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*Biol. Lett.* 2013 **9**, 20130582, published 7 August 2013

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**Cite this article:** Betini GS, Griswold CK, Norris DR. 2013 Density-mediated carry-over effects explain variation in breeding output across time in a seasonal population. *Biol Lett* 9: 20130582.  
<http://dx.doi.org/10.1098/rsbl.2013.0582>

Received: 26 June 2013

Accepted: 15 July 2013

### Subject Areas:

ecology

### Keywords:

seasonality, density-dependence, *Drosophila*

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Electronic supplementary material is available at <http://dx.doi.org/10.1098/rsbl.2013.0582> or via <http://rsbl.royalsocietypublishing.org>.

## Population ecology

# Density-mediated carry-over effects explain variation in breeding output across time in a seasonal population

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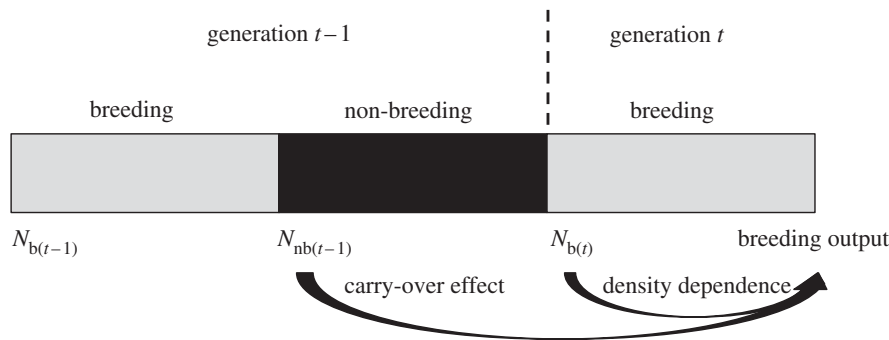
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In seasonal environments, where density dependence can operate throughout the annual cycle, vital rates are typically considered to be a function of the number of individuals at the beginning of each season. However, variation in density in the previous season could also cause surviving individuals to be in poor physiological condition, which could carry over to influence individual success in the following season. We examine this hypothesis using replicated populations of *Drosophila melanogaster*, the common fruitfly, over 23 non-overlapping generations with distinct breeding and non-breeding seasons. We found that the density at the beginning of the non-breeding season negatively affected the fresh weight of individuals that survived the non-breeding season and resulted in a 25% decrease in *per capita* breeding output among those that survived to the next season to breed. At the population level, *per capita* breeding output was best explained by a model that incorporated density at the beginning of the previous non-breeding season (carry-over effect, COE) and density at the beginning of the breeding season. Our results support the idea that density-mediated COEs are critical for understanding population dynamics in seasonal environments.

## 1. Introduction

Negative feedback caused by density is a key mechanism for understanding the dynamics of populations [1]. In seasonal environments, where density dependence can operate in more than one season, it is typically assumed that vital rates within a season are determined by the number of individuals that survive the previous season [2,3]. However, variation in density in one season could also influence the physiological condition of surviving individuals, which could then carry over to influence individual success the following season [4,5]. Such delayed density dependence caused by density-mediated, non-lethal carry-over effects (COEs) could play an important role in understanding the dynamics of populations in a seasonal environment [3,6]. For example, evidence from a model system using *Drosophila* showed that high density at the beginning of the non-breeding season caused lower *per capita* breeding output among the individuals that survived to breed [6], suggesting that variation in density in one season can have non-lethal effects on *per capita* rates in the following season. These results also demonstrated a clear interaction between non-breeding and breeding density, such that *per capita* breeding output was most strongly influenced by non-breeding density only when breeding density was below carrying capacity [6]. Despite experimental evidence demonstrating that density-mediated COEs can influence *per capita* rates, there is no empirical evidence that COEs play an important role in the dynamics of seasonal populations over multiple generations.

Here, we used 45 replicate populations of *Drosophila melanogaster* over 23 non-overlapping generations with distinct breeding and non-breeding seasons



**Figure 1.** Schematic diagram of the population with two distinct breeding and non-breeding seasons.  $N_{nb}$  represents the number of individuals at the beginning of the non-breeding season and  $N_b$  is the number of individuals at the beginning of the breeding season. Traditionally, breeding output is considered to be a function of the number of individuals that started the breeding season at time  $t$  ( $N_{b(t)}$ ) (density dependence arrow). Density-mediated COEs could also influence the number of individuals at time  $t$  by affecting the physiological conditions of individuals through variation in density during the non-breeding season at time  $t - 1$  ( $N_{nb(t-1)}$ ) (COE arrow).

to investigate whether COEs could influence individual condition and explain long-term variation in breeding output. If density at the beginning of the non-breeding season influences the physiological condition of surviving individuals, then high density at that time of the season should result in lower condition among those that survive and reduce *per capita* breeding output in the following season (non-lethal COE; figure 1). Moreover, the decrease in breeding output should be stronger when breeding density is low, which would weaken the strength of density dependence in the breeding season. Thus, we predict that both non-breeding density and an interaction between non-breeding density and breeding density should explain variation in *per capita* breeding output.

## 2. Material and methods

### (a) Experimental system

To simulate seasonality in populations with non-overlapping generations, we used *D. melanogaster* and changed food composition to generate two distinct ‘seasons’ ([6]; see electronic supplementary material). During the ‘breeding season’, flies were allowed to lay eggs for 24 h (day 0) in a dead yeast–sugar medium, after which adults were discarded and larvae were allowed to mature to adults. On day 17, flies were lightly anesthetized with  $\text{CO}_2$ , counted and placed into the non-breeding vials. The ‘non-breeding season’ consisted of an empty vial of the same size as the breeding vials and a pipette tip filled with 0.200 ml of 5% water–sugar solution per day. This medium provided food for the flies but prevented females from producing eggs [6]. After 4 days in the non-breeding season, flies were counted and the cycle was repeated. We randomly removed 5% of the population each time they were moved between seasons to mimic migratory mortality and dispersal. This procedure was repeated for 23 generations in 45 populations (figure 2a).

### (b) Testing for density-mediated carry-over effects

First, to test whether the condition of flies entering the breeding season was influenced by density at the start of the previous non-breeding season, we used a linear mixed model with fresh weight at the beginning of the breeding season as a response variable, density at the beginning of the non-breeding season as an explanatory variable and population as random variable. We also used natal breeding density as an explanatory variable in our model to control for body size, because size in flies is a function of parental density [7]. Fresh weights were obtained

from survivor females ( $n = 356$ ) that were randomly selected at the end of the non-breeding season. We sampled females at generations 15, 16, 21 and 22, from 16 to 25 replicates arbitrarily selected from each generation (see electronic supplementary material). A log-likelihood ratio test (LRT) was used to assess whether density at the beginning of the non-breeding season improved the model compared with a model with only natal breeding density (see electronic supplementary material).

To test whether density at the beginning of the non-breeding season (COE) could affect *per capita* breeding output, we compared three linear mixed effect models with population as random variable in all models, using Akaike’s information criterion [8]. The null model represented the hypothesis that *per capita* breeding output was solely a function of variation in density at the beginning of the breeding season. The COE model also included density at the beginning of the previous non-breeding season to explain *per capita* breeding output, and the interaction model included the interaction between breeding and non-breeding density (figure 1).

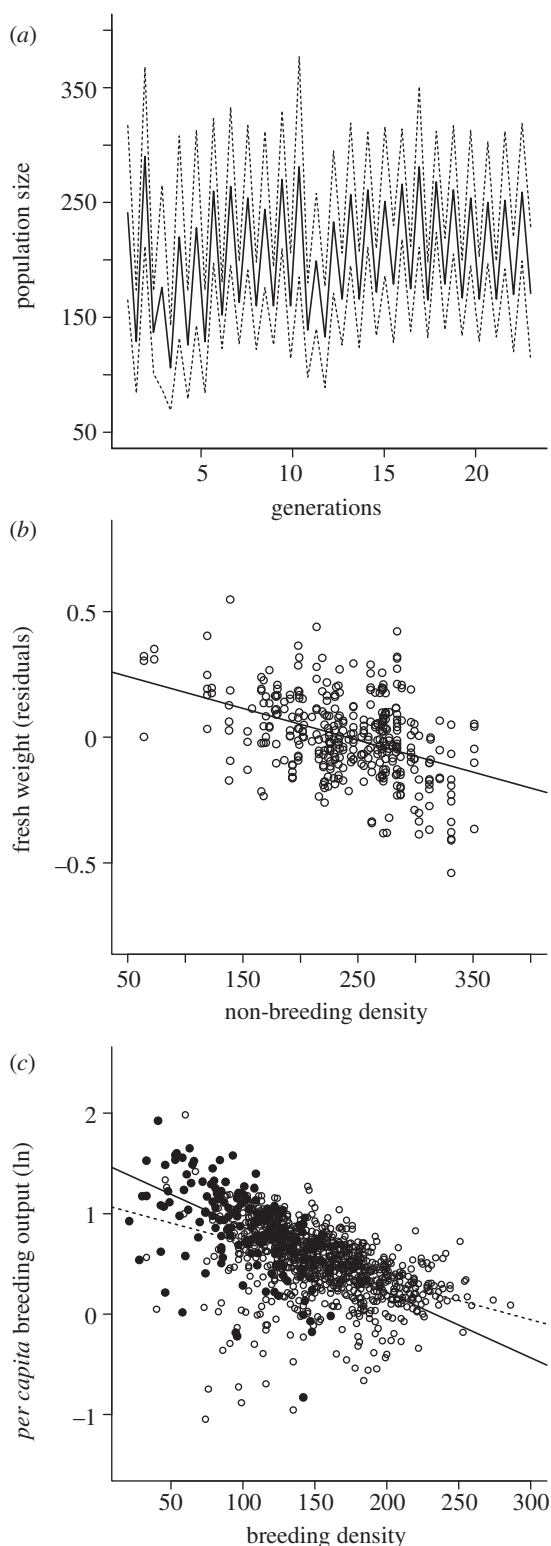
To quantify the change in *per capita* breeding output caused by COE, we divided our dataset into low (less than or equal to 180) or high (greater than 180) non-breeding density and used a Welch two sample  $t$ -test ( $t$ ) to compare *per capita* breeding output for generations with ‘high’ and ‘low’ non-breeding density. This cut-off value was used because the previous experiment showed that COEs influenced *per capita* output when non-breeding density was higher than 180 [6].

*Per capita* breeding output was defined as the ratio of the log of the number of individuals at the end of the breeding season to the number of individuals that started the breeding season (i.e. the number of survivors from the previous non-breeding season less 5%). All variables were standardized before analysis (see electronic supplementary material) and all analyses were performed using R [9].

## 3. Results

At the individual level, fresh weight at the end of the non-breeding season was negatively influenced by density at the beginning of the non-breeding season after controlling for parental breeding density (LRT = 75.13, d.f. = 1,  $p < 0.001$ ; figure 2b and electronic supplementary material, table S1), suggesting that the density affected body condition.

At the population level, the most parsimonious model for explaining *per capita* breeding output included the interaction between density at the beginning of the breeding season and density at the beginning of the previous non-breeding season (AIC weight 1; table 1 and electronic supplementary material,



**Figure 2.** (a) Time series obtained from 23 generations of *Drosophila melanogaster* in a seasonal environment. Solid line denotes mean population size for each generation from 45 replicates. Dotted lines denote  $\pm$  s.d. (b) Density at the beginning of the non-breeding season caused a significant decrease in adult fresh weight. (c) The significant interaction between density at the beginning of the breeding and the previous non-breeding season that predicted *per capita* breeding output (ln) from the time series. Points represent *per capita* breeding output for either low (less than or equal to 180, solid circles) or high (greater than 180, open circles) density at the beginning of the previous non-breeding season. The solid line represents the regression line for low non-breeding density and the dotted line is the regression line for the high non-breeding density.

table S2), suggesting that high non-breeding density (i.e. high COE) not only caused a decrease in breeding output, but also interacted with breeding density to change the strength of density dependence (figure 2c). When populations experienced high density at the beginning of the previous non-breeding season, *per capita* breeding output was on average 25% lower compared with the *per capita* breeding output for low density at the beginning of the previous non-breeding season ( $t = -5.99$ , d.f. = 284.87,  $p < 0.001$ ;  $0.58 \pm 0.37$ , mean  $\pm$  s.d. for high non-breeding density and  $0.80 \pm 0.41$  for low non-breeding density).

## 4. Discussion

Our results provide direct evidence that non-lethal, individual-level effects that carry over across seasons affect long-term population dynamics. At the individual level, we show that the density at the beginning of one season influences the condition of surviving individuals in the following season. At the population level, we show, for the first time, that a model including density-mediated COE improves the ability to explain long-term variation in *per capita* breeding output in a seasonal population, challenging the conventional view that vital rates are mainly a function of number of individuals moving between successive seasons. We also show that density-mediated COEs can weaken the strength of density dependence in the breeding season, suggesting that COEs can influence the long-term stability of populations [6]. Although delayed density dependence has been traditionally investigated between generations [1,3], we showed that, in seasonal environments, density-mediated COE could be a new mechanism that causes lags in population dynamics.

Although our model system is artificial, the results presented here provide important insights into how density-mediated COEs may affect natural populations. For example, lineages characterized by high fecundity and low survival, such as insects and fishes typically realize a high growth rate only at low abundance, resulting in a concave relationship between population growth rate and density. This might explain why density-mediated COEs were strong only for low breeding densities in our experimental system. On the other hand, lineages characterized by low fecundity and high survival, such as in mammals and birds, typically maintain their growth rate for densities close to carrying capacity, resulting in a convex relationship between population growth and density [10]. Thus, it is possible that density-mediated COEs might be strong in mammals and birds for densities close to carrying capacity and more common than in fish and insects.

Our results also have important implications for management and conservation. Most harvesting programmes are based on the idea of compensation, for example mortality during one season would be compensated by higher than usual breeding output in the following season, so that the rate of increase would tend to zero [11]. The compensation hypothesis has strong support from mathematical models [12,13] because one common feature of sequential density-dependence models is (over) compensation. However, if density dependence operates in the non-breeding season to affect individual condition, then density-mediated COE could act to decrease breeding output, challenging the compensation hypothesis.

**Table 1.** Akaike's information criterion model selection parameters and regression coefficients from competing models used to explain *per capita* breeding output in a seasonal population. The null model contained generation and breeding density  $B_{(t)}$ , the COE model included breeding and non-breeding density in the previous season ( $NB_{(t-1)}$ ) and the interaction model contained the interaction between those two variables. LogLik, log-likelihood values for each model;  $AIC_c$ , Akaike's information criterion corrected for small samples;  $\Delta AIC_c$ , difference for model relative to the smallest  $AIC_c$  in the model set;  $W_i$ , Akaike weight is the approximate probability in favour of the given model from the set of models considered.

model	intercept	$B_{(t)}$	$NB_{(t-1)}$	$B_{(t)} \times NB_{(t-1)}$	LogLik	$AIC_c$	$\Delta AIC_c$	$W_i$
null model	$-8.567 \times 10^{-17}$	-0.503			-1287	2542	41	0
COE model	$1.557 \times 10^{-16}$	-0.431	-0.156		-1276	2563	21	0
interaction model	-0.057	-0.439	-0.092	0.109	-1265	2542	0	1

A growing body of work has shown that COEs can be an important driver of fitness [5], indirectly suggesting that COEs influence population abundance. But linking COEs to population dynamics has been difficult because estimates of the strength of COEs are few and challenging to obtain [5]. Here, we provided a simple way to test for density-mediated COEs in a time series. Such a test requires only observations on seasonal abundance and information on breeding output and could be coupled with information on how density influences individual condition. As long as other factors, such as competition and predation that are known to be influenced

by density are also accounted for, this test could be applied to a wide range of field data.

**Acknowledgements.** We thank A. Pardy, J. Pakkala and S. Wood for help in the laboratory and T. Flockhart, J. Fryxell and A. McAdam for valuable comments.

**Data accessibility.** Data were deposited in the Dryad repository: <http://dx.doi.org/10.5061/dryad.nh43g>.

**Funding statement.** Research was supported by Discovery grants from the Natural Sciences and Engineering Research Council of Canada (D.R.N. and C.K.G.), an Early Researcher Award (D.R.N.) and an Ontario Graduate Scholarship (G.S.B.).

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