.2011.01702.x)
- Ziebarth NL, Abbott KC, Ives AR. 2010 Weak population regulation in ecological time series. *Ecol. Lett.* **13**, 21–31. (doi:10.1111/j.1461-0248.2009.01393.x)
- Hutchinson GE. 1948 Circular causal systems in ecology. *Ann. N Y Acad. Sci.* **50**, 221–246. (doi:10.1111/j.1749-6632.1948.tb39854.x)
- Turchin P. 1990 Rarity of density dependence or population regulation with lags? *Nature* **344**, 660–663. (doi:10.1038/344660a0)
- Ginzburg LR, Taneyhill DE. 1994 Population cycles of forest Lepidoptera: a maternal effect hypothesis. *J. Anim. Ecol.* **63**, 79–92. (doi:10.2307/5585)
- Benton TG, Ranta E, Kaitala V, Beckerman AP. 2001 Maternal effects and the stability of population dynamics in noisy environments. *J. Anim. Ecol.* **70**, 590–599. (doi:10.1046/j.1365-2656.2001.00527.x)
- Hanski I. 1999 *Metapopulation ecology*. Oxford, UK: Oxford University Press.
- Chambers DL. 1977 Quality control in mass rearing. *Annu. Rev. Entomol.* **22**, 289–308. (doi:10.1146/annurev.en.22.010177.001445)
- Cohen D. 1967 Optimization of seasonal migratory behavior. *Am. Nat.* **101**, 5–17. (doi:10.1086/282464)
- Lundberg P. 1988 The evolution of partial migration in birds. *Trends Ecol. Evol.* **3**, 172–175. (doi:10.1016/0169-5347(88)90035-3)
- Griswold CK, Taylor CM, Norris DR. 2010 The evolution of migration in a seasonal environment. *Proc. R. Soc. B* **277**, 2711–2720. (doi:10.1098/rspb.2010.0550)
- Holt RD. 2008 Theoretical perspectives on resource pulses. *Ecology* **89**, 671–681. (doi:10.1890/07-0348.1)