

Modeling Quantitative Traits and Evolution by Natural Selection Using Cichlids of Lake Victoria Fish

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Abstract: Life is a study in contrasts between randomness and determinism. Scientists often reconcile the stochastic and the deterministic by appealing to the statistics of large numbers for variations among individuals in a population. And in natural populations, variation in most characters takes the form of a continuous phenotypic range rather than discrete phenotypic classes. In other words, the variation is quantitative, not qualitative. Mendelian genetic analysis is extremely difficult to apply to such continuous phenotypic distributions, so statistical techniques are employed instead. A major task of quantitative genetics is therefore to determine the ways in which genes interact with the environment to contribute to the formation of a given quantitative trait distribution. Furthermore, the genetic variation underlying a continuous character distribution can be the result of segregation at a single genetic locus or at numerous interacting loci that produce cumulative effects on the phenotype. Thus, this study was aimed at modeling quantitative traits and evolution by natural selection using some traits related to trophic adaptation of Lake Victoria cichlid fish. And we showed that disruptive natural selection is acting upon the traits investigated (i.e., Lower Jaw Length (LJL), Lower Jaw Length (LJW), Snout Length (SnL) and Snout Width (SnW)).

Keywords: Evolution, natural selection, quantitative genetics

INTRODUCTION

To evolutionary biologists, *natural selection* and an *evolutionary response to natural selection* are different phenomena. It is generally accepted truth, for a population to experience natural selection, two conditions must be met:

- Individuals must vary from one another for a particular trait.
- An individual's survival and reproductive success must be affected by which of the traits it possesses.

Some traits will be well adapted to a given environment and some will not. For example Darwin's finches, a favorite model of evolutionary biologists, are highly variable in beak size and individuals with larger beaks tend to survive periods of drought more successfully than those with smaller beaks (Grant and Grant, 1993). This is an example of natural selection where during drought; birds with small beaks are more likely to be eliminated from the population. However, it has to be noted that selection happens in generations. Nevertheless, natural selection says nothing about what happens to beak size in the subsequent generations. Since evolution can be broadly defined as a change in genetic make-up over time, we need to examine future generations to determine if natural selection is a mechanism that causes an evolutionary change in organisms. If natural selection does indeed lead to

changes in future generations, then it is claimed that an evolutionary response to natural selection or evolution by natural selection has been observed (Levins, 1968).

As a rule of thumb, for evolution by natural selection to take place three criteria must be fulfilled:

- Individuals in a population must vary from one another.
- Survival and reproduction must be affected by that variation existed in the population.
- The variation revealed within the population must be heritable.

Heritability is a concept best dealt with by quantitative genetics. To this end, the field of quantitative genetics examines quantitative (measurable) traits that vary continuously over a range of values such as beak size in birds or caterpillar weight, percentage of unicuspidness in cichlid fish, human height etc., Falconer (1989) and Weiner (1995). Suppose we consider human height is a quantitative rather than a qualitative trait and is influenced by numerous genes and by the environment. However, at this point it is important to remember that, unlike population genetics approach, most of the mathematical equations used by a quantitative geneticist do not require knowing the genotype of individuals (Griffiths *et al.*, 2000). They have developed a fundamental equation that quantifies the evolutionary response to natural selection (Falconer, 1989):

$$R = S \times h^2 \quad (1)$$

where, R stands for evolutionary response to natural; S is the selection differential (the strength of selection) and h^2 is heritability.

The objective of this study was to model quantitative traits using data from cichlid fish of Lake Victoria. The Lake Victoria cichlid fish species flock presents a text book example of adaptive radiation and spectacular diversity in terms of morphology, ecology and behavior (Axel *et al.*, 2012; Seehausen, 2008). We tested how genomic differentiation varies with steepness of ecological gradient using population of *Neochromis spp.* that live along environmental gradients created by water depth and associated light condition. We hypothesized that variation in gradient steepness induced by variation in shore slope, water clarity and rock size explains variation between islands in the extent of trophic adaptation and genetic differentiation.

METHODOLOGY

With the aforementioned theoretical background we have developed a model of a population of 133 individuals *Neochromis spp.* from Lake Victoria that undergoes natural selection. In 2011, at the department of biology, Mekelle University, Northern Ethiopia, A Hypothetical trait of individuals was taken for the model and several variable like: the mean and variance of a trait in the parental population, the “quality” of breeding habitat, how the individuals are distributed across breeding habitats, the degree of environmental and genetic influence on the offspring trait (a modeling surrogate for heritability) and how natural selection favors individuals of various traits were manipulated during modeling to see how they affect S , R and the course of evolution.

To start the modeling, first the parental fish population was defined to have a particular mean and standard deviation for a 3 traits under investigation namely Lower Jaw Length (LJL), Lower Jaw Length (LJW), Snout Length (SnL) and Snout Width (SnW) given in Table 1.

For the model the environmental conditions in which the parents breed and produce offspring was established depending on the mean and standard values set, suggesting that on average (genetics aside), most parents nest in environments that produce offspring with 10.6, 7.1, 9.5 and 10.9 mm for LJL, LJW, SnL and SnW, respectively. Furthermore, the variation in the environment is set to 10. This means that the population is nesting in a very heterogeneous environment; some individuals will nest in high-quality environments that generate large offspring with values greater mean, while others will nest in lower - quality environments that generate smaller offspring with values smaller than mean. However, we have not tested the variation with very small

Table 1: Parameters used as starting points for modeling

	LJL	LJW	SnL	SnW
Mean	10.66143	7.104248	9.534361	10.980790
St. dev	1.383622	1.346625	1.327889	1.513487

Table 2: Initial parameters used for modeling

Initial population trait	Offspring trait	
Mean trait value	10.9	“heritability factor”
Variation in trait	1.5	“environmental factor”
Environmental condition		sselection values
Mean condition	50	select parents above 0
Variation in environment	10	select parents below 0

values, such as 1 to indicate that parents are breeding in a similar (homogeneous) environment because researchers claim (Liem, 1973; Seehausen, 2008) that Lake Victoria at first was such a heterogeneous environment that leads to over 500 spp. fish to evolve in a short period of time. Therefore, using 10 for the variation in the environment for modeling sounds persuasive and the other part of the model was run to check how natural selection will “select” or pick which parents will breed. This was done to indicate that only large or small parents breed (directional selection), both small and large parents breed (disruptive selection), or only medium-sized parents breed (stabilizing selection) were selected. Besides, at first selection values were set to 0, which indicates that all parents are able to breed and natural selection will not discriminate among the parent trait size given in Table 1.

The “heritability factor” and the “environmental factor,” which define the extent to which an offspring’s trait size will be controlled by its parental genotype or by the environment in which it was raised were set to 0.5 values (this is an arbitrary value). We have used a spreadsheet to draw a random cumulative probability (the RAND () portion of the formula) from a distribution whose mean and standard deviation is given in Table 1. And this probability is converted into an actual data point by the NORMINV function of excel 2007. We’ll assume that this data point represents the average of the male and female size for the parameters (Table 1) under consideration.

RESULTS AND DISCUSSION

The initial parameters used for initial population trait is 10.9 and the variation in trait considered is 1.5 the standard deviation calculated from ($n = 160$) Table 2.

Furthermore, the heritability factor and environmental factors in the model were set to 0.5 indicating that each of the traits will be equally affected by both genotype of the individual and environment of individual organism. Using these conditions the model was run several hundred times to get the frequency distribution of parents before and after natural selection (Table 3).

The frequency distribution generated from the model (Table 3) significantly differ from 11 to 89 for the first generation (p_1) individuals and shift towards the highest

Table 3: Frequency distribution of parents after and before natural selection

Frequency distribution			Frequency distribution			Frequency distribution		
"Bin"	Trait size	Frequency of parents	"Bin"	Trait size	Frequency of parents	"Bin"	Trait size	Frequency of offspring
		Before			Before			
9	<10	11	9	<10	0	9	<10	0
19	<20	89	19	<20	1	19	<20	0
29	<30	0	29	<30	2	29	<30	1
39	<40	0	39	<40	16	39	<40	8
49	<50	0	49	<50	25	49	<50	35
59	<60	0	59	<60	31	59	<60	44
69	<70	0	69	<70	18	69	<70	11
79	<80	0	79	<80	6	79	<80	1
89	<90	0	89	<90	1	89	<90	0
	<100	0		<100	0		<100	0

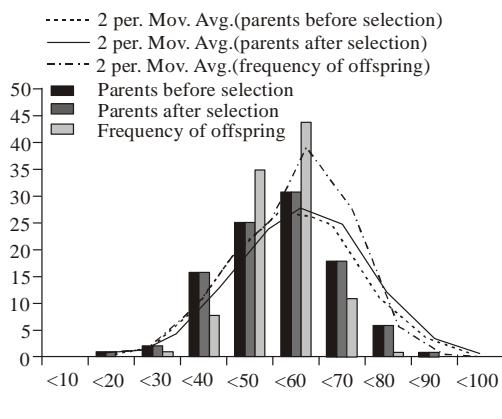


Fig. 1: Natural selection using the selection statistics calculated

value trait size value of 50 (Table 3). Furthermore, frequency of offspring shifted to the right (towards highest trait size value) and this shift is pronounced in the second generation (Table 3). This strongly suggests that disruptive natural selection is acting upon the traits investigated (i.e., Lower Jaw Length (LJL), Lower Jaw Length (LJW), Snout Length (SnL) and Snout Width (SnW)).

Using the selection statistics calculated from the model (Fig. 1), We found that the population will be right skewed indicating that disruptive natural selection does really have great impact on the traits we investigated for this model.

Furthermore, the individuals with lower values are selected against by natural selection in a heterogeneous environment unlike the individuals with highest value for trait under investigation (i.e., Lower jaw length, Lower Jaw width and Snout length). This is in line with molecular studies by Marten and van Nes (2006) snails

with larger but unlike the results by Isabel (2009) on where divergent selection due to resource competition where two extremes are selected against the modalities. It is clear those extensive model parameters (where, here simplified models are used). In natural setting it is obvious that both directional and stabilizing selection can take place provided that natural selection occurs whenever survivorship or reproductive success is nonrandom with respect to a particular trait. With this in mind biologist have accepted that selection can be directional, *stabilizing*, or *disruptive* in different study organism and study traits. From our modeling, the disruptive selection, which claims that individuals in the population with *either* high or low extremes for a trait survive better than individuals with an intermediate-sized trait (modality traits) seems to be operating in cichlids. Thus it looks argumentative to suggest that cichlids with higher traits are selected for by natural selection operating in the environment. Our theoretical finding is in line with data on molecular analysis for sexual selection in Haplochromine cichlid of east Africa (Isabel, 2009). However, unlike Marten and van Nes (2006) the numerical experiments suggest that on an evolutionary time scale self-organization may be a strong directional force creating stable lumps of similar species even in the face of stochasticity in competitive power and evolutionary dynamics. Supporting our data are myriads of experimental data's on three spine stickleback and cichlid fish of east African rift valley lakes.

CONCLUSION

In natural populations, variation in most characters takes the form of a continuous phenotypic range rather than discrete phenotypic classes. In other words, the variation is quantitative, not qualitative. Mendelian genetic analysis is extremely difficult to apply to such continuous phenotypic distributions, so statistical techniques are employed instead just like what we have done here. A major task of quantitative genetics is therefore to determine the ways in which genes interact with the environment to contribute to the formation of a

given quantitative trait distribution. Furthermore, the genetic variation underlying a continuous character distribution can be the result of segregation at a single genetic locus or at numerous interacting loci that produce cumulative effects on the phenotype. The estimated ratio of genetic to environmental variation is *not* a measure of the relative contribution of genes and environment to phenotype. Estimates of genetic and environmental variance are specific to the single population and the particular set of environments in which the estimates are made.

REFERENCES

- Axel, M., F. Shaohua, R. Kathryn and Elmer, 2012. Genomics of adaptation and speciation in cichlid fishes: Lineages recent advances and analyses in African and Neotropical. Phil. Trans. R. Soc. B. 367: 385-394. DOI: 10.1098/rstb.2011.0247.
- Falconer, D.S., 1989. Introduction to Quantitative Genetics. 3rd Edn., Longman Scientific and Technical, Essex.
- Grant, B.R. and P.R. Grant, 1993. Evolution of Darwin's finches caused by a rare climatic event. Proc. Royal Soc. London B, 251: 111-117.
- Griffiths, A.J.F., J.H. Miller, D.T. Suzuki R.C. Lewontin and W.M. Gelbart, 2000. An Introduction to Genetic Analysis. 7th Edn., W. H. Freeman, New York, ISBN: 10: 07167-35202.
- Isabel, M., 2009. The Roles of Divergent Selection and Environmental Heterogeneity in Speciation of Lake Victoria Cichlid Fish. Inaugural Faculty of Science, University of Bern, Germani, pp: 220.
- Levins, R., 1968. Evolution in Changing Environments: Some Theoretical Explorations. Princeton Univ. Press, Princeton.
- Liem, K.F., 1973. Evolutionary strategies and morphological innovations: Cichlid pharyngeal jaws. Syst. Zool., 22: 425-441, (DOI: 10.2307/2412950).
- Marten, S. and E.H. van Nes, 2006. Self-organized similarity, the evolutionary emergence of groups of similar species. PNAS, 103(16).
- Seehausen, O., 2008. Speciation through sensory drive in cichlid fish. Nature, 455: 620-626, (DOI:10.1038/Nature07285).
- Weiner, J., 1995. The Beak of the Finch. Vintage Books, New York.