
Article:

Rodríguez-Muñoz, R., Hopwood, P.E., Slate, J. et al. (2025) Fluctuating selection among years in a wild insect. Evolution, 79 (6). pp. 973-982. ISSN: 0014-3820

https://doi.org/10.1093/evolut/qpaf042

Evolution, 2025, **79(6)**, 973–982
https://doi.org/10.1093/evolut/qpaf042
Advance access publication 27 February 2025
Original Article

OXFORD

Fluctuating selection among years in a wild insect

Rolando Rodríguez-Muñoz[1], Paul E. Hopwood[1], Jon Slate[2], Craig A. Walling[3], Thomas M. Houslay[1], Tom Tregenza[1]

[1]Centre for Ecology & Conservation, University of Exeter, Penryn Campus, Penryn, United Kingdom
[2]School of Biosciences, The University of Sheffield, Sheffield, United Kingdom
[3]Institute of Ecology and Evolution, Ashworth Laboratories, University of Edinburgh, Edinburgh, United Kingdom

Corresponding author: T. Tregenza, Centre for Ecology and Conservation, University of Exeter, Penryn Campus, Penryn TR10 9FE, United Kingdom. Email: T.Tregenza@exeter.ac.uk

Abstract

Temporal or spatial variation in selection has the potential to explain long-standing evolutionary problems such as evolutionary stasis and the maintenance of genetic variation. Long-term field studies of plants and wild vertebrates have provided some insights, but multigenerational measures of selection in wild invertebrates remain scarce. Short-lived ectothermic animals are likely to experience more pronounced environmental variation across generations than longer-lived and endothermic species. As a result, variation in selection may be particularly significant in these groups. Over 10 years, we have monitored an individually tagged population of wild crickets (*Gryllus campestris*) using a network of up to 133 day–night video cameras. The over a million hours of video that we watched allowed us to capture detailed information about naturally and sexually selected traits and life history parameters. Over 10 discrete generations, the population size ranged from 51 to 546 adults. There were also substantial differences among years in the average values of traits including adult emergence date, body size, lifespan, and several behavioral traits. We combined measurements of these traits with individual fitness, measured as the number of adult offspring inferred from genetic-marker-based parentage assignments. This revealed substantial variation in selection gradients across years in several traits, with evidence that in one trait, adult emergence date, selection switched from positive to negative over the years. Our findings suggest that fluctuations in selection gradients are common but complete reversals in the direction of selection may not be very frequent.

Keywords: genetic variation, *Gryllus campestris*, lifespan, mating rate, polyandry, selection gradient

Introduction

Understanding how genetic variation is maintained in the face of selection and genetic drift remains one of the major challenges facing evolutionary biology (Roff, 1997; Charlesworth & Hughes, 1999; Walsh & Lynch, 2018). One potential explanation is that selection acting on specific traits varies in time or space. If this variation includes reversals in the direction of selection, then allelic variation can be maintained through the rescue by positive selection of variants that are under negative selection in other places or at other times (Bell, 2010; Abdul-Rahman et al., 2021; Acker et al., 2021; Johnson et al., 2023; de Villemereuil et al., 2020; Yamamichi et al., 2023). Net selection on a trait can fluctuate between positive and negative because the trait optimum varies as a result of environmental or demographic variation. It can also vary because the mean expression of the trait changes due to maladaptive plasticity, even if the trait optimum does not change (Chevin et al., 2010, 2013; Gauzere et al., 2020). If we consider these possibilities in terms of among-year variation; in the fluctuating optimum scenario (Bell, 2010) the mean value of a trait expressed in the population may be relatively stable across years, but in some years, the balance of trade-offs in the costs and benefits of the trait may mean that higher expression individuals are more fit, and in other years, lower expression individuals have higher fitness. In the maladaptive phenotypic plasticity scenario (Chevin et al., 2010), net selection can fluctuate even if the trait optimum remains constant across years. For instance, in a year with very low food availability, individuals may be smaller than is optimal, creating a selection for larger size. In another year where food is more abundant, the average size may be larger and there may be no directional selection or even selection for smaller size. This will create a fluctuating selection of size even though the optimal size has not changed. In either of these two scenarios, if fluctuations in selection are persistent, it could allow substantial genetic variation to be maintained by selection rather than eroded by it (Bell, 2010; Nevo, 1988).

Meta-analyses of published estimates of selection on traits in wild populations have frequently concluded that the strength of selection varies substantially over the years (Bell, 2010; de Villemereuil et al., 2020; Siepielski et al., 2009). Bell (2010) reviewed long-term studies that provide demographic surveys of genotype frequencies or direct measures of survival and fecundity. His conclusion was that selection often reverses in direction. Taking a more quantitative meta-analytical approach, Siepielski et al. (2009) collated 89 studies, concluding that changes in the direction of selection are frequent. However, the robustness of this conclusion has been questioned because of issues related to sampling error (Morrissey & Hadfield, 2012) and ecological variation in

Received February 12, 2024; revisions received January 28, 2025; accepted February 25, 2025

Associate editor: Yimen Araya-Ajoy; Handling editor: Hélène Morlon

trait repeatability (Dingemanse et al., 2021). de Villemereuil et al., (2020) examined the evidence for temporal variation in selection on breeding date across 39 populations of 21 wild animals. They found substantial variation in the magnitude of selection on laying and parturition date among years, but no evidence that the direction of selection changed among years.

There does not appear to be a clear consensus on how much selection fluctuates in natural populations. What is clear, is that there is an imbalance in the representation of taxa in studies of selection on wild animals, which are dominated by mammals and birds. For example, the study by de Villemereuil et al., (2020) is one of the largest collated datasets of its kind, but only includes birds and mammals. Terrestrial homeotherms represent only a tiny fraction of animal biodiversity. Also, they are frequently at the extreme end of trait distributions (e.g., in size, lifespan, and fecundity) relative to vastly more diverse and numerous invertebrates. This bias may be a major contributor to the current picture we have, which is of relatively weak evidence for fluctuations in the direction of selection. Long-lived birds and mammals are heavily buffered against environmental fluctuations and may have the option of reducing investment in reproduction for long periods. In contrast, annual insects and other short-lived organisms may be unable to avoid the selective effects of within and among-year environmental variation (Ellner & Hairston, 1994).

A handful of invertebrate examples have been included in selection meta-analyses (Kingsolver et al., 2001; Siepielski et al., 2009), these examples are very welcome although they are typically short-term, with only four of the invertebrate studies in those reviews including more than two generations. Also, they depend upon male reproductive success being estimated through counting numbers of mates or matings, despite it being well established that males can trade-off investment in gaining matings against success in sperm competition (e.g., Evans, 2010; Kingsolver et al., 2001; Siepielski et al., 2009; Simmons et al., 2017).

Behavioral traits are particularly interesting in relation to responses to environmental variation because they are potentially extremely plastic. Whether this plasticity means that we do not observe variation in selection resulting from environmental variation is an open question. However, in addition to the taxonomic bias in existing quantifications of selection across years, there has historically been a severe underrepresentation of behavioral traits. There are only three studies of behavioral traits (<1%) in Siepielski et al.'s (2009) influential meta-analysis of the temporal dynamics of phenotypic selection in the wild. These comprise Wagner and Sullivan's (1995) study of sexual selection across 2 and 3 years in two populations the Gulf Coast toad, *Bufo valliceps*; a study of boldness in bighorn sheep (*Ovis canadensis*) (Réale & Festa-Bianchet, 2003) and of number of mating partners in the sand lizard *Lacerta agilis* (Olsson & Madsen, 2001). More studies are beginning to accumulate including studies of the Siberian chipmunk (*Tamias sibiricus)* (Le Cœur et al., 2015) showing that the likelihood of being trapped is a heritable trait that is positively selected in some years and selected against in other years. Similarly, Nicolaus et al. (2016) found that in great tits (*Parus major*) selection on the speed of exploration varied according to local density. A larger-scale study of five populations of the same species (Mouchet et al., 2021) also found that selection on exploratory behavior varied both in space and in time. Studies on European shags (*Phalacrocorax aristotelis*) have identified fluctuating selection on migration vs. residency in juveniles (Ugland et al., 2024) and adults (Acker et al., 2021).

Crickets have become a major laboratory model for studies of sexual selection, revealing females exercising pre- and post-copulatory mate choice among males according to factors such as their size (Simmons, 1987), songs (Simmons & Ritchie, 1996), dominance (Bretman et al., 2006; Rantala & Kortet, 2004), immunocompetence (Tregenza et al., 2006), and relatedness (Bretman et al., 2011). They are also a model system for neurobiology, particularly in relation to phonotaxis (Hedwig, 2006; Poulet & Hedwig, 2005; Sarmiento-Ponce et al., 2021). Our model species is the field cricket *Gryllus campestris*, which has been extensively studied, particularly in relation to male sexually selected traits (Hissmann, 1990; Jacot et al., 2004; Rost & Honegger, 1987; Simmons, 1995) and senescence (Hissmann, 1990; Jacot et al., 2004; Makai et al., 2020; Rodríguez-Muñoz et al., 2019a, 2019b, 2019c, 2019d; Rost & Honegger, 1987; Simmons, 1995). Between 2006 and 2017, we studied a population of field crickets in a meadow in Northern Spain which they have inhabited for at least 50 years. We have collected detailed information about individual traits and assigned parentage to each generation of newly emerging adults from amongst the adults sampled in the previous breeding season (see *Methods* section).

Some of the traits we have measured have obvious potential relationships with fitness, and we have chosen to focus on these. Morrisey and Hadfield (2012) point out that among studies that quantify selection, there is a clear negative relationship between how strong the apparent evidence for variation in selection among years is, and how reliably estimated are the parameters upon which that claim is based. This makes interpreting patterns across studies problematic. It also leads them to argue that identifying the ecological basis of selection is likely to be more informative than studying trait-fitness correlations alone. However, this is a demanding requirement (Milesi et al., 2016). It has been achieved by experimentally intervening to drastically alter selection pressures, as in Losos et al.'s (2006) introduction of a novel predator to six small Bahamian islands. Their manipulation shifted selection on resident *Anolis sagrei* lizards first to longer, and then to shorter legs as *A. sagrei* adopted a more arboreal habit. However, where naturally occurring variation in selection has been studied, it has only been possible to identify the environmental source of selection in a small number of studies where either obvious climatic events have occurred, or unusually dominant sources of selection exist. The classic example is Gibbs and Grant's (1987) study of the finch *Geospiza forth* where directional selection in favor of large adult size under (typical) drought conditions reversed in response to an exceptionally wet climate event. A related example is the observation that in sockeye salmon (*Oncorhynchus nerka*) variation in lake water level caused selective mortality of larger individuals creating variation in selection on body size (Carlson & Quinn, 2007). Climate change has also provided the opportunity to identify relationships between spring temperatures and selection on bird populations such as earlier breeding times in great tits (Husby et al., 2011). Predictable seasonal variation has also been shown to cause fluctuating selection in *Drosophila melanogaster* where generation times of a few weeks occur within seasonally fluctuating temperature regimes (Bergland et al., 2014).

Our population of field crickets lives in an environment that varies substantially among annual generations. This is apparent from the fact that adult population sizes varied between 51 and 546 among years, and the sex ratio (males to females) at adult emergence varied from 0.52 to 1.11 (see Supplementary Table S1). These demographic fluctuations are presumably the result of environmental variation occurring along a very large number of axes including air temperature, availability of sunshine, levels of rainfall, the prevalence of a range of vertebrate and invertebrate predators, and many others, all of which vary in importance through the lifecycle. In the absence of a specific environmental parameter that we could test for a relationship with selection, our aim is to quantify selection across a range of traits. We examine the relationship between the level of expression of these traits and the number of offspring the individual has in the next generation. We do this for eight independent annual generations and determine whether selection (irrespective of its provenance) fluctuates significantly over the years. We use the term "fluctuating selection" to refer to changes in the strength or direction of selection through time following Johnson et al. (2023) and Bonnet and Postma (2018). We are particularly interested in whether there are reversals in the direction of selection on traits among years, and in whether the extent of among-year variation in behavioral traits is comparable or systematically different to that in size and life history traits.

Material and methods

Study system

Our data are the product of WildCrickets, a long-term project monitoring of a wild population of field crickets *G. campestris* in a meadow in northern Spain (Rodríguez-Muñoz et al., 2019d). This species has a single generation each year, with the first adults emerging in mid to late April and the last adults dying in mid-July. Individuals of both sexes build burrows as a refuge from predation and bad weather. Most interesting events occur at burrow mouths (Rost & Honegger, 1987) with individuals spending only short periods moving between them. This lifestyle allows us to record the adult lives of the entire population in great detail, by attaching unique tags to individuals as they become adult and monitoring the population through daily surveys and a network of up to 133 day/night video cameras. During the adult season, males call from their burrows to attract females and both sexes move around the meadow, displacing members of the same sex from burrows and sharing burrows with a single member of the opposite sex (Fisher et al., 2016). We take a DNA sample at adult emergence, allowing us to assign the parentage of each generation from amongst the adults sampled in the previous breeding season. Details on how the meadow is managed every year, our monitoring protocol and parentage assignment to estimate fitness, are available in Rodriguez-Muñoz et al. (2010) and Rodriguez-Muñoz et al. (2019d). The data included in this study cover eight generations within the period 2006–2014 and comprise 364,902 hr of video where a cricket was present under the camera. We did not include the years 2009, 2015, and 2016 as we do not have parentage assignments for offspring from those years.

Parentage assignment

Genetic profiling with microsatellite loci was performed to conduct parentage analysis. Details of this procedure are provided elsewhere (Bretman et al., 2011; Rodríguez-Muñoz et al., 2019d). Briefly, we used between 14 and 21 autosomal loci. Genotyping was performed on an ABI3730 capillary sequencer, using standard protocols (Ball et al., 2010) and scoring was performed using GeneMapper v3.7 software. Parentage analysis was performed using genotype data combined with spatial and mating information in a Bayesian framework using the MasterBayes package (Hadfield et al., 2006; Koch et al., 2008). We estimated the pedigree on a year-by-year basis rather than as a single run, as field crickets are annual, and thus generations are not overlapping. Using the modal parentage assignment for each individual, maternity was assigned to a sampled individual in the population for 1,326 out of 1,568 individuals (0.85 of the population) and paternity to a sampled individual for 1,441 individuals (0.92 of the population). These figures, and our observation that during the breeding season, new adults (that we have not observed having overwintered there) occasionally appear in the meadow, indicate that there is limited immigration into our meadow (see also Bretman et al., 2011). The median confidence of maternity assignments, to known individuals, was 0.985 and in paternity assignments was 0.987.

Description of traits

We explored variation in selection by analyzing the relationship between fitness (response variable) and eight morphological, behavioral, and life history traits (predictors) that could affect reproductive success. We quantified fitness as the number of offspring produced per adult cricket in year t that survived to adulthood in year $t + 1$. This fitness measure has the weakness that it is affected by both parent and offspring traits (as offspring traits will affect their survival to adulthood). This means there is the potential for our selection metrics to be affected by direct and indirect effects of traits on juvenile survival. However, our metric does provide a clear measure of each parent's count of offspring that have the potential to pass their genes on to the next generation. In common with most invertebrates, counting the eggs laid by female crickets living in the wild is an impossible task, as each female injects hundreds of eggs into the soil in multiple locations. Our predictors included adult size, timing of adult emergence and longevity, and traits that quantified the intensity of polygamy, mobility (in relation to both time and space), and effort in attracting mates (for males only).

In our study population, sexual activity does not start until about 5 days after adult emergence (Rodríguez-Muñoz et al., 2019a). We therefore only included data from events that happened at least 5 days post-adult emergence. Adult crickets move frequently between burrows, leaving one burrow and arriving at another a few minutes later (median duration of each visit to a burrow is 1.2 hr). Because we often have more burrows than cameras to monitor them, there are some crickets where we only have a small amount of observational data, perhaps from a single period during the individual's life. Cricket behavior is dependent on the weather (for instance, crickets avoid leaving their burrows when it is raining). It is also affected by the seasonal changes that occur as spring progresses and there are systematic changes in behavior with age (Makai et al., 2020). These effects mean that parameter estimates from crickets where we only have a few hours of observational data are likely to be very unreliable. To avoid the noise from these poorly sampled, but otherwise random individuals masking biologically relevant patterns, we excluded crickets observed for less than 96 hr over their reproductive lives. For those living more than 35 d, at least 24 hr out of the total observation time had to happen after that age, this meant that we had between 787 and 1,374 unique individuals for each trait that we studied. This data exclusion is not based on any characteristics of the crickets, but on chance in relation to their visits to our cameras, so we do not expect it to cause any bias. The number of individuals per year and sex before the removal of poorly sampled crickets is shown in Supplementary Table S2. We quantified our predictors as follows:

Thorax width: Measured from a digital picture using imageJ analysis software (Schneider et al., 2012).

Emergence date: Day of the year when the cricket reached adulthood (counted from day 1 on 1 Jan).

Lifespan: Number of days alive as an adult. For individuals whose death date was not observed, we assume they died on the day after the last available observation.

Mates per day: This is the mean number of unique partners a cricket mated with per day, over its whole life. We calculated it by dividing the total number of different mates an individual was observed mating with by the total number of days of video observation we had of that cricket.

Burrows per day: Mean number of different burrows visited per day. We calculated it by dividing the total number of unique burrows visited when under observation by the total number of days we observed the cricket with a camera.

Distance among burrows: Maximum distance between any two pairs of burrows from among all the burrows where we observed the cricket during its adult life. Moving exposes crickets to the risk of predation and reflects investment in reproduction, as food resources are hyper-abundant through the meadow. To control for the effect of time under observation, we divided the maximum distance by the total number of days the target individual was observed.

Time at burrow: Median duration of time spent on each visit to any burrow, calculated from all the visits recorded for this individual over its life. Usually, sexual activity starts a few days after adult emergence. Hence, for crickets with known emergence date, we excluded all the movements happening before 5 days of age.

Calling effort (males only): We recorded point samples every 2 min during the first 10 min of every hour where we observed the target male with a camera. If we saw the male calling at any of those point samples, we recorded him as calling. We then calculated calling effort as the proportion of hourly observations when the male was calling. As for the previous trait and for the same reason, we excluded the first 5 days after adult emergence. We also excluded all individuals with less than 10 samples in total to avoid very unreliable estimates due to the small sample size.

Statistical analyses

To compare selection among years, we need a common model to describe the relationship between traits and fitness. Inspection of graphs for individual years indicated that the dominant patterns we observed were either no effect or directional selection within years, we therefore estimated linear selection gradients. To test for variation in selection gradients, we followed the common approach of running generalized linear mixed models independently for each trait. To simplify the analyses, we ran separate models for each sex. This approach is also appropriate because it is likely that the same traits are under different selection regimes in males and females; for instance, movements around the meadow have a completely different function in mate-searching males than they do in females (who are surrounded by the singing of potential mates). We did not include age in our analyses because our species has discrete generations; adults emerge in early to mid-spring and die between late spring and early summer within the same year. We ran analyses in R (R Development Core Team, 2020, v. 4.0.3) and RStudio (RStudio Team. 2020, v. 1.3.1093) using the lme4 package (Bates et al., 2015) with a negative binomial family distribution to cope with overdispersion. This approach uses a log-link function by default, which puts fitness on a relative scale equivalent to the traditional approach of dividing by mean fitness and using linear regression (e.g., Bonnet & Postma, 2018; Lande & Arnold, 1983). This means that our fitness gradients can be directly compared with those estimated using earlier methods. We checked whether the output of the models showed overdispersion by using the method proposed by Harrison (2014). Before the analyses, we centered all traits within years (by subtracting the mean of the year) and standardized them across years by dividing by the standard deviation of the centered values. The phenotypic traits of small ectotherms like these crickets are extremely dependent on weather conditions which vary substantially from year to year. A cold winter will affect the size and emergence date of the entire cohort and failing to control for this means that variation is dominated by environmental effects. In view of this, we centered traits within years. For those traits, where means are similar across years, centering within years will not make a relevant difference. However, in the Supplementary information, we have also included the same analyses based on data-centered among years, so that it is possible to compare results between both approaches.

We estimated selection gradients separately for each trait using mixed models with Fitness as the response variable, focal Trait (as described above) as a fixed effect, and Year as a random effect. In each case, our main "random slopes" model allowed both the average Fitness and the effect of the focal Trait on Fitness to vary across each Year in the random effects (i.e., Fitness ~ 1 + Trait + (1 + Trait|Year)). We then ran a second model whereby the effect of the Trait on Fitness was constrained to be the same across all Years, with the "random intercepts" allowing Years to vary only in their average Fitness (i.e., Fitness ~ 1 + Trait + (1|Year)). We then compared these models using a likelihood ratio test to assess whether the contribution of the random slopes term for Year was significant. We followed Visscher (2006) and assumed the difference in log likelihood between the models was distributed as a 50:50 mix of χ^2_1 and χ^2_2. This contribution indicates whether the selection gradient varies over the years. When a gradient varies, it can do so without changing the direction of selection, so that the differences are just in the intensity of selection. Alternatively, variation can involve changes in the direction of selection (reversals); i.e., a trait can have a positive or negative effect on fitness depending on the year. To provide insights into how selection gradients vary among years, we extracted the coefficients per year from the random effects and estimated their confidence intervals by bootstrapping using the bootMer function in *lme4*.

Results

Overall relationships between traits and fitness

Descriptive statistics for traits are provided in Supplementary Table S3. We describe our confidence in results using the language of evidence as suggested by Muff et al. (2022). Five traits showed moderate or greater evidence of having an overall positive or negative effect on fitness across years when all years are considered together (see estimated effects and *p*-values for random intercepts models in Table 1). This included three traits for both sexes (lifespan, mates per day, and time at burrow), one male trait (calling effort), and one female trait (burrows per day) (Figure 1). Longer lifespan was associated with higher fitness in both males and females with our data providing very strong evidence to support this relationship. The rate of mating with new partners measured as mates per day (decoupling it from lifespan) was also associated with higher fitness in both sexes, with this relationship very strongly supported by our data. There were also relationships between how individuals used burrows and their fitness: We found strong support for the observation that crickets of both sexes that spent more time at each burrow they visited had lower fitness. In females, there was also moderate support for a positive association between the mean number of burrows visited per day and their fitness. Time spent at each burrow and number of unique burrows per day are variables that we would expect to be negatively related to one another, and there was a negative correlation between them (Spearman rank correlation, $r_{\text{males}} = -0.29$, $r_{\text{females}} = -0.39$). However, because some crickets move repeatedly between the same burrows on a single day, whereas others remain for a long time in the same burrow and then move to a different one, the two measures do capture independent variation. The sex-limited, sexually selected trait of male calling effort (the number of hours each day during which a male was observed singing to attract a mate) had a very strongly supported positive relationship with fitness. We found no evidence of an overall relationship with fitness in either body size or date of emergence to adulthood. We also found no effect of home-range size measured as the greatest distance between any two burrows visited by an individual (controlling for observational effort) and fitness.

As expected, the overall effect on fitness across years was nearly identical for all traits between models with data-centered within vs. among years (Table 1 and Supplementary Table S4; Figure 1 and Supplementary Figure S1). The only difference was the size of the error estimates for emergence date in males, which were slightly larger when centering among years. This difference is a consequence of the differences in average emergence date among years.

Evidence for fluctuating selection

Of the eight traits that we studied, we found weak to strong evidence for fluctuating selection in four traits (lifespan in both sexes, and emergence date, mates per day and calling effort in males). This fluctuation is identified as the contribution of random slopes to the model fit; see *p*-values for the comparison between the random intercepts and random slopes models, right-hand column in Table 1. Fluctuation was most evident in the relationship between lifespan and fitness which varied between some of the strongest selection we observed in 2008, 2012, and 2013 to relatively weak selection in 2014 (Figure 2). In males, there was strong evidence

Table 1. Selection gradients for behavioral, morphological, and life history traits in a wild population of the field cricket *G. campestris* estimated from two mixed models; either with year as random intercepts or as random slopes. These models are then compared to assess the evidence for among-year fluctuations in selection using likelihood ratio tests as described in the methods, assuming a 50:50 mix of χ^2_1 and χ^2_2. Data were centered within years and standardized across years. Estimate: estimated selection gradient; SE: standard error; Var RE (95% CI): variance of slopes for the random term (year) with 95% CI calculated by bootstrapping using the confint function in *lme4*, for traits with fluctuating slopes only; chi-sq: chi-squared value; *P*: *p*-values corrected according to Visscher (2006) (values smaller than 0.05 in bold).

Trait	Random intercepts			Random slopes				Likelihood ratio test	
	Estimate	SE	*P*	Estimate	SE	*P*	Var RE	Chi-sq	*P*
Females									
Thorax width	−0.015	0.067	0.821	−0.012	0.068	0.860	0.002	0.472	0.641
Emergence date	0.014	0.059	0.806	0.006	0.063	0.923	0.001	0.187	0.788
Lifespan	0.642	0.056	**<0.001**	0.674	0.112	**<0.001**	0.070 (0.001–0.187)	15.695	**<0.001**
Mates per day	0.341	0.087	**<0.001**	0.381	0.099	**<0.001**	0.012	2.450	0.206
Burrows per day	0.201	0.090	**0.025**	0.211	0.114	0.063	0.000	0.021	0.938
Distance burrows	0.116	0.085	0.175	0.135	0.095	0.155	0.004	0.695	0.556
Time at burrow	−0.256	0.090	**0.004**	−0.193	0.111	0.081	0.021	2.089	0.250
Males									
Thorax width	0.063	0.070	0.367	0.062	0.073	0.398	0.004	0.805	0.519
Emergence date	−0.030	0.060	0.620	−0.056	0.092	0.543	0.037 (0.000–0.130)	8.547	**0.009**
Lifespan	0.667	0.057	**<0.001**	0.688	0.086	**<0.001**	0.031 (0.000–0.110)	6.708	**0.022**
Mates per day	0.426	0.076	**<0.001**	0.456	0.115	**<0.001**	0.056 (0.001–0.201)	9.796	**0.005**
Burrows per day	0.134	0.091	0.140	0.285	0.143	**0.046**	0.020	2.640	0.186
Distance burrows	0.076	0.082	0.354	0.164	0.113	0.146	0.021	3.028	0.151
Time at burrow	−0.202	0.065	**0.002**	−0.305	0.120	**0.011**	0.031	2.053	0.255
Lifetime calling effort	0.473	0.070	**<0.001**	0.506	0.098	**<0.001**	0.032 (0.000–0.122)	4.389	0.074

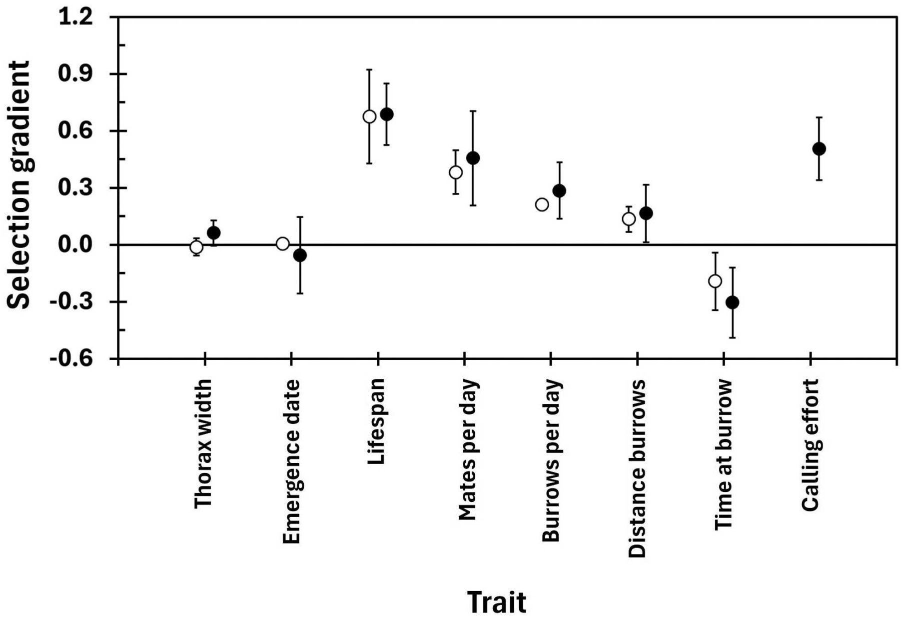

Figure 1. Selection gradients for a number of morphological, life history, and behavioral traits, separated by sex (empty circles, females; filled circles, males). We have estimated the values from a mixed model including year as random effects (intercepts) for data of eight consecutive generations of a wild population of *G. campestris*, using the *lme4* R package (Bates *et al.*, 2015). Trait values are centered within years and standardized across years. Error bars show the SD of the annual coefficients for each trait and sex.

of fluctuating selection on the effect of number of mates per day (Table 1, Figure 1). There was also moderate evidence of fluctuating selection on emergence date in males, despite there being no overall consistent pattern of selection on this trait across years (Table 1). This male trait is particularly interesting in this context because it also shows evidence of reversals in the direction of selection among years (Figure 2). In 2007, 2011, and 2014, early emergence in males was associated with higher fitness whereas in 2008 and 2012, late emerging males had higher fitness, and in 2006, 2010, and 2013, there seems to be no effect of emergence date on fitness.

Centering among years did not change the traits that showed evidence of fluctuating selection gradients based on the likelihood ratio test comparing random intercepts and random slopes models (Table 1 and Supplementary Table S4). Nor did it change the direction and significance of the overall effect of each trait on fitness. When plotting the annual coefficients, centering among years caused a small increase in the confidence intervals. As with the overall effect, this increase in the estimated error was larger for the emergence date of males (Figure 2 and Supplementary Figure S2). The widening of confidence intervals meant they overlap with zero for some of the years that where clearly non-overlapping when based on data-centered within years.

Discussion

Siepielski et al. (2009) considered the existence of fluctuating selection in the context of its potential contribution to evolutionary stasis, i.e., to the maintenance of genetic variation. They concluded that changes in the direction of selection are relatively common but warned that sampling error could impose bias on estimates of variation. Morrissey and Hadfield (2012) showed that after accounting for this bias, re-analysis of the same data revealed that directional selection is the rule and that even if there is fluctuating selection, evidence for reversal is uncommon. The studies used in these analyses were mainly focused on vertebrate morphological traits, with poor representation of other animal groups and other types of traits (Siepielski et al., 2009).

We used a multigenerational dataset from a wild population of an annual field cricket, to analyze morphological, life history, and behavioral traits that we expected to affect fitness. Around half the traits we studied fulfilled that expectation and showed an overall (across years) relationship to fitness. As would be expected, there were particularly strong effects in traits that have been identified as fitness-related in other species because of their role in sexual selection (lifetime calling effort) or lifetime breeding success (lifespan). However, body size, which is frequently associated with phenotypic traits that are correlated with fitness (Blanckenhorn, 2000) including in crickets (Simmons, 1995) does not appear to be under directional selection in our population.

The general pattern we observed was quite a lot of among-year variation in selection gradients. In three of these traits, there was moderate or strong evidence that fluctuations in the strength of selection were greater than we would expect by chance. For male emergence time, these fluctuations meant that selection was positive in some years and negative in others, with average values within years that varied between positive and negative (Figure 1). In addition, in evolutionary terms, eight generations is not very long, and a larger number of years would increase the likelihood of observing reversals, which could contribute to the maintenance of genetic variation even if they are not very common.

Two traits, lifespan and calling effort, were under consistent directional selection across years (Figure 1) but still showed large among-year fluctuations in the strength of selection on them. Consistent directional selection is not inconsistent with fluctuating selection at the genotype level (different genotypes could confer longer lives in different years), but it is interesting to consider what might cause the fluctuations we observe.

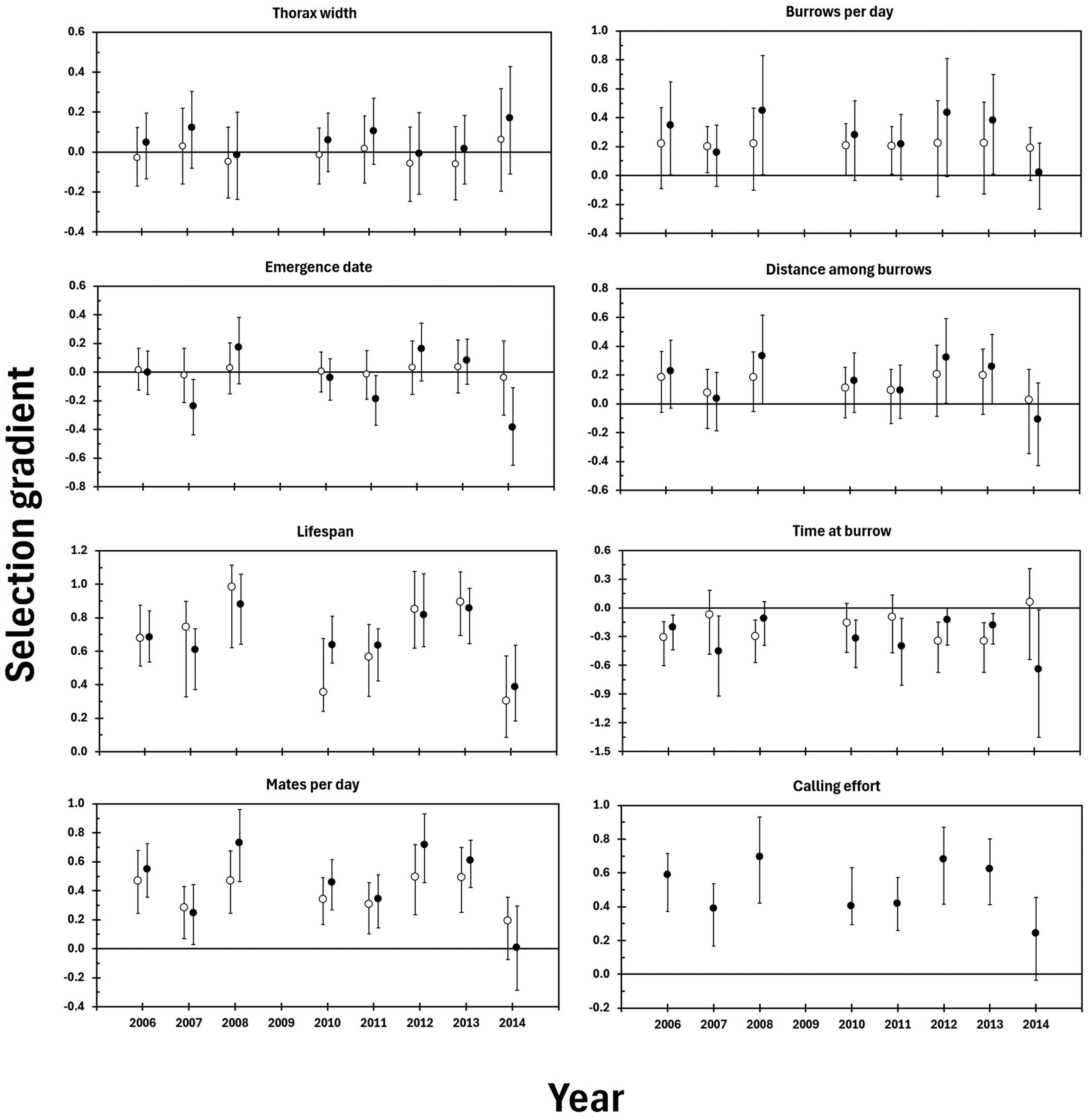

Figure 2. Selection gradients (± 95% CI) for behavioral, morphological, and life history traits in a wild population of *G. campestris* over 8 years, separated by sex (empty circles, females; filled circles, males), with data standardized across years, after centering the data within years. Analyses carried out with the *lme4* package (Bates et al., 2015) using a random slopes mixed model with year as random effects. Values show the slope (selection gradient) coefficient for each year; the confidence intervals have been estimated by bootstrapping.

For lifespan, the observation of consistent directional selection is not surprising since reproduction occurs continuously throughout the breeding season, so dying early will often reduce fitness. Environmental factors that affect how lifespan relates to fitness are likely to vary more among years than environmental effects on selection gradients in some other traits. For example, if there is a cool period toward the end of the breeding season this may mean that crickets are unable to mate and lay eggs during the later part of their lives because the temperature is too low. As a result, in such years longer lifespan will have a weaker relationship with fitness. In contrast, years with a long hot summer may allow crickets to continue to reproduce in later life creating a stronger relationship between lifespan and fitness. The positive relationship between calling effort and fitness we observe fits with our previous studies of a single year of data (Rodríguez-Muñoz et al., 2010) and numerous studies of sexual selection on male signaling (Andersson, 1994). However, as well as males attracting females with song, we frequently observe males arriving at female burrows (Fisher et al., 2015), something reported by other researchers (Hissmann, 1991). This indicates that calling is not essential for mating in males and may be less important in years with a high population density, which may explain variable effects on fitness.

Looking at the overall pattern of selection on traits when all years are combined (Figure 1) the pattern is of traits having similar effects on fitness in both sexes (Figure 1). Although our analysis is not designed to test for differences between the sexes, this finding is noteworthy bearing in mind that our expectation would be that the drivers of reproductive success would be very different between the sexes, particularly in a species with such obvious male secondary sexual traits in the form of male singing and frequent fights between males (Fisher et al., 2019). This is clearly a point that deserves further study.

Our analysis also allows us to compare patterns of variation in selection in behavior as opposed to other types of traits. We hypothesized that the potential plasticity of behavioral traits could allow adaptive phenotypic plasticity to reduce fluctuations in their effects on fitness. We predicted that this might contrast with morphological or life history traits, which may be more tightly linked to environmental parameters. However, our data do not seem to support this: there is no obvious difference in how variable selection is on the three types of traits.

As discussed in our introduction, identifying the environmental variation that drives fluctuating patterns of selection is a very tall order. Eight generations are not enough to determine which of the numerous axes of environmental variation among years are causes of variation in selection. The only way to find out would be to either continue the study for a great deal longer or it might be possible to conduct an experiment in the wild manipulating parameters hypothesized to drive the observed variation. There was 1 year in our study (2008) when the population size was substantially lower than in other years (Supplementary Table S1). This year was not associated with any obvious climatic or other environmental anomaly of the sort that Gibbs and Grant (1987) identified as responsible for a change in the direction of selection in the beak size of their finches. Although selection on the number of burrows that males visited in 2008 was more negative that year than in other years, it is clear from Figure 1 that it is not the case that this year alone is responsible for fluctuations that we observe. Because all physiological and behavioral processes in ectotherms are dependent on body temperature, it is tempting to speculate that climatic variation will be important in driving variation in selection. However, whether there are times of the year when annual insects are particularly sensitive to some specific aspect of climate, whether it is the average level of a parameter like temperature or the minimum or maximum, and whether effects are direct or result from impacts on parasites or predators and so-on are all question that remain to be studied.

A key issue in evaluating our results is around the relationship between the strength of selection and whether reversals in the direction of selection are evolutionarily important. It is difficult to determine whether the modest evidence for a reversal in selection on the emergence date that we find (Table 1, Figure 2) is important in maintaining variation in this trait. Analyzing the heritability of each trait and the change in breeding values from 1 year to the next as in Bonnet and Postma (2018) might help. Although ours is by far the largest and most ambitious study of selection in a wild invertebrate to date, we have only studied eight generations with limited power within years due to sample size. Within this snapshot, we find substantial evidence that selection varies in strength over the years, but only modest evidence for a reversal in selection in one trait. Whether one views this as evidence that fluctuating selection makes an important contribution to the maintenance of genetic variation depends on temporal and spatial patterns of environmental variation and population size and structure. These parameters are very demanding to estimate in wild invertebrates. How frequent reversals in selection need to be to maintain variation, and how common they are in the small animals that dominate most ecosystems is likely to remain the subject of speculation for some time to come.

Supplementary material

Supplementary material is available online at *Evolution*.

Data availability

Data are available in Dryad at DOI: 10.5061/dryad.rxwdbrvm8.

Author contributions

R.R.M., T.T., and J.S. designed the research; R.R.M., P.H., and T.T. performed the research on the living crickets; J.S. and C.W. created the pedigree; R.R.M., T.H., and C.W. performed all statistical analyses; and R.R.M. and T.T. wrote the article with input from all other authors.

Funding

This work was supported by the Natural Environment Research Council (NERC); standard grants: NE/E005403/1, NE/H02364X/1, NE/L003635/1, NE/R000328/1, NE/V000772/1 and the Leverhulme Trust.

Conflict of interest: We have no competing interests.

Acknowledgments

We thank Luis Rodríguez and María del Carmen Muñoz for unconditional support, providing access to facilities including the WildCrickets study meadow. The following people contributed to video processing and data recording: David Fisher, Ian Skicko, Xing P. Liu, Thor Veen, Carlos Rodríguez del Valle, Alan Rees, Sophie Haugland Pedersen, Hannah Hudson, Jasmine Jenkin, Lauren Morse, Emma Rogan, Emelia Hiorns, Sarah Callow, Jamie Barnes, Chloe Mnatzaganian, Olivia Pearson, Adèle James, Robin Brown, Chris Shipway, Luke Meadows, and Peter Efstratiou. We also thank www.icode.co.uk for modifications to their i-catcher video recording package to optimize it for behavioral research. Erik Postma, Timothée Bonnet, and Alastair Wilson advised on statistical analysis and interpretation of our results. Three anonymous reviewers and Joel Pick provided numerous constructive comments that helped to improve the manuscript.

References

Abdul-Rahman, F., Tranchina, D., & Gresham, D. (2021). Fluctuating environments maintain genetic diversity through neutral fitness effects and balancing selection. *Molecular Biology and Evolution*, *38*(10), 4362–4375. https://doi.org/10.1093/molbev/msab173

Acker, P., Burthe, S. J., Newell, M. A., Grist, H., Gunn, C., Harris, M. P., Payo-Payo, A., Swann, R., Wanless, S., Daunt, F., & Reid, J. M. (2021). Episodes of opposing survival and reproductive selection cause strong fluctuating selection on seasonal migration versus residence. *Proceedings of the Royal Society of London, Series B: Biological Sciences*, *288*(1951), 20210404. https://doi.org/10.1098/rspb.2021.0404

Andersson, M. (1994). *Sexual selection*. Princeton University Press.

Ball, A. D., Stapley, J., Dawson, D. A., Birkhead, T. R., Burke, T., & Slate, J. (2010). A comparison of SNPs and microsatellites as linkage mapping markers: Lessons from the zebra finch (*Taeniopygia guttata*). *BMC Genomics*, *11*, 218. https://doi.org/10.1186/1471-2164-11-218

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, *67*(1), 48.

Bell, G. (2010). Fluctuating selection: the perpetual renewal of adaptation in variable environments. *Philosophical Transactions of the Royal Society of London, Series B: Biological Sciences*, *365*(1537), 87–97. https://doi.org/10.1098/rstb.2009.0150

Bergland, A. O., Behrman, E. L., O'Brien, K. R., Schmidt, P. S., & Petrov, D. A. (2014). Genomic evidence of rapid and stable adaptive oscillations over seasonal time scales in drosophila. *PLoS Genetics*, *10*(11), e1004775. https://doi.org/10.1371/journal.pgen.1004775

Blanckenhorn, W. U. (2000). The evolution of body size: What keeps organisms small? *The Quarterly Review of Biology*, *75*(4), 385–407. https://doi.org/10.1086/393620

Bonnet, T., & Postma, E. (2018). Fluctuating selection and its (elusive) evolutionary consequences in a wild rodent population. *Journal of Evolutionary Biology*, *31*(4), 572–586. https://doi.org/10.1111/jeb.13246

Bretman, A., Rodriguez-Muñoz, R., & Tregenza, T. (2006). Male dominance determines female egg laying rate in crickets. *Biology Letters*, *2*(3), 409–411. https://doi.org/10.1098/rsbl.2006.0493

Bretman, A., Rodríguez-Muñoz, R., Walling, C., Slate, J., & Tregenza, T. (2011). Fine-scale population structure, inbreeding risk and avoidance in a wild insect population. *Molecular Ecology*, *20*(14), 3045–3055. https://doi.org/10.1111/j.1365-294X.2011.05140.x

Carlson, S. M., & Quinn, T. P. (2007). Ten years of varying lake level and selection on size-at-maturity in sockeye salmon. *Ecology*, *88*(10), 2620–2629. https://doi.org/10.1890/06-1171.1

Charlesworth, B., & Hughes, K. A. (1999). The maintenance of genetic variation in life-history traits. In R. S. Singh, & C. B. Crimbas, (Eds.), *Evolutionary genetics: from molecules to morphology* (pp. 369–392). Cambridge University Press.

Chevin, L. -M., Collins, S., & Lefèvre, F. (2013). Phenotypic plasticity and evolutionary demographic responses to climate change: Taking theory out to the field. *Functional Ecology*, *27*(4), 967–979. https://doi.org/10.1111/j.1365-2435.2012.02043.x

Chevin, L. -M., Lande, R., & Mace, G. M. (2010). Adaptation, plasticity, and extinction in a changing environment: Towards a predictive theory. *PLoS Biology*, *8*(4), e1000357. https://doi.org/10.1371/journal.pbio.1000357

de Villemereuil, P., Charmantier, A., Arlt, D., Bize, P., Brekke, P., Brouwer, L., Cockburn, A., Côté, S. D., Dobson, F. S., Evans, S. R., Festa-Bianchet, M., Gamelon, M., Hamel, S., Hegelbach, J., Jerstad, K., Kempenaers, B., Kruuk, L. E. B., Kumpula, J., Kvalnes, T., & Chevin, L. M. (2020). Fluctuating optimum and temporally variable selection on breeding date in birds and mammals. *Proceedings of the National Academy of Sciences of the United States of America*, *117*, 31969.

Dingemanse, N. J., Araya-Ajoy, Y. G., & Westneat, D. F. (2021). Most published selection gradients are underestimated: Why this is and how to fix it. *Evolution*, *75*(4), 806–818. https://doi.org/10.1111/evo.14198

Ellner, S., & Hairston, N. G. J. (1994). Role of overlapping generations in maintaining genetic variation in a fluctuating environment. *The American Naturalist*, *143*, 403–417.

Evans, J. P. (2010). Quantitative genetic evidence that males trade attractiveness for ejaculate quality in guppies. *Proceedings of the Royal Society of London, Series B: Biological Sciences*, *277*(1697), 3195–3201. https://doi.org/10.1098/rspb.2010.0826

Fisher, D. N., James, A., Rodriguez-Muñoz, R., & Tregenza, T. (2015). Behaviour in captivity predicts some aspects of natural behaviour, but not others, in a wild cricket population. *Proceedings of the Royal Society of London, Series B: Biological Sciences*, *282*(1809), 20150708. https://doi.org/10.1098/rspb.2015.0708

Fisher, D. N., Rodríguez-Muñoz, R., & Tregenza, T. (2016). Wild cricket social networks show stability across generations. *BMC Evolutionary Biology*, *16*(1). https://doi.org/10.1186/s12862-016-0726-9

Fisher, D. N., Rodríguez-Muñoz, R., & Tregenza, T. (2019). Dynamic networks of fighting and mating in a wild cricket population. *Animal Behaviour*, *155*, 179–188. https://doi.org/10.1016/j.anbehav.2019.05.026

Gauzere, J., Teuf, B., Davi, H., Chevin, L. -M., Caignard, T., Leys, B., Delzon, S., Ronce, O., & Chuine, I. (2020). Where is the optimum? Predicting the variation of selection along climatic gradients and the adaptive value of plasticity. A case study on tree phenology. *Evolution Letters*, *4*(2), 109–123. https://doi.org/10.1002/evl3.160

Gibbs, H. L., & Grant, P. R. (1987). Oscillating selection on Darwin's finches. *Nature*, *327*(6122), 511–513. https://doi.org/10.1038/327511a0

Hadfield, J. D., Richardson, D. S., & Burke, T. (2006). Towards unbiased parentage assignment: Combining genetic, behavioural and spatial data in a Bayesian framework. *Molecular Ecology*, *15*(12), 3715–3730. https://doi.org/10.1111/j.1365-294X.2006.03050.x

Harrison, X. A. (2014). Using observation-level random effects to model overdispersion in count data in ecology and evolution. *PeerJ*, *2*, e616. https://doi.org/10.7717/peerj.616

Hedwig, B. (2006). Pulses, patterns and paths: Neurobiology of acoustic behaviour in crickets. *Journal of Comparative Physiology. A, Neuroethology, Sensory, Neural, and Behavioral Physiology*, *192*(7), 677–689. https://doi.org/10.1007/s00359-006-0115-8

Hissmann, K. (1990). Strategies of mate finding in the European Field Cricket (*Gryllus campestris*) at different population densities: A field study. *Ecological Entomology*, *15*(3), 281–291. https://doi.org/10.1111/j.1365-2311.1990.tb00810.x

Hissmann, K. (1991). Phonotaxis of male crickets (*Gryllus campestris*) in a field population as an indication of territoriality (Orthoptera: Gryllidae). *Journal of Insect Behavior*, *4*(5), 675–681. https://doi.org/10.1007/bf01048078

Husby, A., Visser, M. E., & Kruuk, L. E. B. (2011). Speeding up microevolution: The effects of increasing temperature on selection and genetic variance in a wild bird population. *PLoS Biology*, *9*(2), e1000585. https://doi.org/10.1371/journal.pbio.1000585

Jacot, A., Scheuber, H., & Brinkhof, M. W. G. (2004). Costs of an induced immune response on sexual display and longevity in field crickets. *Evolution*, *58*(10), 2280–2286. https://doi.org/10.1554/03-660

Johnson, O. L., Tobler, R., Schmidt, J. M., & Huber, C. D. (2023). Fluctuating selection and the determinants of genetic variation. *Trends in Genetics*, *39*(6), 491–504. https://doi.org/10.1016/j.tig.2023.02.004

Kingsolver, J. G., Hoekstra, H. E., Hoekstra, J. M., Berrigan, D., Vignieri, S. N., Hill, C. E., Hoang, A., Gibert, P., & Beerli, P. (2001). The strength of phenotypic selection in natural populations. *The American Naturalist*, *157*(3), 245–261. https://doi.org/10.1086/319193

Koch, M., Hadfield, J. D., Sefc, K. M., & Sturmbauer, C. (2008). Pedigree reconstruction in wild cichlid fish populations. *Molecular Ecology*, *17*(20), 4500–4511. https://doi.org/10.1111/j.1365-294X.2008.03925.x

Lande, R., & Arnold, S. J. (1983). The measurement of selection on correlated characters. *Evolution*, *37*(6), 1210–1226. https://doi.org/10.1111/j.1558-5646.1983.tb00236.x

Le Cœur, C., Thibault, M., Pisanu, B., Thibault, S., Chapuis, J. -L., & Baudry, E. (2015). Temporally fluctuating selection on a personality trait in a wild rodent population. *Behavioral Ecology*, *26*(5), 1285–1291. https://doi.org/10.1093/beheco/arv074

Losos, J. B., Schoener, T. W., Langerhans, R. B., & Spiller, D. A. (2006). Rapid temporal reversal in predator-driven natural selection. *Science*, *314*(5802), 1111. https://doi.org/10.1126/science.1133584

Makai, G., Rodríguez-Muñoz, R., Boonekamp Jelle, J., Hopwood, P. E., & Tregenza, T. (2020). Males and females differ in how their behaviour changes with age in wild crickets. *Animal Behaviour*, *164*, 1–8.

Milesi, P., Lenormand, T., Lagneau, C., Weill, M., & Labbé, P. (2016). Relating fitness to long-term environmental variations in natura. *Molecular Ecology*, *25*(21), 5483–5499. https://doi.org/10.1111/mec.13855

Morrissey, M. B., & Hadfield, J. D. (2012). Directional selection in temporally replicated studies is remarkably consistent. *Evolution*, *66*(2), 435–442. https://doi.org/10.1111/j.1558-5646.2011.01444.x

Mouchet, A., Cole, E. F., Matthysen, E., Nicolaus, M., Quinn, J. L., Roth, A. M., Tinbergen, J. M., Oers, K. van, Overveld, T. van, & Dingemanse, N. J. (2021). Heterogeneous selection on exploration behavior within and among West European populations of a passerine bird. *Proceedings of the National Academy of Sciences of the United States of America*, *118*, e2024994118.

Muff, S., Nilsen, E. B., O'Hara, R. B., & Nater, C. R. (2022). Rewriting results sections in the language of evidence. *Trends in Ecology & Evolution*, *37*(3), 203–210. https://doi.org/10.1016/j.tree.2021.10.009

Nevo, E. (1988). Genetic diversity in nature: Patterns and theory. *Evolutionary Biology*, *23*, 217–246.

Nicolaus, M., Tinbergen, J. M., Ubels, R., Both, C., & Dingemanse, N. J. (2016). Density fluctuations represent a key process maintaining personality variation in a wild passerine bird. *Ecology Letters*, *19*(4), 478–486. https://doi.org/10.1111/ele.12584

Olsson, M., & Madsen, T. (2001). Between-year variation in determinants of offspring survival in the sand lizard, *Lacerta agilis*. *Functional Ecology*, *15*(4), 443–450. https://doi.org/10.1046/j.0269-8463.2001.00544.x

Poulet, J. F. A., & Hedwig, B. (2005). Auditory orientation in crickets: Pattern recognition controls reactive steering. *Proceedings of the National Academy of Sciences of the United States of America*, *102*(43), 15665–15669. https://doi.org/10.1073/pnas.0505282102

R Development Core Team. (2020). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing.

Rantala, M. J., & Kortet, R. (2004). Male dominance and immunocompetence in a field cricket. *Behavioral Ecology*, *15*, 187–191.

Réale, D., & Festa-Bianchet, M. (2003). Predator-induced natural selection on temperament in bighorn ewes. *Animal Behaviour*, *65*(3), 463–470. https://doi.org/10.1006/anbe.2003.2100

Rodríguez-Muñoz, R., Boonekamp, J. J., Liu, X. P., Skicko, I., Fisher, D. N., Hopwood, P., & Tregenza, T. (2019b). Testing the effect of early-life reproductive effort on age-related decline in a wild insect. *Evolution*, *73*(2), 317–328. https://doi.org/10.1111/evo.13679

Rodríguez-Muñoz, R., Boonekamp, J. J., Liu, X. P., Skicko, I., Haugland Pedersen, S., Fisher, D. N., Hopwood, P., & Tregenza, T. (2019c). Comparing individual and population measures of senescence across 10 years in a wild insect population. *Evolution*, *73*(2), 293–302. https://doi.org/10.1111/evo.13674

Rodríguez-Muñoz, R., Boonekamp Jelle, J., Fisher, D., Hopwood, P., & Tregenza, T. (2019a). Slower senescence in a wild insect population in years with a more female-biased sex ratio. *Proceedings of the Royal Society of London, Series B: Biological Sciences*, *286*, 20190286.

Rodríguez-Muñoz, R., Bretman, A., Slate, J., Walling, C. A., & Tregenza, T. (2010). Natural and sexual selection in a wild insect population. *Science*, *328*(5983), 1269–1272. https://doi.org/10.1126/science.1188102

Rodríguez-Muñoz, R., Hopwood, P., Fisher, D., Skicko, I., Tucker, R., Woodcock, K., Slate, J., Walling, C., & Tregenza, T. (2019d). Older males attract more females but get fewer matings in a wild field cricket. *Animal Behaviour*, *153*, 1–14. https://doi.org/10.1016/j.anbehav.2019.04.011

Roff, D. A. 1997. The maintenance of genetic variation. In *Evolutionary quantitative genetics* (pp. 339–387). Springer. https://doi.org/10.1007/978-1-4615-4080-9_9

Rost, R., & Honegger, H. W. (1987). The timing of premating and mating behavior in a field population of the cricket *Gryllus campestris* L. *Behavioral Ecology and Sociobiology*, *21*(5), 279–289. https://doi.org/10.1007/bf00299965

RStudio Team. (2020). RStudio: Integrated Development for R. RStudio, PBC, Boston, MA http://www.rstudio.com/

Sarmiento-Ponce, E. J., Rogers, S., & Hedwig, B. (2021). Does the choosiness of female crickets change as they age? *Journal of Experimental Biology*, *224*(11), jeb241802. https://doi.org/10.1242/jeb.241802

Schneider, C. A., Rasband, W. S., & Eliceiri, K. W. (2012). NIH Image to ImageJ: 25 years of image analysis. *Nature Methods*, *9*(7), 671–675. https://doi.org/10.1038/nmeth.2089

Siepielski, A. M., DiBattista, J. D., & Carlson, S. M. (2009). It's about time: The temporal dynamics of phenotypic selection in the wild. *Ecology Letters*, *12*(11), 1261–1276. https://doi.org/10.1111/j.1461-0248.2009.01381.x

Simmons, L. W. (1987). Heritability of a male character chosen by females of the field cricket, *Gryllus bimaculatus*. *Behavioral Ecology and Sociobiology*, *21*(2), 129–133. https://doi.org/10.1007/bf02395441

Simmons, L. W. (1995). Correlates of male quality in the field cricket, *Gryllus campestri*s l: Age, size, and symmetry determine pairing success in field populations. *Behavioral Ecology*, *6*(4), 376–381. https://doi.org/10.1093/beheco/6.4.376

Simmons, L. W., Lüpold, S., & Fitzpatrick, J. L. (2017). Evolutionary trade-off between secondary sexual traits and ejaculates. *Trends in Ecology & Evolution*, *32*(12), 964–976. https://doi.org/10.1016/j.tree.2017.09.011

Simmons, L. W., & Ritchie, M. G. (1996). Symmetry in the songs of crickets. *Proceedings of the Royal Society of London, Series B: Biological Sciences*, *263*, 1305–1311.

Tregenza, T., Simmons, L. W., Wedell, N., & Zuk, M. (2006). Female preference for male courtship song and its role as a signal of immune function and condition. *Animal Behaviour*, *72*(4), 809–818. https://doi.org/10.1016/j.anbehav.2006.01.019

Ugland, C. R., Acker, P., Burthe, S. J., Fortuna, R., Gunn, C., Haaland, T. R., Harris, M. P., Morley, T. I., Newell, M. A., Swann, R. L., Wanless, S., Daunt, F., & Reid, J. M. (2024). Early-life variation in migration is subject to strong fluctuating survival selection in a partially migratory bird. *The Journal of Animal Ecology*, *93*(10), 1567–1581. https://doi.org/10.1111/1365-2656.14172

Visscher, P. M. (2006). A note on the asymptotic distribution of likelihood ratio tests to test variance components. *Twin Research and Human Genetics*, *9*(4), 490–495. https://doi.org/10.1375/183242706778024928

Wagner, W. E., & Sullivan, B. K. (1995). Sexual selection in the Gulf Coast toad, *Bufo valliceps*: Female choice based on variable characters. *Animal Behaviour*, *49*, 305–319.

Walsh, B. & M. Lynch. 2018. *Evolution and selection of quantitative traits*. Oxford University Press.

Yamamichi, M., Letten, A. D., & Schreiber, S. J. (2023). Eco-evolutionary maintenance of diversity in fluctuating environments. *Ecology Letters*, *26*(Suppl 1), S152–S167. https://doi.org/10.1111/ele.14286