

Project Carboniferous: Implementing principles of Darwinian agriculture to increase size and palatability of domesticated crickets

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*Nothing in game theory makes
sense except in the light of
evolution*

Theodosius Dobzhansky

Introduction

A major challenge for the longevity and well-being of the human species is to cultivate enough food to feed a growing population. By 2050 there will be 10 billion people on the planet. Estimates suggest we need 70–100% increases in food yields [1, 2, 3], and many of the production-limiting resources, such as fossil fuels, land, and fresh water are only diminishing [3]. This challenge is exacerbated by climate change, which will add unpredictable obstacles to agriculture. Advances in methodology and technology are required to feed the future without destroying the Earth.

Insects as food provide a potential solution to the problem [2]. Insects already form part of the diets of an estimated 2 billion people, mainly in developing countries. Compared to traditional meats, insects use less land and water, convert feed to food more efficiently, and produce far fewer greenhouse gases [3]. In addition, insects have significantly higher protein concentrations than traditional foods, which is important because protein is a major limiting nutrient globally [2, 4, 3]. If more people globally started farming and eating insects, we could produce more food (and especially protein-rich foods) with fewer resources, potentially curbing a global food disaster.

However, a major obstacle to increasing global entomophagy (human consumption of insects) is palatability. In societies where insects do not form a part of the traditional diet, many people find insects unpalatable, as is often the case with foreign or novel foods [3]. Insects may be particularly problematic, because they appear so alien to the foods we already eat. For example, someone may be more willing to try bear meat than a cricket, because bear meat is quite similar to beef or venison.

A potential solution, then, is to look to the foods in our diets most similar to insects. Fortunately, in many of the societies where insects are eaten, their close relatives, crustaceans, are not only eaten but prized. Crustaceans and insects likely form a single monophyletic branch of the tree of life. Both have three segmented body parts and six legs, surrounded by an hard exoskeleton. Indeed, lobsters, now a highly valuable food source, were once considered ‘junk food’. If insects were more similar to edible crustaceans, this might help overcome the palatability problem.

The most obvious axis on which they could become more similar is size. Insects are limited in size, in large part, by environmental oxygen concentrations and humidity [5]. Insects breath through passive diffusion, opening holes in their body to let air in. However, each time they open these holes, they also lose water due to evaporation. Their maximum size, then, is limited by how much water they lose and how much oxygen they receive when opening their breathing holes. This is most strongly evidenced by the fact that, during the Carboniferous period in Earth’s history (360 Ma - 300 Ma), when atmospheric oxygen concentrations were 27-35 kPa (compared to today’s 21 kPa), and the climate was relatively cool and humid, insects experienced gigantism, with, for example, dragonflies reaching wingspans of 70cm. This fact could be exploited to evolve significantly larger insects.

We propose to utilise experimental evolution to evolve insects to significantly larger body sizes. Our study insect is the house cricket, *Acheta domesticus*, a widely consumed edible insect. By constructing hyperoxic (higher oxygen than 21 kPa) conditions, increasing humidity and decreasing temperature (relative to current standard cultivation methods), and implement artificial selection on size, we expect to increase the body size of insects relative to extant sizes. By achieving this, we aim to make their appearance, and the process of eating them, more similar to traditional foods. It’s important to note, that, as with most scientific papers, nothing in this paper matters except for the figures and their captions.

Methods and Results

The study organism

We used *Acheta domesticus*, a species of cricket commonly cultivated for human consumption. *A. domesticus* has a generation time of roughly 2-3 months. Crickets had access to water (water + Polyacrylamide Copolymer), dry feed (Fluker Farms High Calcium Cricket Feed) and shelter, and were reared with a natural day/night ratio (12 hr), using artificial lighting (standard ambient lighting). We housed crickets in 8 separate units (4 for control, 4 for experiment), with approximately $N = 2500$ crickets in each.

Puzzles in Biology

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Step 1: Genetic Code of Study Organism. DNA translation has become much more affordable thanks to advances in technology. Completing step one will take you to step two.

The environment

To construct hyperoxic conditions, we housed crickets in an acrylic subunit inside an oxygen-controlled chamber (Coy Labs, O2 Control InVivo Cabinet, Model 60). We used pure oxygen and N2 as an inert gas to maintain the oxygen levels at 35 kPa, the maximum percentage reached during the Carboniferous period. Waste ammonia and CO2 produced by the crickets was filtered out using a Carbolime mixture at the bottom of the unit. A temperature and

humidity control unit mounted at the back of the unit held the temperature at 20 degrees C and 80% humidity.

Artificial selection

The acrylic subunit which housed the crickets was subdivided into three adjacent sections, separated by walls, but connected by tubes such that crickets could walk between them. These tubes were size restricting, such that only the smallest crickets could reach the third container, and medium crickets being able to reach the second container. Due to the ideal free distribution, the crickets should have separated across the different containers roughly by size [5]. Therefore, we could impose positive artificial size selection by only rearing the eggs in the first container.

Nymphs were reared until sexual maturity (approximately 40 days). Adult Crickets are left to mate for 3 days, after which females from the largest container were isolated using black tubing. Individual females were placed in their own incubation chamber, which has food, water, and vermiculite for laying. Females are left to lay eggs for 10 days, at which point they are removed, and returned to the original chamber, completing the life cycle.

Experimental evolution

We evolved the crickets over 6 generations, measuring the body length, width, and mass of 30 randomly selected adults each generation.

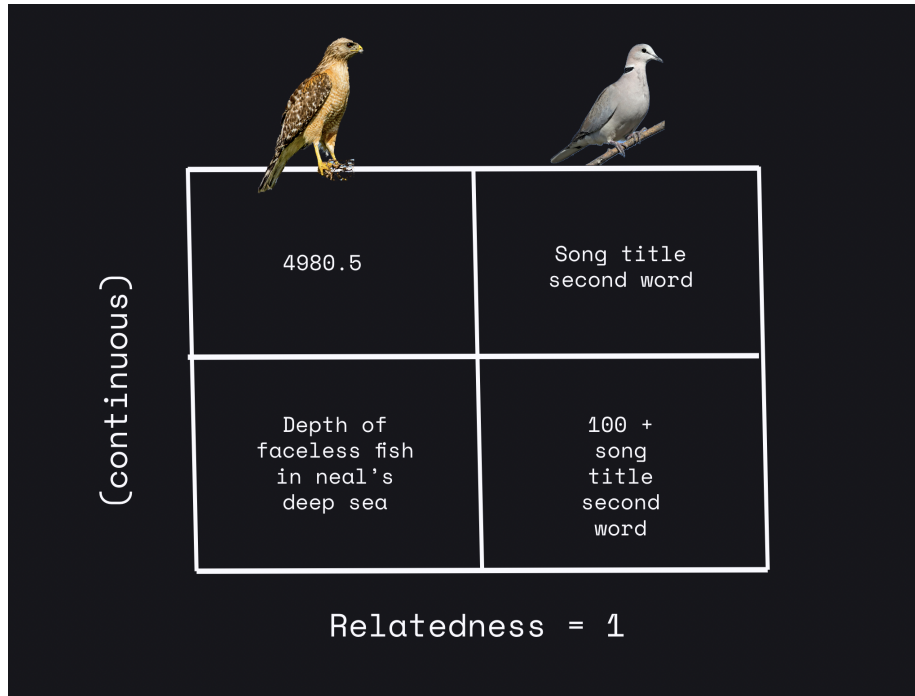
Results

Discussion

Natural Selection

Natural selection favours genes which increase their representation in the population. Such genes have higher relative ‘fitness’, a measure of the long term contribution of genes to future generations [7]. Over time, organisms accrue traits which increase the fitness of the genes which underpin those traits. Traits can increase the spread of genes either directly, by increasing the offspring number of their bearer, or indirectly, by increasing the offspring number of gene-sharing relatives.

The combination of indirect and direct genetic fitness can be captured in a single, individual level metric, called ‘inclusive fitness’ [8]. Inclusive fitness measures an individual’s adult offspring number in the absence of any effects from other individuals (baseline asocial fitness), plus weighted effects on offspring number that individual has on all other individuals in the population, including itself. The weightings are genetic relatedness, a measure of the likelihood of



Step 3: Input results from Step 1 and 2 here. Return to findmykiller.xyz/ifwedontplaygodwhowill?splash=1 to enter your Evolutionarily Stable Strategy (ESS) [6].

sharing genes at a given locus, with 1 for self and 0 for a random member of the population [8, 9, 10].

A wide body of theoretical and empirical work suggests that this quantity, inclusive fitness, is maximised by natural selection (for theory, see; 8, 9, 10, 11, 12, 13, 14, 15, 16, 17; for a summary of empirical results see 5, 18, 19, 20. Accordingly, at equilibrium, we can conceive of organisms as rational agents, trying to maximise a utility function for which the payoffs are inclusive fitness [21, 22, 17].

This fact is invaluable to the Darwinian Farmer, because it allows us to design farming equipment and methodology with evolutionary goals in mind, without knowing the underlying genetics or mapping between genotype and phenotype. Instead, we can treat the farmed organism as an agent trying to maximise its inclusive fitness, and plan accordingly.

Darwinian agriculture

Our solution is to create a farming system in which, by maximising personal inclusive fitness, organisms will also be increasing yield. Formally, we are cre-

ating an environment in which the organismal strategy which maximises their utility function, inclusive fitness, also delivers close to optimal payoffs for our utility function, yield. Evolutionary theory has shown us that we can capture this metric in a single equation [17].

References

- [1] R Ford Denison. *Darwinian agriculture: how understanding evolution can improve agriculture*. Princeton University Press, 2012.
- [2] FAO. Global agriculture towards 2050, 2009.
- [3] FAO. The future of food and agriculture, 2017.
- [4] FAO. Edible insects, 2013.
- [5] David Westneat and Charles W Fox. *Evolutionary behavioral ecology*. Oxford University Press, 2010.
- [6] Alan Grafen. The hawk-dove game played between relatives. <https://users.ox.ac.uk/~grafen/cv/hawkdove.pdf>, 1979.
- [7] Ronald A Fisher. *The genetical theory of natural selection*. Oxford University Press, 1930.
- [8] William D Hamilton. The genetical theory of social behavior. i and ii. *Journal of Theoretical Biology*, 7(1):1–52, 1964.
- [9] William D Hamilton. Selfish and spiteful behaviour in an evolutionary model. *Nature*, 228(5277):1218–1220, 1970.
- [10] Alan Grafen. A geometric view of relatedness. *Oxford surveys in evolutionary biology*, 2(2), 1985.
- [11] David C Queller. A general model for kin selection. *Evolution*, 46(2):376–380, 1992.
- [12] Steven A Frank. *Foundations of social evolution*. Princeton University Press, 1998.
- [13] Alan Grafen. Optimization of inclusive fitness. *Journal of Theoretical Biology*, 238(3):541–563, 2006.
- [14] Andy Gardner, Stuart A West, and Geoff Wild. The genetical theory of kin selection. *Journal of evolutionary biology*, 24(5):1020–1043, 2011.
- [15] Laurent Lehmann and François Rousset. Fitness, inclusive fitness, and optimization. *Biology & Philosophy*, 29(2):181–195, 2014.
- [16] Peter Taylor. Inclusive fitness in finite populations – effects of heterogeneity and synergy. *Evolution*, 71(3):508–525, 2017.

- [17] Samuel R Levin and Alan Grafen. Inclusive fitness is an indispensable approximation for understanding organismal design. *Evolution*, 73(6):1066–1076, 2019.
- [18] NB Davies, JR Krebs, and SA West. *An introduction to behavioural ecology. 4th edition*. Oxford: Wiley-Blackwell, 2012.
- [19] Patrick Abbot, Jun Abe, John Alcock, Samuel Alizon, Joao AC Alpedrinha, Malte Andersson, Jean-Baptiste Andre, Minus Van Baalen, Francois Bal-loux, Sigal Balshine, et al. Inclusive fitness theory and eusociality. *Nature*, 471(7339):E1, 2011.
- [20] David C Queller. Kin selection and its discontents. *Philosophy of Science*, 83(5):861–872, 2016.
- [21] Samir Okasha and Johannes Martens. Hamilton’s rule, inclusive fitness maximization, and the goal of individual behaviour in symmetric two-player games. *Journal of evolutionary biology*, 29(3):473–482, 2016.
- [22] Laurent Lehmann, Ingela Alger, and Jörgen Weibull. Does evolution lead to maximizing behavior? *Evolution*, 69(7):1858–1873, 2015.