NATURAL SELECTION IN THE FIELD *AND* THE CLASSROOM

by

Tessa Marie Andrews

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ABSTRACT

This dissertation examined natural selection in westslope cutthroat trout *(Oncorhynchus clarkii lewisi*) and undergraduate learning in the subject area natural selection. Translocation—moving individuals to a new habitat to establish, re-establish or supplement a population—is a crucial management strategy for cutthroat trout. One of the major questions managers face in a translocation is which population(s) should contribute individuals? Unfortunately, we often know little about the differences among potential contributing population. The goal of the first half of this dissertation was to look for differences in performance among individuals from five populations of westslope cutthroat trout. I assessed survival, growth, and condition (Chapter 2) and dispersal (Chapter 3) following the translocation of embryos from these five populations to six introduction sites in Cherry Creek. No differences existed among these populations in relative survival, growth, or condition at age 1 or 2. In contrast, statistically significant differences existed in dispersal distance among these populations. These differences were consistent across some, but not all, introduction locations.

As our knowledge of evolutionary biology has continued to grow, so too has our knowledge of how students learn evolution. Students taught using active learning strategies can learn substantially more about complex scientific concepts than students taught using primarily lectures. The goal of the second half of this dissertation was to further examine how students learn natural selection and how instructors facilitate that learning. I conducted a national survey of the relationship between an instructor's use of active learning strategies and how much students learned about natural selection (Chapter 4). I used a random sample of instructors from the largest and most prestigious universities in the country so that my results could be inferred to this large population of instructors. The degree to which instructors used active learning was NOT associated with student learning in this population of typical biology instructors. However, I found that a discussion of contemporary human evolution that used active learning strategies could effectively facilitate student learning of natural selection (Chapter 5).

CHAPTER ONE

INTRODUCTION TO DISSERTATION

Universities hire biology faculty to conduct research to expand and refine our understanding of the biological world *and* to help students learn biology by teaching. Traditionally, future faculty members have received little or no training as teachers. Instead, they have received essentially the same training as graduate students who go on work in government research positions and private sector jobs. This training system assumes that expertise in a subject area prepares someone to effectively teach that subject area.

Students in college courses are failing to learn fundamental scientific concepts. Many students in introductory physics courses that focus on mechanics leave courses without understanding force. Students with degrees in mechanical engineering do not understand basic electrical circuits. In biology, we find the same pattern. Students are not learning natural selection, photosynthesis, or basic genetics.

The accumulation of evidence showing that undergraduate students are not learning science has led to numerous national calls for reforming undergraduate science education. One focus of these calls has been “scientific teaching.” Essentially, scientific teaching consists of applying the same scientific rigor to teaching that we apply to research. This approach to reforming undergraduate science education is promising because it emphasizes skills and knowledge biologists already have.

If biologists are passionate about improving student learning, they can lead the way to effective undergraduate biology education using their scientific expertise. The same study design expertise needed to design an experiment comparing the performance of different stocks of fish in different water temperatures in the lab can be used to design an experiment comparing the performance of different teaching modules in the classroom. The same analysis expertise necessary to assess survival in a complex system that requires numerous control variables and nested data is necessary to assess learning in a system of diverse classrooms within different institutions. In collaboration with education experts who have a rich and nuanced background in learning theory and research, biologists could make great strides in reforming college biology education.

Reform occurs in individual classrooms and in a growing community of biology researchers dedicated to improving biology education. In classrooms, instructors teach scientifically when they objectively assess student learning and the effectiveness of their own instruction. On a larger scale, biology education researchers are addressing questions about how students learn biology and how instructors facilitate that learning. To make meaningful strides on these questions, we need researchers with expertise in biology *and* education.

This dissertation is the product of such training. The second and third chapters focus on evolutionary biology and the conservation consequences of a population’s evolutionary history. These chapters describe a common-garden experiment used to look for differences in survival, growth, and condition (Chapter 2) and differences in dispersal (Chapter 3) among individuals from different populations of westslope cutthroat trout introduced as embryos to common habitats. Differences among stocks indicate diverse evolutionary pasts and inform future conservation strategies.

The fourth and fifth chapters of this dissertation focus on how students learn natural selection biology and how science faculty facilitate (or fail to facilitate) student learning in the subject area of evolutionary biology. The fourth chapter describes a national survey of the effectiveness of active learning methods used by typical college faculty to teach natural selection in introductory biology courses. The fifth chapter describes a classroom exercise that uses a discussion of contemporary human evolution to engage students and efficiently and effectively change their ideas about natural selection.

Reforming undergraduate biology education requires collaborations among biology and education faculty. Faculty with expertise in both areas can create bridges among these disparate fields. They can also use the most effective and efficient research, theory, and methodology from both areas to engender meaningful and lasting improvement in what students learn in college biology courses. Training graduate students to be proficient in both fields is a nascent endeavor. Programs are underway around the country, but much debate remains about the optimal training for these interdisciplinary scholars. This dissertation is one model of the products of doctoral training in biology education.

CHAPTER TWO

PERFORMANCE OF CUTTHROAT TROUT FROM FIVE POPULATIONS TRANSLOCATED AS EMBRYOS INTO A FISHLESS COMMON HABITAT IN MONTANA

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Abstract

Translocations are a key conservation strategy for many imperiled fish species, but important questions about what maximizes the success of these projects remain unanswered. For example, how much does it matter which populations contribute individuals? We used an experimental translocation to look for evidence of genetic differences among three wild and two hatchery populations of westslope cutthroat trout. We translocated embryos into six locations within a fishless watershed containing prime cutthroat habitat. We examined relative survival, annual growth rates, and condition at ages 1 and 2. All three wild populations performed similarly. Little evidence of local adaptation to stream temperature existed and no evidence existed of decreased population fitness that could be caused by inbreeding depression. The hatchery populations performed as well or better than the wild populations. A translocation project using any of these five populations would have had a similar outcome. Further research should examine reproductive success to directly compare fitness among these populations.

Introduction

Tranlocations are an important management practice in fisheries. Managers use translocations to supplement small populations threatened by inbreeding depression or demographic stochasticity or to expand the range of a species. Many management decisions influence the success of a translocation, not the least of which is the selection of a source population. Genetic differences among populations can affect the fitness of individuals translocated into a new habitat (Griffith et al. 1989, Dunham et al. 2011). In wild populations, genetic differences caused by local adaptation can threaten the success of a translocation. In hatchery populations, genetic differences caused by adaptation to captivity can jeopardize a translocation. In both wild and hatchery populations, inbreeding can reduce the ability of fish to survive and reproduce in any environment.

Local adaptation is natural selection that causes traits beneficial in a local habitat to become more common within the local population (Kawecki and Ebert 2004). In a translocation designed to found or re-found a population, a mismatch between the habitat in a contributing population's native site and the habitat in the translocation site could affect the ability of the introduced fish to successfully establish a population. In a translocation used to augment an existing population, local adaptation can cause even larger problems. These translocations are generally meant to improve population fitness by ameliorating the effects of inbreeding depression, but the fitness of the existing population can be *reduced* if the fish introduced into the threatened population are adapted to a different environment. In the worse case scenario, the translocation could cause the extinction of the native population (Greig 1979).

Hatchery environments present unique opportunities for local adaptation. Hatchery populations are a convenient source of individuals for translocation projects and so are commonly used (e.g., Harig et al. 2000), but hatchery fish may be adapted to grow and survive in artificial environments and these adaptations can decrease the ability of hatchery fish to live and reproduce in the wild. For example, Araki et al. (2007) estimated that each generation steelhead (*Oncorhynchus mykiss*) were raised in captivity decreased their ability to reproduce in the wild by 40% (also see Christie et al. 2012). This may be why translocations involving only wild stocks of fish have been twice as likely to establish a self sustaining population as translocations using hatchery populations (Griffith et al. 1989).

In both hatchery and wild populations, genetic differences caused by mating between relatives and genetic drift can lower population fitness, potentially affecting translocations. Individuals from these populations are more likely to be homozygous for deleterious alleles, making them less likely to survive or thrive in a translocation (Frakham et al. 2002). Additionally, these populations have reduced genetic variability (Hedrick and Kalinowski 2000), hindering their capacity to adapt to new or changing conditions. Fish species in need of translocations often consist of small, isolated populations (e.g., Young 2009), so low population fitness is a major concern.

Westslope cutthroat trout (*Oncorhynchus clarkii lewisi*) are the most widespread of the eight major extant subspecies of cutthroat trout and (despite their name) occupy both slopes of the Continental Divide in the northern Rocky Mountains (Allendorf and Leary 1988, Behnke 1992). Westslope cutthroat trout (WCT) populations in Montana have been heavily affected by hybridization with non-native rainbow trout, competition with non-native brook trout, and habitat degradation caused by cattle grazing, mining, logging and other types of development (Liknes and Grahm 1988, Behnke 1992, McIntyre and Rieman 1995). Currently, WCT occupy 59% of their historical range and population sizes are declining range-wide (Shepard 2005, May 2009). In addition, many WCT populations have undergone severe population bottlenecks (Liknes and Graham 1988). Many of the remaining genetically pure WCT populations are now isolated above barriers that prevent immigrants from entering populations. These barriers protect WCT populations from hybridization and competition with non-native trout (Shepard et al. 2005), but increase the threat of inbreeding and demographic stochasticity (Kruse et al. 2001, Novinger and Rahel 2003).

Given the challenges to persistence faced by WCT, their long-term viability may depend on translocations. However, selecting source populations for these translocations would be difficult because little is known about the functional genetic differences among populations of WCT. Drinan et al. (2011) showed large genetic differences among WCT populations at neutral genetic loci. There are a few reasons to suspect that such differences are present: WCT are distributed in discrete populations (Shepard et al. 2005), occupy divergent habitats (Liknes and Graham 1988), and have been isolated for a long time (Behnke 1992, Drinan et al. 2011). All of these conditions promote local adaptation. Furthermore, laboratory experiments (Drinan et al. in press) showed that WCT may be adapted to their native water temperature. As for domestication selection, no research exists on whether hatchery stocks of WCT have adapted to their captive environment, but Montana Fish, Wildlife, and Parks' principal hatchery stock (which has frequently been used to establish new populations) has been reared in captivity since 1984, affording ample opportunity for domestication selection. Little research exists on inbreeding depression in WCT, but compelling indirect evidence exists of inbreeding depression in some populations of WCT (Allendorf and Phelps 1980, Leary et al. 1985), including documented albinos in at least one population.

The specific genetic characteristics of fish populations used in translocations could influence the success of the translocation, but in most cases little is known about the genetic traits of potential donor populations that might affect a project. Because translocations are a major conservation strategy for many imperiled fish species and because the cost of these projects is considerable, further investigation is necessary regarding the influence on translocation success of genetic differences among populations.

The goal of this project was to identify differences among populations of WCT by performing an experimental translocation and monitoring survival, growth, and condition. We looked for evidence of genetic differences caused by local adaptation, adaptation to captivity (i.e., a form of local adaptation), and inbreeding depression. We compared the performance of individuals from five WCT populations introduced as embryos, including two hatchery and three wild populations. We used a classic common-garden experiment in the wild that consisted of six distinct locations in an extensive, fishless stream system. Using a historically fishless stream system eliminated the possibility of jeopardizing existing populations.

Materials and Methods

Project Design and Study Site

The study described in this paper was part of a large conservation project to create a genetically diverse WCT conservation population within a secure refuge in Cherry Creek, a tributary of the Madison River (Bramblett 1998). The Cherry Creek project took place in two phases. During the first phase, the study site was treated with the piscicides antimycin and rotenone to remove non-native fish species. During the second phase, in which this study took place, wild and hatchery WCT embryos were introduced throughout the fishless drainage and the individuals resulting from those introductions were monitored using electrofishing sampling and genetic identification.

The study site consisted of upper Cherry Creek and its tributaries (Fig. 2.1), which included over 90 km of stream and a 2.84 ha lake. The site provided high quality WCT habitat and refuge (Bramblett 1998). An 8-m waterfall prevented re-colonization of non-native fish species. Additionally, the majority of the study site flows through a remote portion of the Lee Metcalf Wilderness area and private property owned by Turner Enterprises, Inc. providing protection from anthropogenic threats.

We introduced fertilized embryos to six different locations in the Cherry Creek system over three years (Fig. 2.1). We choose these introduction sites to ensure that introductions were spread throughout the watershed and because they had different stream temperature regimes (Fig. 2.2). We gathered water temperature data in introduction sites and the native streams of wild populations using Onset Optic Stowaway and HOBO TempPro (www.onsetcomp.com) recording temperature monitors that recorded stream temperature hourly. We collected data June through mid-September. We used average daily temperatures to compare habitats. Temperature data collected in the introduction sites was less extensive than in the native habitats of the donor populations because of accessibility. Additionally, much of the temperature data from the unnamed tributary was lost, such that our estimates of temperature in this site are less precise than in other sites (Fig. 2.2).

Donor Populations

Embryos introduced to the study site came from five donor populations, including two hatchery and three wild populations. One of the hatchery populations was the state of Montana's captive WCT conservation population, which is reared at Washoe Park Hatchery. This population (WPH) was founded in 1984 from populations of WCT in the upper Flathead and Clark Fork river drainages. The population was infused with additional gametes from the Flathead drainage about 20 years later. The WPH population differs from the other donor populations in two important ways: it is the most genetically diverse and it originated from populations west of the Continental Divide whereas Cherry Creek and the other donor populations originated east of the divide. The Continental Divide is associated with substantial genetic variation among WCT populations (Drinan et al. 2011). The WPH population served as both a treatment and a control population.

The other hatchery population came from a private hatchery on the Sun Ranch in southwestern Montana. This population (SRH) was founded in 2002 from embryos donated by WCT populations east of the Continental Divide. The three wild populations used in this study were also the principal donors to this outbred population. Because this captive population is relatively new, some of the broodstock probably descended directly from crosses of individuals from the same donor population, rather than from outbred crosses between populations. No embryos from the SRH population could be introduced in 2009. Otherwise, embryos from all donor populations were introduced to all sites.

The three wild populations that donated embryos are large, genetically pure populations that inhabit mountain streams east of the Continental Divide. Ray Creek supports the most pristine of the three wild populations. This population (Ray) consists of about 2,500 individuals and is isolated from non-native fish by a perched culvert (L. Nelson, Montana Fish, Wildlife and Parks, Helena, MT, personal communication, 2011). The populations in Muskrat Creek (Muskrat) and White's Creek (White's) required intensive restoration management in recent years, including the construction of manmade barriers and brook trout removals (Shepard et al. 2002; L. Nelson, personal communication, 2011). The state relocated some WCT in Muskrat above a headwater barrier to expand the upper distribution of this population and completed extensive habitat restoration in White's to ameliorate effects of past placer mining. In 2007, the Muskrat population has about 3,500 individuals inhabiting over 8 km of stream, but this population may have been as small as 100 individuals before aggressive management began in 1997 (L. Nelson, personal communication, 2011). The White's population decreased to about 100 individuals in the 1990s, but later increased to about 1,000 individuals inhabiting slightly over 3 km of stream (Shepard et al. 2002).

We choose these donor populations because of their physical proximity to the study site, genetic purity, ability to provide enough embryos, and the thermal regimes of the streams that supported them. Westslope cutthroat trout populations could conceivably be adapted to many characteristics of their environment, but water temperature may be the most likely candidate because water temperature affects all aspects of poikiloform life and therefore has probably imposed strong selective pressure on WCT populations. Water temperature strongly governs growth, development, reproductive cycles, migrations and other life history traits concomitant to salmonid survival (Liknes and Graham 1988, McIntyre and Rieman 1995, Bear et al. 2005). Because these populations come from streams with different water temperature regimes, we were able to test for local adaptation to stream temperature. We gathered temperature data as described above. Stream temperatures of the donor populations' natal streams differed in both degree and variation. The stream temperature of White's Creek tended to be warmer and less variable than the other two wild donor streams (Fig. 2.3). In the warmest part of the summer, White's Creek had an average daily temperature about one degree (C) higher than Muskrat and Ray Creek, but most of the year the water temperature in White's was considerably warmer than in Muskrat or Ray (Fig. 2.3).

Embryo Collection, Incubation, and Introduction

We collected embryos from the source populations by spawning adults from each population. In the wild, we captured adults using a backpack electrofisher and confined them in in-stream containers until they were ready to spawn. After spawning, we released adults and marked them by clipping their dorsal fins so that they would not be spawned again. At the Washoe Park Hatchery, we collected embryos from ripe adults once a week for several weeks to have eyed hatchery embryos to introduce at the same time as each wild embryos introduction. At the Sun Ranch, we captured adults from a holding pond with seines and spawned all ripe males and females that had not previously contributed embryos to the project. We collected a small pelvic fin clip for genetic analysis from each adult that contributed gametes.

We followed the same spawning procedure for each donor population, using protocols designed specifically for WCT. We stripped each female of eggs and split the eggs among two to four thermoses. The eggs in each thermos were fertilized with milt from a different male to produce a unique male × female cross, hereafter called a "lot." Next we added water and left the embryos undisturbed for at least 30 minutes to water harden before rinsing the fertilized eggs. Wild embryos were re-suspended in fresh water and packed in coolers for transport to Sun Ranch Hatchery, where they were incubated alongside embryos from the SRH population. Embryos from the WPH population were incubated on site at the Washoe Park Hatchery. We held all embryos in Heath tray incubators until the eyed stage and treated them with formalin every three to seven days to prevent fungus. After the embryos had eyed, we removed dead embryos, and counted and packed live embryos in thermoses for transport to the study site. Embryos from each female were generally split between the two introduction sites used in a year. embryos from a single lot were introduced to the same incubator, with the exception of lots from WPH, which were sometimes split among several incubators. The number of embryos introduced from each stock varied among stocks and across years (Table 2.1) depending on the availability of embryos from the donor populations.

We used in-stream remote-site incubators (RSIs) to plant eyed embryos in introduction sites. RSIs are designed to consistently supply embryos with fresh water while avoiding the sedimentation associated with buried incubators. They have previously been used to successfully reestablish Arctic grayling (*Thymallus arcticus*) and WCT to native streams in Montana (Kaeding and Boltz 2004). embryos absorb the yolk sac in the RSI. After swimming up, the fry follow the outflow of water through a tube and into a receiving bucket. We counted and then released fry in calm water downstream of the RSIs. We monitored RSIs for function and fry emergence every two to three days from the day of planting until the last fry emerged.

Fish Sampling

We used a systematic sampling design with a non-random start to estimate the relative survival rate, size, and condition of fish from the five populations introduced into Cherry Creek starting in 2008 when the first fish introduced were age 1. We began sampling at each introduction site and attempted to sample throughout the introduced population's current range. We sampled 100-m sections every 300 m for about 600 m above and from 1 to 5 km below introduction sites. Fish densities tended to decrease abruptly at some point below each introduction site. At that point, we decreased our sampling frequency to sample one 100-m section per 500 m of stream. We continued downstream from the introduction sites until few or no fish were collected in several sequential sections. In some cases, such as in Cherry Lake Creek, our most downstream sections were spread out to avoid terrain that prohibited efficient sampling. We sampled age 1 fish from each introduction site and age 2 fish from the two sites used for the first year of introductions.

We sampled in late summer using two to four-person backpack electrofishing crews. Electrofishing efficiently captures salmonids, particularly those over 4 inches long (Bohlin et al. 1989), and has minimal long-term effects on WCT at the electrofishing settings we used (Dwyer et al. 2001). When shocked, fish become immobilized and lose equilibrium (Reynolds 1996). We caught immobilized fish in nets and held them until they were completely recovered. We weighed and measured the length of each fish, and removed a small portion of the pelvic fin for genetic analysis. We recorded the GPS location of the section in which each fish was captured before releasing fish within 100 m of their capture location.

Genetic Analysis and Parentage Assignment

To determine the donor population of each captured fish, we used unique genetic markers to match parents and offspring. We extracted genomic DNA using Qiagen DNeasy Blood & Tissue Kits (Qiagen, Valencia, CA). To determine the donor population of each captured individual, we genotyped 12 microsatellite loci (loci and laboratory conditions are described by Vu and Kalinowski 2009). We scored genotypes using Genemapper v. 3.7 (Applied Biosystems, Carlsbad, CA).

We assigned offspring to parent pairs by counting Mendelian exclusions (e.g., Muhlfeld et al. 2009). We accepted a parentage assignment if an offspring had two or fewer loci mismatched with only one parent pair. Any offspring that could not be matched to at least one parent pair with two or fewer mismatches was excluded from further analysis; 5.3% (n = 77) of offspring were excluded at this point in the analysis.

When an offspring was assigned to more than one parent pair with an equal number of two or fewer mismatches, we accepted the assignment to each parent pair and fractionally allocated the offspring to parent pairs for the analysis of survival data. For example, if an offspring was assigned to two parent pairs, we would assign 0.5 offspring to each parent pair. Ninety-two individuals (6.3%) were assigned to two or more parent pairs. These individuals were excluded from analyses on annual growth rate and condition because they could not be assigned to a single lot.

Statistical Analysis

We used linear mixed models to compare the mean relative survival rate, median growth rate, and median condition of individuals from the five populations of cutthroat trout introduced into the Cherry Creek watershed. For each response variable, we fit linear mixed models using SAS. Linear mixed models can control for a lack of independence caused by clustering or repeated sampling (Gelman and Hill 2007). For example, in our linear mixed models, we accounted for the fact that RSIs were nested within introduction sites in our study design. We also accounted for the fact that individuals were nested within lot, which was nested within female. Finally, we also included introduction year as a random effect to control for variability across time. In all models, we included donor population, introduction site, and the interaction between them as fixed effects.

For each response variable, we considered age 1 and age 2 individuals separately. The only differences between age 1 and age 2 analyses were the number of introduction sites included. For age 1 models, there were six introduction sites, whereas there were two introduction sites for the age 2 models. The sites included for age 2 analyses were from the same introduction year, precluding the need to include introduction year as a random effect.

We used a two-step analysis. We began by fitting a full linear mixed model that included an interaction between introduction site and donor population for each response variable at age 1 and age 2. A significant interaction indicates that the pattern of the response variable among donor populations varies across introduction sites. If local adaptation has caused differences among populations, we would find a significant interaction. When we found a significant interaction, we used plots of estimated means or medians and 95% confidence intervals for each donor population × introduction site combination to further examine differences. For those models with significant interactions, we stopped analyzing at this point because it is challenging to interpret main effects such as the effect of donor population when an interaction is present (Ramsey and Schafer 2002).

For models in which the interaction was not significant, we proceeded to the second step of analysis. We fit a model that excluded the interaction to test for a main effect of donor population. A significant main effect of donor population would indicate populations performed differently across introduction sites. When we found a significant effect of donor population, we estimated population means or medians and 95% confidence intervals to further examine differences. The comparison of CIs provides information about precision as well as statistical significance and circumvents inflated error values associated with multiple comparisons (Cumming and Finch 2001). Non-overlapping CIs imply there is a significant difference between two means or medians. If two means or medians are from independent populations with large enough sample sizes and the CIs widths are similar, the difference between them will be significant at an alpha level of about 0.006 (Cumming and Finch 2005).

Our first response variable was relative survival. Calculations of relative survival do not assume that capture efforts and efficiencies were equal across space and time. We calculated relative survival as the proportion of a lot captured (number of fish captured/number of embryos introduced) divided by the median proportion of a lot captured for the WPH population in that introduction site and year. The WPH population was the most appropriate baseline because embryos from this population were introduced across a wider timeframe than the other populations. For example, embryos from White's Creek and the SRH population were ready for introduction earlier in the season than embryos from Muskrat and Ray Creeks, but WPH embryos could be introduced throughout the season.

We calculated the other two response variables as follows. We calculated annual growth rate as weight in grams divided by age and used logged growth rate as the response variable because the distribution was skewed. We calculated condition using Fulton's condition factor after examining simple linear regressions of log(weight) and log(length) and determining the slopes were near 3.0 (Pope and Kruse 2007). Again, we used a log transformation because of a skewed distribution. We conducted the growth and condition analyses at the level of the individual, rather than the level of the lot, to capture individual variation.

The annual growth rate analyses differed slightly from the relative survival and condition analyses. Individuals in our study site varied in the degree to which they dispersed. Because this was a fishless habitat, dispersing individuals were likely to encounter less occupied habitats and therefore less competition for resources than sedentary individuals. Therefore, growth may have been mediated by dispersal distance in this system. We have calculated dispersal distance as the distance in meters between the site fry were released and the capture location at age 1 or age 2. The parameterization of dispersal distance does not take into account the direction of dispersal (i.e., upstream or downstream), but most individuals dispersed downstream. Annual growth rate was strongly correlated with dispersal distance at age 1 ($r = 0.61$, $P < 0.0001$) and age 2 ($r = 0.61$, $P < 0.0001$). Stream width and dispersal distance were not correlated at age 1 ($r = 0.003$, $P = 0.92$), but were significantly correlated at age 2 ($r = 0.59$, $P < 0.0001$). Therefore, we did not include stream width in the age 2 analysis. Dispersal distance data were unavailable for one of the six introduction sites because sampling locations were not recorded, so the age 1 growth analysis included five introduction sites, rather than six.

Results

Relative Survival

Little evidence existed of differences among populations in relative survival rates. Across six introduction locations at age 1 and two locations at age 2, the pattern of relative survival among populations was similar (Fig. 2.4). In particular, the relative survival of the three wild populations from White's, Ray, and Muskrat creeks was nearly indistinguishable.

Although survival was similar for most of the stocks at most of the introduction sites, some notable differences existed. One of these was the unusually high survival of the SRH population in the unnamed tributary (Fig. 2.4). At age 1, a significant interaction existed between donor population and introduction site (*F*(13, 66) = 2.53, *P* = 0.007), which indicates that the pattern of relative survival among populations differed in at least one introduction location. Examination of a plot of relative survival rates (Fig. 2.4) showed that the performance of the SRH in the unnamed tributary was the largest difference in survival rates among populations at all sites. We removed the SRH data from the unnamed tributary and tested to see if the interaction was still significant; it was not (*F*(12, 66) = 1.01, *P* = 0.450), meaning no other significant differences existed among introduction locations in the pattern of relative survival among populations.

Another notable difference in relative survival was the performance of WPH relative to the performance of the wild populations. We used WPH to calculate relative survival, so each estimate of mean relative survival in Fig. 2.4 is a ratio of the survival of the population listed on the x-axis divided by the survival of WPH in that introduction site. Therefore, if the 95% confidence interval around estimated relative survival does not cross the horizontal line at one, we can conclude that the survival of WPH is significantly different from the survival of the other population. At age 1, the survival of the wild populations in the four coldest introduction sites tended to be significantly lower than the survival of WPH (Fig. 2.4). By contrast, the survival rates of some of the wild populations in the two warmest sites were significantly greater than the survival of WPH (Fig. 2.4). The same general pattern was present at age 2, but the differences between the wild and WPH populations were not statistically significant as often (Fig. 2.4).

Other than these differences, our analyses revealed only similarities in relative survival among populations. We removed the interaction from the age 1 model to see if the relative survival of populations differed across all introduction locations. We did not find a significant main effect of donor population (*F*(3, 66) = 1.01, *P* = 0.395), meaning that no population stood out as having higher or lower overall survival than the other populations. At age 2, there was not a significant donor population × introduction site interaction (*F*(3, 21) = 1.44, *P* = 0.260), meaning the pattern of relative survival among populations was the same at both introduction sites. When we fit a model excluding the interaction, donor populations did not differ (*F*(3, 21) = 1.14, *P* = 0.355), meaning survival was equivalent among populations when we looked across both introduction sites.

Annual Growth Rate

We found some evidence of differences in annual growth rates among populations at both ages. At age 1, we did not find a significant interaction (*F*(13, 600) = 1.34, *P* = 0.185), which means that the pattern of median growth rates among populations was the same at all introduction sites. However, when we removed the interaction, we found significant differences among populations (*F*(4, 607) = 28.23, *P* < 0.0001). The median annual growth rate of the two hatchery populations was 1.5 to over 2 times greater than that of the three wild populations (Fig. 2.5).

At age 2, a significant interaction existed between introduction site and donor population (*F*(4, 218) = 2.46, *P* = 0.047), meaning that the pattern of annual growth rate among populations was different in the two introduction locations. Graphically, non-parallel lines represent an interaction when each line represents a donor population and connects estimates of median survival at the two introduction locations (e.g., Fig. 2.6).

Examination of a plot indicated that White's is the only populations with a line not parallel to the others (Fig. 2.6). Median annual growth rates at age 2 of the other four populations were about twice as great in Cherry Creek as in Cherry Lake Creek, whereas the growth rate of individuals from White's was almost four times higher in Cherry Creek than in Cherry Lake Creek (Fig. 2.6).

Condition

Some evidence of differences in condition existed among donor populations at both age 1 and age 2. At age 1, no significant donor population × introduction site interaction existed ($F(17,796) = 1.03$, $P = 0.420$), meaning the pattern of median condition among populations was similar across sites. When we removed the interaction from the statistical model, significant differences existed among populations ($F(4, 805) = 3.28$, $P = 0.011$). The median condition factor of fish from Muskrat was lower than that of the other populations (Fig. 2.7). At age 2, a significant interaction existed ($F(4, 219) = 2.45$, $P = 0.047$), and a plot revealed that Muskrat was different from the other populations (e.g., the line representing Muskrat had a different slope in Fig. 2.8). Individuals from all of the other populations were in poorer condition in Cherry Creek than in Cherry Lake Creek, but individuals from Muskrat were in similar condition in both sites (Fig. 2.8).

Discussion

Few differences existed among populations in relative survival, growth, and condition. This suggests these populations do not have genetic differences that affect translocation success and using any one of these populations would have led to similar outcomes in the first two years following a translocation. Although similarities among populations outnumbered differences, we did find several differences, most notably that WPH fish outperformed the three wild populations of fish in cold water locations, and underperformed (or performed as well as) the wild populations in warmer waters. These results have a few implications for what we can infer about the genetic characteristics of the five populations of WCT that we studied; we will discuss implications regarding local adaptation, domestication selection, and inbreeding depression in turn.

One potential cause of genetic differences in wild WCT populations is local adaptation. Westslope cutthroat trout populations could conceivably be adapted to many characteristics of their environment, but water temperature may be the most likely candidate because water temperature affects all aspects of poikiloform life and therefore has probably imposed strong selective pressure on WCT populations. Water temperature strongly governs growth, development, reproductive cycles, migrations and other life history traits concomitant to salmonid survival (Liknes and Graham 1988, McIntyre and Rieman 1995, Bear et al. 2005). Because we conducted this study in a historically fishless stream, none of the wild populations are "local" to the Cherry Creek drainage. However, we can compare the stream temperature of a wild populations' native stream with the stream temperature of the introduction locations to determine if a wild population is likely to be adapted to that site. White's Creek is much warmer and more moderate than Ray or Muskrat Creek (Fig. 2.3), so if WCT populations are adapted to their native water temperature we would expect individuals from White's to perform better in a warm introduction location such as Cherry or Carpenter Creek. On the other hand, we would expect individuals native to Muskrat and Ray Creeks to be adapted to cold introduction sites such as Cherry Lake Creek or South Fork. These expectations were met for only one population in one introduction site.

One piece of evidence existed for local adaptation to stream temperature among the three wild populations we examined. A significant interaction between introduction site and donor population is an initial indicator of local adaptation. A significant interaction existed when we modeled annual growth rate at age 2. Large error bars prevent definitive conclusions, but our data suggest White's may be locally adapted to warm water temperatures. All three wild populations had higher growth rates in Cherry Creek (warm site) than in Cherry Lake Creek (cold site), but this difference (i.e., the slope of the line in Fig. 2.6) was most pronounced for White's. This suggests that the White's population may benefit from the warm water more than the two populations from colder native streams because White's has adapted to the warm water in its native creek.

A significant interaction existed for condition at age 2, but further investigation revealed that this result did not provide evidence for local adaptation. The population with the aberrant pattern of condition across introduction sites (i.e., the line in Fig. 2.8 that is NOT parallel with the other lines) was from Muskrat, which is a cold (Fig. 2.8). Individuals from Muskrat were in similar condition in both Cherry Creek and Cherry Lake Creek, whereas the condition of individuals from White's and Ray was similar to that of Muskrat in Cherry Lake Creek (cold site) and lower than Muskrat in Cherry Lake Creek (Fig. 2.8). Muskrat's native stream is substantially colder that Cherry Creek, so individuals from Muskrat have not undergone selection for water temperatures such as that in Cherry Creek. In other words, this result is not evidence for local adaptation.

These results add to a growing body of research questioning the ubiquity of local adaptation. Recent meta-analyses have independently concluded that local adaptation is less common than generally assumed (Leimu and Fischer 2008, Fraser et al. 2011). Local plants significantly outperformed foreign plants in about 50% of comparisons (Leimu and Fisher 2008). Similarly, local salmonids significantly outperformed foreign salmonids in about 50% of 76 comparisons (Fraser et al. 2011). The preponderance of cases that did NOT provide evidence for local adaptation is particularly notable in salmonids, because these populations so often exist in conditions expected to promote local adaptation (Kawecki and Ebert 2004, Fraser et al. 2011). One possible explanation is that small population size and the associated deficiency of genetic diversity make adaptation unlikely in these populations (Jakobsson and Dinnetz 2005, Leimu and Fisher 2008, Fraser et al. 2011).

Another explanation for the fact that we found little evidence of local adaptation is that we compared individuals too late in life. A companion laboratory study (Drinan et al. in press) found WCT populations from cold native streams exhibited a greater decline in embryonic survival when incubated at warm temperatures than populations native to warm streams. After incubation was over, however, they found no evidence of local adaptation (Drinan et al. in press). All embryos in our study were incubated in similar environments to the eyed stage and then released into the wild using RSIs. As such, they were not subjected to different temperature regimes during embryonic development in this generation. If embryonic survival in the wild is strongly related to temperature, then second generation survival rates among populations should provide evidence of local adaptation to water temperature. Assessing natural reproduction in this study system would provide a more rigorous test for genetic differences caused by local adaptation.

No evidence existed that hatchery populations performed more poorly than wild populations of WCT. The state of Montana manages a WCT hatchery population that would be a convenient source of individuals for translocations, but concern exists that these individuals are not as fit in the wild as individuals from wild populations because reproductive capability of captive-reared salmonids in the wild can be reduced (e.g., Christie et al. 2012). Therefore, we looked for differences in performance between hatchery and wild WCT populations. We found several notable differences. When we examined survival to age 1, we found evidence that WPH had higher survival rates than wild populations in four colder introduction sites, but lower survival rates than wild populations in two warm introduction sites. SRH also had an unusually high survival rate in one introduction location. These results suggest that, at least to age 2, individuals from the hatchery populations survive well, in some cases at greater rates than individuals from wild populations.

Additionally, hatchery populations had higher growth rates than the wild populations (Fig. 2.5). Domestication selection or maternal effects could cause this pattern. Growth rate in trout is correlated with embryo size, and embryo size is affected by female size (Beacham and Murray 1985, Einum and Fleming 1999). If hatchery females were larger than their wild counterparts, this could cause their offspring grow faster (and this difference could be caused solely by the hatchery environment). To test the hypothesis that greater egg weight led to higher growth rates, we compared the mean length of females from each population. We compared the lengths of females that donated eggs to Pika Creek and the unnamed tributary in 2008. WPH female length data was not collected in 2007, so we could not compare lengths in Cherry Creek and Cherry Lake Creek.

If embryo size caused the differences in growth rate we found among donor populations, we would expect the largest females to come from the population that had the highest growth rate in Cherry Creek, namely SRH. When we compared the lengths of females, we found that the largest females were indeed from SRH; the mean ± SD length of females from SRH was 396.8 ± 21.4 mm. The second largest females were from WPH; the mean ± SD length of females from WPH was 276.7 ± 36.9 mm. In comparison, the mean length of females in wild populations ranged from 177.5 mm for White's to 200.33 and 202.1 for Ray and Muskrat, respectively. The pattern of female length among populations is exactly the same as the pattern of annual growth rate (i.e., a graph of female size by population would look very similar to Fig. 2.5), suggesting the superior growth rates of the hatchery populations may result from the effect of the hatchery environment on donor females, rather than genetic differences.

In summary, we did not observed any compelling evidence that the SRH and WPH populations were suffering from domestication selection. However, if we had examined different traits or a more direct indicator of fitness, we may have found that captive reared individuals had lower fitness than wild reared individuals. Compelling studies have demonstrated decreased reproductive success resulting from captive rearing (e.g., Fleming et al. 2000, Christie et al. 2012), and we did not examine reproductive success in this study. Further research examining the reproductive success of the hatchery and wild populations in Cherry Creek is necessary to rigorously compare the fitness of these populations.

We looked for any pattern of low fitness in a population across all of the introduction locations. A pattern of inferior performance across habitats could indicate genetic differences caused by genetic drift and inbreeding depression. At least two of the wild populations we used in this study have undergone relatively recent population bottlenecks that could have led to inbreeding depression. In one of these populations, Muskrat Creek, managers have observed albino fish, a trait that is undoubtedly detrimental in the wild. However, none of the populations displayed low overall fitness in our study. No population performed poorly on all three of our indices of fitness: relative survival, annual growth rate, and condition. In some instances, a population performed more poorly than the other populations on one of our response variables (e.g., age 1 individuals from Muskrat were in poorer condition than individuals from other wild populations, Fig. 2.7), but all in all, we found no clear evidence that any wild population was different from the others.

The most important management implication of this study is that individuals from five different WCT populations performed similarly during the first two years of life following introduction as embryos to a fishless and protected habitat. Individuals from three different wild populations had similar survival rates, annual growth rates, and condition suggesting that local adaptation and inbreeding depression have not created genetic differences that affect the post-embryonic juvenile performance of these populations. Additionally, individuals from both a recently created and a well-established hatchery population survived and thrived and their performance was not any worse than the performance of wild populations. Though our results suggest populations perform similarly following a translocation, the best test of the effectiveness of a translocation project is whether it establishes a self-sustaining and thriving population. Future studies should examine multiple generations in this study system to see if genetic differences among populations affect the long-term success of this translocation.

Tables and Figures

Table 2.1. Number of embryos introduced by donor population, introduction site and introduction year

	2007		2008		2009	
Donor population	Cherry Creek	Cherry Lake Creek	Tributary	Pika Creek	Carpenter Creek	South Fork
Muskrat	2790	2655	1621	1583	2113	1891
Ray	1919	1548	810	890	1022	889
White’s	351	664	565	409	314	322
Outbred	1533	1522	1565	1712	0	0
Hatchery	553	568	1394	1251	792	922
Total	*7146*	*6957*	*5955*	*5845*	*4214*	*4024*

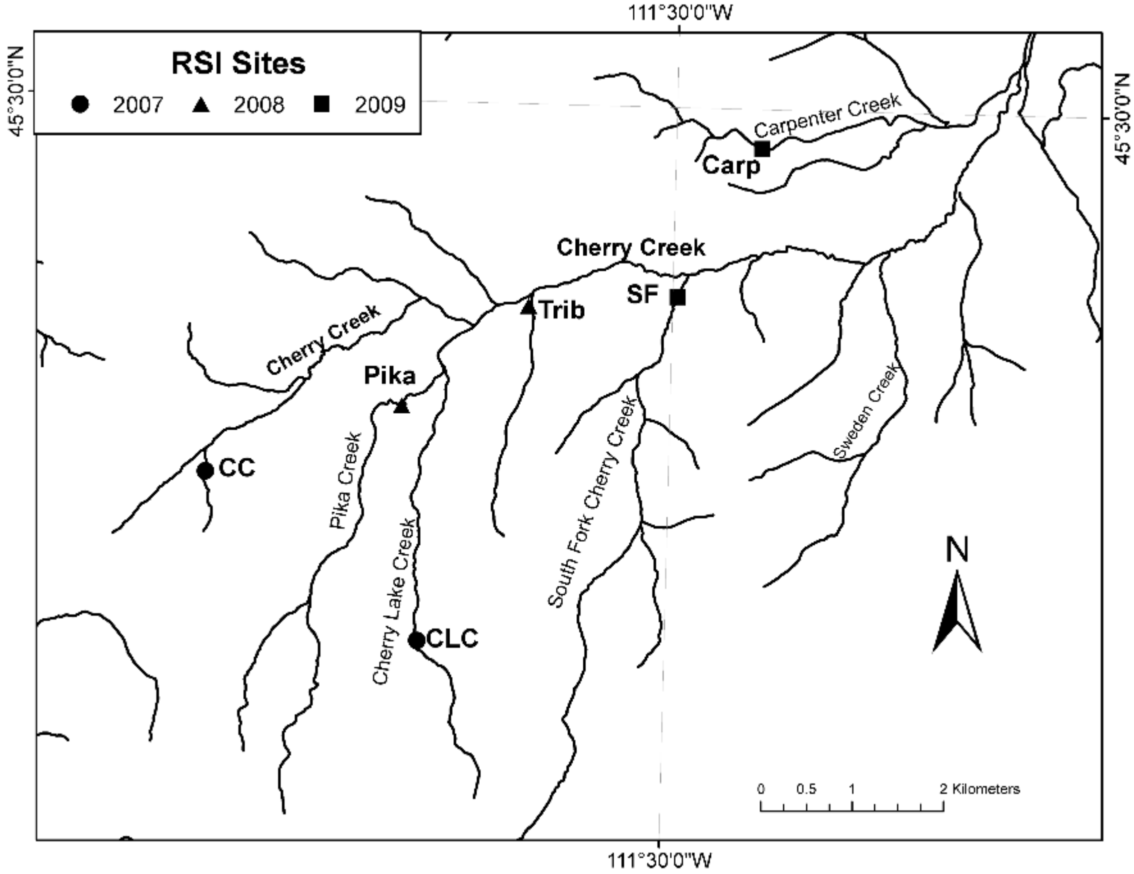

Figure 2.1 Study site showing RSI sites where embryos were introduced. CC = Cherry Creek; CLC = Cherry Lake Creek; Pika = Pika Creek; Trib = the unnamed tributary; Carp = Carpenter Creek; SF = South Fork Cherry Creek.

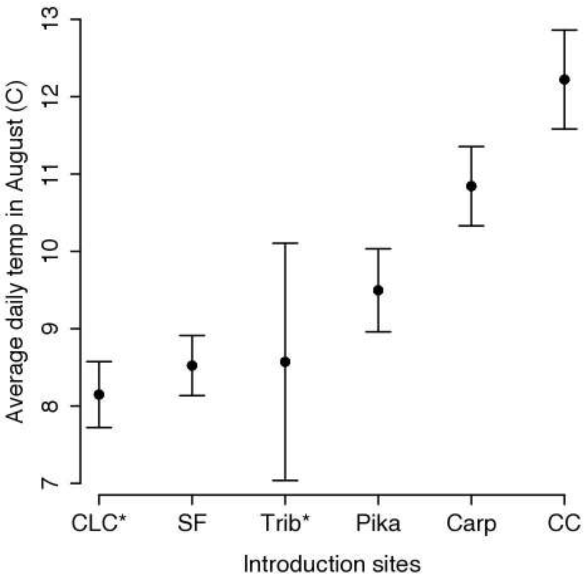

Figure 2.2. Average daily temperatures and associated 95% confidence intervals in August for our six introduction sites in 2009, or 2008 for sites marked with an asterisk (*). This same order of introduction sites from the coldest (CLC) to the warmest (CC) is used in the graphs presenting results.

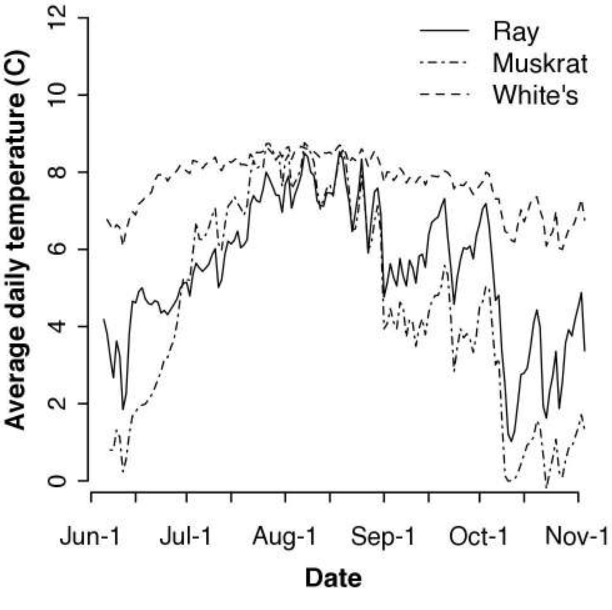

Figure 2.3. Average daily summer temperatures in the three wild donor streams. Though summer temperatures undergo annual variation, the relationship among the temperature regimes at White's, Ray, and Muskrat Creek is well-represented by this data from 2008. White's Creek tends to have higher water temperature than Ray or Muskrat, even during the hottest part of the year.

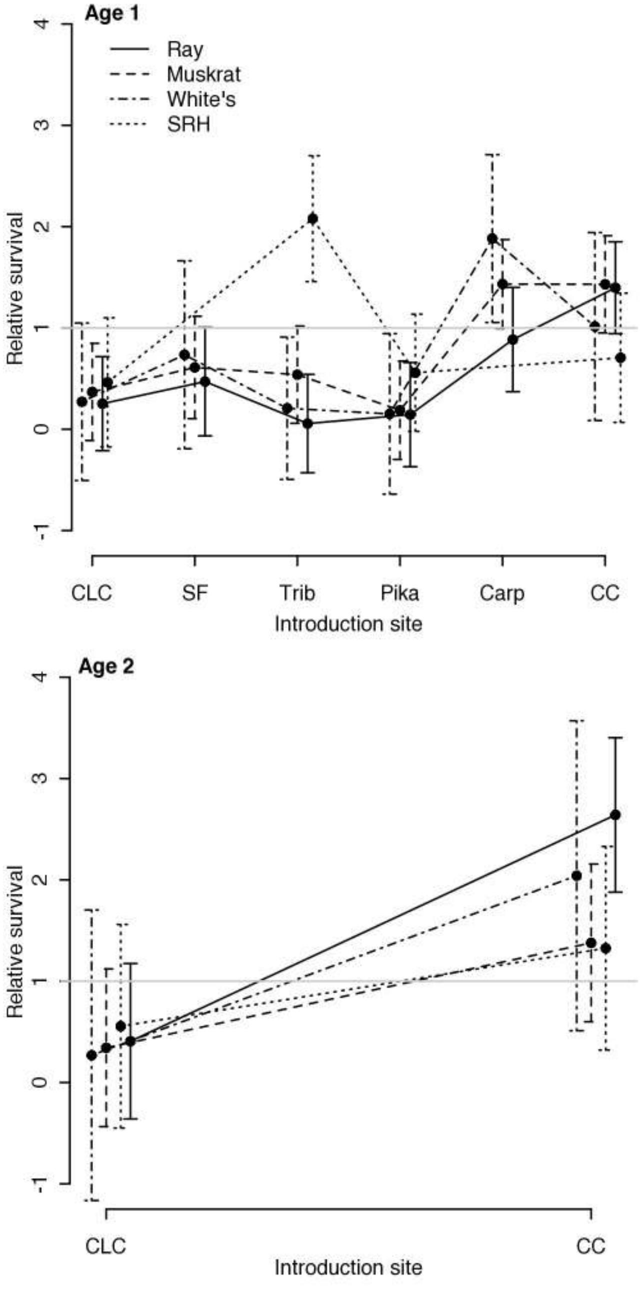

Figure 2.4. Estimated mean relative survival and associated 95% confidence intervals across donor populations and introduction sites at age 1 and age 2. When the lines representing different populations are parallel it indicates that the pattern of survival among populations is the same across introduction sites (i.e., no significant interaction exists between donor population and introduction site).

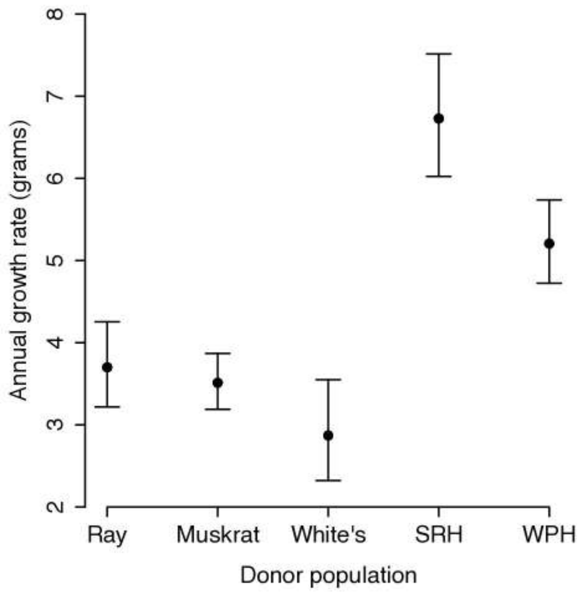

Figure 2.5. Estimated median annual growth rate at age 1 and associated 95% confidence intervals by donor population. Significant differences existed among populations (*F*(4, 607) = 28.23, *P* < 0.0001).

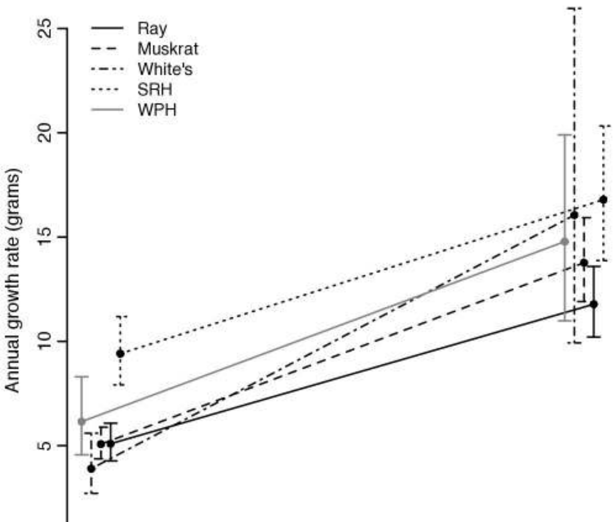

Figure 2.6. Estimated median annual growth rate at age 2 and associated 95% confidence intervals across donor populations and introduction sites. If the lines representing different populations are parallel it indicates that the pattern of survival among populations is the same across both introduction sites (i.e., there is not a significant interaction between donor population and introduction site).

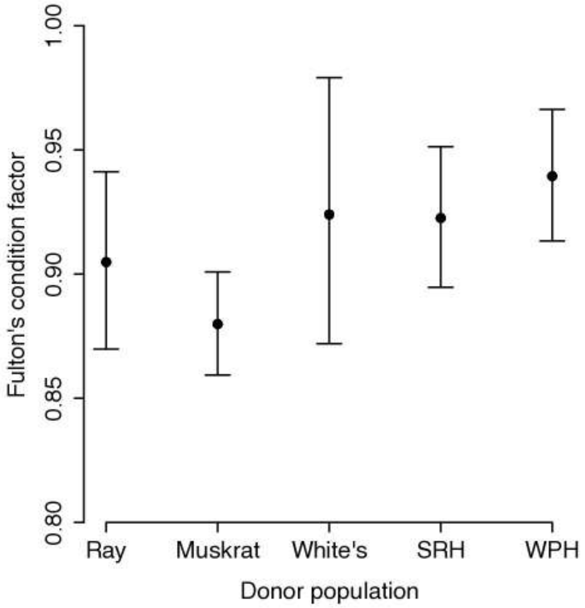

Figure 2.7. Estimated median condition factor at age 1 and associated 95% confidence intervals by donor population. There were significant differences among populations ($F(4, 805) = 3.28$, $P = 0.011$).

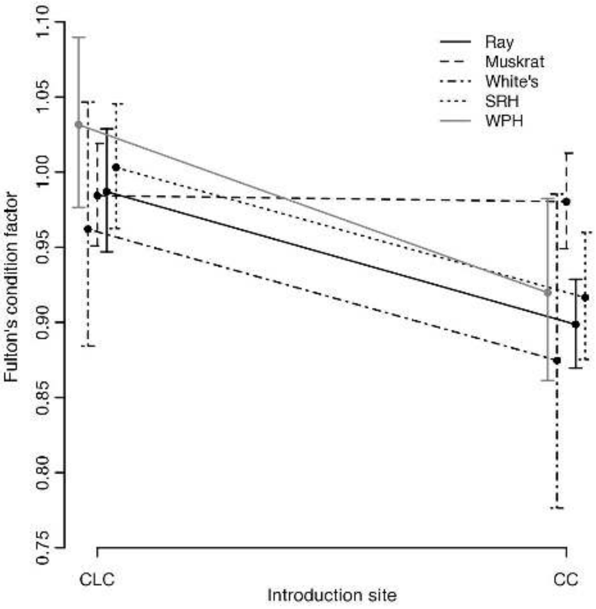

Figure 2.8. Estimated median condition factor at age 2 and associated 95% confidence intervals across donor populations and introduction sites. If the lines representing different populations are parallel it indicates that the pattern of survival among populations is the same across both introduction sites (i.e., there is not a significant interaction between donor population and introduction site).

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CHAPTER THREE

JUVENILE DISPERSAL AMONG CUTTHROAT TROUT INTRODUCED AS EMBRYOS TO VACANT HABITAT

Contribution of Authors and Co-Authors

Manuscript in Chapter 3

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Contributions: Conceived the study, collected and analyzed output data, and wrote the manuscript.

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Contributions: Obtained funding, assisted with study design, discussed the results and implications, and commented on the manuscript.

Co-Author: Andrea R. Litt

Contributions: Assisted with data analysis and commented on the manuscript.

Co-Author: Carter G. Kruse

Contributions: Obtained funding, discussed the results and implications, and commented on the manuscript.

Co-Author: Alexander V. Zale

Contributions: Assisted with study design, discussed the results and implications, and commented on the manuscript.

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Contributions: Obtained funding, assisted with study design, discussed the results and implications, and edited the manuscript at all stages.

Manuscript Information Page

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Abstract

Translocations are frequently used to increase the abundance and range of endangered fishes. One factor likely to affect the outcome of translocations is dispersal behavior. We translocated embryos from five populations of cutthroat trout (including three wild and two hatchery populations) into a five different locations within a fishless stream and determined the dispersal of age 1 and age 2 fish. At age 1, only a small percentage of fish had dispersed more than 1 km, but by age 2 we found numerous fish at locations over 4 km from their hatching location. Dispersal distance varied among introduction locations, suggesting microhabitat may affect juvenile dispersal. Additionally, juveniles from different populations dispersed different distances. We propose these differences may be caused by variation among population in innate tendency to disperse or by among-population variation in other factors affecting dispersal behavior, such as growth rate.

Introduction

Translocating fish is an important conservation strategy for many imperiled fish species, and can be used to create new populations or to supplement existing populations. Translocations can reestablish fish populations in habitats that were historically occupied or establish new populations in historically fishless habitats (e.g., U.S. Forest Service 1998, Colorado Division of Wildlife 2004). Both of these types of translocations can increase the range and abundance of threatened species, which should decrease extinction risk associated with catastrophes and other stochastic processes (Griffith et al. 1989). In addition to creating new populations, wildlife managers use translocations to supplement existing populations. Introducing new individuals can help conserve populations threatened by inbreeding depression (e.g., Madsen et al. 1999, Pimm et al. 2006, Bouzat et al. 2009). It can also speed the recovery of populations following other management interventions, such as non-native species removal or habitat restoration (e.g., Jones 2010).

Cutthroat trout exemplify a species that benefits from translocations. Cutthroat trout have been extirpated from much of their historic habitat (Shepard et al. 2005) and most of the remaining genetically pure populations of cutthroat trout are isolated above barriers that prevent immigration into the population. These barriers protect many cutthroat populations from hybridization and competition with non-native trout, but increase the risk of demographic stochasticity and inbreeding depression. Translocations are an an important conservation tool for cutthroat sub-species because they can be used to ameliorate the negative effects of inbreeding, create artificial gene flow among isolated populations, and establish additional populations (e.g., U.S. Fish and Wildlife Service. 1998; Colorado Division of Wildlife 2004; CRCT Coordination Team. 2006; Idaho Department of Fish and Game 2007; Montana Department of Fish, Wildlife, and Parks 2007).

There are many factors that influence the success of translocation projects, one of which is how transplanted fish disperse in their new habitat. Dispersal may vary depending on the habitat conditions at introduction locations. Dispersal behavior may also vary among potential contributing populations. The degree to which individuals disperse impacts how spatially extensive translocations need to be to meet restoration goals. It also affects whether one translocation is sufficient to establish a robust population or whether multiple translocations across space or time are necessary. In a cutthroat trout translocation project, extensive dispersal over barriers would seriously compromise the project. As such, it is critical we understand the role of dispersal in cutthroat translocations.

The Cherry Creek restoration project in the upper Madison River provides an exceptional system in which to study cutthroat trout dispersal after translocation. Cherry Creek has extensive high-quality habitat for cutthroat trout that is protected from upstream invasion of non-native trout by an 8 m waterfall. Because of the waterfall, Cherry Creek did not historically have cutthroat trout; however, non-native brook trout, rainbow trout, and Yellowstone cutthroat trout were introduced and thrived. Non-native trout have been removed from Cherry Creek using piscicides and multiple agencies recently collaborated to translocate ~30,000 westslope cutthroat trout (*Oncorhynchus clarkii lewisi*) embryos from five populations into Cherry Creek. The translocated population is thriving and should soon be the largest genetically pure westslope cutthroat trout (WCT) population east of the Continental Divide.

The goal of this study was to describe how the translocated WCT in Cherry Creek dispersed. More specifically we looked for differences in dispersal distance among individuals translocated into five different locations within Cherry Creek. We also looked for differences in dispersal distance among individuals from five WCT populations, including two hatchery and three wild populations.

Methods

Study Site

The study described in this paper was part of a larger restoration project to create a genetically diverse WCT population within a secure refuge in Cherry Creek, a tributary of the Madison River (Bramblett 1998). The larger restoration project took place in two phases. During the first phase, the study site was treated with the piscicides antimycin and rotenone to remove non-native fish species. During the second phase, in which this study took place, wild and hatchery WCT embryos were translocated into six locations in the drainage. Juveniles from those translocations were monitored using electrofishing sampling and genetic identification.

The study site included the upper portion of Cherry Creek and its tributaries (Figure 3.1). The study site was separated from lower reaches and the confluence with the Madison River by an 8-m waterfall that prevents rainbow trout and other non-native species from entering the upper portion of Cherry Creek (Bramblett 1998). In total, there were over 90 km of stream available, including extensive high quality WCT habitat (Bramblett 1998). We introduced embryos to six different locations in the Cherry Creek watershed over three years (Figure 3.1). No dispersal data was available for Carpenter Creek, so we will not discuss this introduction site further.

Donor Populations

Embryos introduced to the Cherry Creek study site came from five donor populations, including two hatchery and three wild populations. One of the hatchery populations was the state of Montana’s captive WCT conservation population, which is reared at Washoe Park Hatchery. This population was founded in 1984 from populations of WCT in the upper Flathead and Clark Fork river drainages. The population was infused with additional gametes from the Flathead drainage about 20 years later. We refer to this population as WPH. The other hatchery population was from a private WCT hatchery on the Sun Ranch. This population was founded in 2002 using individuals from the same wild populations that donated embryos to the Cherry Creek project. We will refer to this population as SRH. No embryos from SRH could be introduced in 2009, so only four populations were introduced that year. Otherwise, embryos from all donor populations were introduced to all sites (Table 3.1).

Embryos from three wild donor populations were introduced to Cherry Creek. These included: Ray Creek, Muskrat Creek, and White’s Creek. All three of these wild donor populations are genetically pure WCT conservation populations actively managed by the state of Montana. The population from Ray Creek (Ray) consists of about 2,500 individuals and is isolated from non-native fish by a perched culvert (L. Nelson, Montana Fish, Wildlife and Parks, personal communication). In contrast, the populations in Muskrat Creek (Muskrat) and White’s Creek (White’s) required intensive restoration management in recent years, including the construction of manmade barriers, brook trout removals, and habitat restoration (Shepard et al. 2002; L. Nelson personal communication). In 2007, Muskrat had about 3,500 individuals inhabiting over 8 km of stream, but this population may have been as small as 100 individuals before aggressive management began in 1997 (L. Nelson, personal communication). White’s also decreased to about 100 individuals in the 1990s, but later increased to about 1,000 individuals inhabiting slightly over 3 km of stream (Shepard et al. 2002). We choose these wild populations because of their physical proximity to the study site, genetic purity, and because they are the only source populations east of the Continental Divide that could provide enough embryos.

Embryo Collection and Introduction

We collected embryos from the source populations by spawning adults from each population. In the wild, we captured adults using a backpack electrofisher and confined them in in-stream containers until they were ready to spawn. After spawning, we released adults and marked them by clipping their dorsal fins so that they would not be spawned again. At the Washoe Park Hatchery, we collected embryos from ripe adults once a week for several weeks to have eyed hatchery embryos to introduce at the same time as each wild embryo introduction. At the Sun Ranch hatchery, we captured adults from the facility's holding pond with seines and spawned all ripe males and females that had not previously contributed gametes to the project. We collected a small pelvic fin clip for genetic analysis from each spawning adult, which allowed us to later use genetic testing to identify the parentage of juvenile fish in Cherry Creek.

We followed the same spawning procedure for each donor population, using protocols designed specifically for WCT. We stripped each female of eggs and split the eggs among one-liter thermoses. The eggs in each thermos were fertilized with milt from a different male to produce a unique male × female cross, called a "lot." Next we added water and left the embryos undisturbed for at least 30 minutes to water harden before rinsing the fertilized embryos. Wild embryos were re-suspended in fresh water and packed in coolers for transport to Sun Ranch, where they were incubated alongside embryos from the SRH population. Embryos from the WPH population were incubated on site at that hatchery. We held all embryos in Heath tray incubators until the eyed stage, and treated them with formalin every three to seven days to prevent fungus. After the embryos had eyed, we removed dead embryos, and counted and packed live embryos in thermoses for transport to the study site. Embryos from a single lot were introduced to the same incubator, with the exception of crosses from WPH, which were split among several incubators in some cases. The number of embryos introduced from each population varied depending on the availability of embryos (Table 3.1).

We used in-stream remote-site incubators (RSIs) to plant eyed embryos at introduction sites. RSIs are designed to consistently supply embryos with fresh water, while avoiding the sedimentation associated with buried incubators. They have previously been used to successfully reestablish Arctic grayling (*Thymallus arcticus*) and WCT to native streams in Montana (Kaeding and Boltz 2004; L. Nelson, personal communication). Embryos absorb the yolk sac in the RSI. After swimming up, fry follow the outflow of water through a tube and into a receiving bucket. We counted fry before releasing them. We monitored RSIs for function and fry emergence every two to three days from the day of planting until the last fry emerged.

In most introduction locations, we released fry in calm water just downstream of the RSIs. However, in South Fork we released fry in two different locations: just downstream of the RSIs in South Fork and 400 meters downstream just above the mouth of South Fork in the mainstem of Cherry Creek. To ensure that we could determine dispersal distance of these fish, we released all fish from a single lot in the same location. We released fish from all donor populations at both release sites so that comparisons of dispersal among donor populations should not be affected by the fact that the release method varied in South Fork.

Fish Sampling and Identification

We used a systematic sampling design with a non-random start to estimate the relative survival rate, size, and condition of fish from the five populations introduced into Cherry Creek starting in 2008 when the first fish introduced were age 1. We began sampling at each introduction site and attempted to sample throughout the introduced population's current range. We sampled 100-m sections every 300 m for about 600 m above and from 1to 5 km below introduction sites. Fish densities tended to decrease abruptly at some point below each introduction site. At that point, we decreased our sampling frequency to sample one 100-m section per 500 m of stream. We continued downstream from the introduction sites until few or no fish were found for at least two sections. In some cases, such as in Cherry Lake Creek, our most downstream sections were spread out to avoid terrain that prohibited efficient sampling. We used handheld GPS devices to record the location of each sampling section and each introduction site. Lines in Figures 2 and 3 represent sampled sections in each introduction location. We sampled age 1 fish from each introduction site and age 2 fish from the two sites used for the first year of introductions.

We sampled in late summer using two to four-person backpack electrofishing crews. Electrofishing efficiently captures salmonids, particularly those over 10 mm long (Bohlin et al. 1989), and has minimal long-term effects on WCT at the electrofishing settings we used (Dwyer et al. 2001). When shocked, fish become immobilized and lose equilibrium (Reynolds 1996). We caught immobilized fish in nets and held them until they were completely recovered. We weighed and measured the length of each fish, and removed a small portion of the pelvic fin for genetic analysis. To determine the donor population of each captured individual, we genotyped 12 microsatellite loci (see full list in Table 1 of Vu and Kalinowski 2009) using the laboratory protocols of Vu and Kalinowski (2009).

We assigned offspring to parent pairs by counting Mendelian exclusions (e.g., Muhlfeld et al. 2009). We accepted a parentage assignment if an offspring had two or fewer loci mismatched with only one parent pair. Any offspring that could not be matched to at least one parent pair with two or fewer mismatches was excluded from further analysis; 5.3% (*n* = 77) of offspring were excluded at this point in the analysis. Ninety-two individuals (6.3%) were assigned to two or more parent pairs with two or fewer mismatches. These individuals were excluded from analyses.

Determining Dispersal Distance

Hereafter, we refer to the distance between the location a fish was released after fry emergence and the location a fish was captured at age 1 or age 2 as “dispersal distance.” We have qualified this with “age 1” or “age 2” when we are referring to the subset of distances between fry emergence and capture location at age 1 and age 2, respectively. When we have used “dispersal distance” without a qualifier, we are referring to dispersal distances at both ages.

We computed dispersal distances using an “NHD plus” hydrography layer (http://nhd.usgs.gov) and Network Analyst within ArcGIS (version 9.3.1; http://www.esri.com). These values were then used to compute dispersal distance in meters to the nearest 100 m using simple arithmetic. We used negative number to designate downstream movement and positive number to designate upstream movement.

Statistical Analysis

We used non-parametric statistical analyses to compare median dispersal distances across donor populations and introduction sites. We used non-parametric tests because the distributions of dispersal distance in our data were highly skewed. We used Kruskal-Wallis one-way analyses of variance to compare dispersal distances across donor populations and across introduction locations. The null hypothesis for this test is that the populations from which the samples originate have the same median. In cases where the null hypothesis was rejected, we completed post-hoc pairwise comparisons, using Wilcoxson rank-sum tests. We adjusted *P*-values for multiple comparisons using the Bonferonni method.

Results

Over 90% (n = 761) of captured individuals introduced to the Cherry Creek system were captured within 1 km of their introduction location at age 1 (Figure 3.2). The remaining 9% ($n = 75$) were in locations 1.2 to 4.2 km from their introduction site. By age 2, 44% ($n = 123$) of individuals were more than 1 km from their introduction location (Figure 3).

As described above, we released fry in the South Fork in two different locations, while in the other introduction sites we released fry in only one location. Therefore, before comparing the dispersal distances among populations and among introduction sites, we looked more closely at dispersal distance in South Fork to see whether where fry were released affected how far they dispersed. We compared the median dispersal distances of the individuals released at the two South Fork release sites. These groups dispersed equivalent distances (Wilcoxson's rank-sum test, $W = 1562$, $P = 0.159$). We also compared the pattern among populations at both of the South Fork release sites. The among-population patterns were the same. In the South Fork release site, no differences existed among populations (Kruskal-Wallis: $KW = 4.795$, $df = 3$, $P = 0.188$). Furthermore, no differences existed among populations in the Cherry Creek release site (Kruskal-Wallis: $KW = 5.297$, $df = 3$, $P = 0.151$). Therefore, for all additional analyses, we pooled the dispersal distances of the two release sites in South Fork; we use "South Fork" to refer to the combined data henceforth.

When we compared dispersal distance among donor populations and introduction sites, we found two notable results. First, significant differences existed in dispersal distance among introduction sites at age 1and age 2. Median dispersal distances were not equivalent across introduction sites (Kruskal-Wallis $P < 0.0001$). Post-hoc pairwise comparisons revealed that the median dispersal distance in Cherry Creek was significantly greater than the median dispersal distance in any other location (Table 3.2, Figure 3.4). In contrast, the median dispersal distance in Cherry Lake Creek was significantly less than the median dispersal distance in three of the four other sites (Table 3.2, Figure 3.4). At age 2, the median dispersal distance in Cherry Creek was significantly greater than that in Cherry Lake Creek ($W = 14{,}013$; $P < 0.0001$).

Our second notable result was that significant differences existed in dispersal distance among populations in four out of the five introduction sites at age 1 and both of the introduction sites at age 2. At age 1, statistically significant differences existed among the median dispersal distance of donor populations in every introduction site except South Fork (Cherry Creek, Pika Creek, Unnamed tributary, and Cherry Lake Creek: Kruskal-Wallis $P < 0.0001$, South Fork: Kruskal-Wallis $P = 0.105$). At age 2, statistically significant differences existed among the median dispersal distance of donor populations in Cherry Creek (Kruskal-Wallis $P < 0.0001$) and Cherry Lake Creek (Kruskal-Wallis $P < 0.0001$). The rest of the results presented below pertain to the sites in which there were significant differences among populations.

Post-hoc pairwise comparisons of dispersal distance at age 1 showed that WPH and White’s most often differed from the other populations because individuals from WPH and White’s tended to disperse shorter distances (Table 3.3). The median dispersal distance of WPH was significantly less than the median dispersal distances of SRH, Ray, and Muskrat at every site and significantly less than that of White’s in two of five sites (Table 3.3). The median dispersal distance of White’s was significantly less than that of Muskrat in two of four introduction sites and significantly less than SRH in one introduction site (Table 3.3). Ray and White's could only be compared in two sites due to low survival of Ray; there was no difference between their median dispersal distances in those sites (Table 3.3).

At age 2, pairwise comparisons revealed a slightly different pattern than we found at age 1. Dispersal distance of WPH was not as consistently different from the other populations. Instead, Muskrat stood out as the most disparate population because individuals from that population dispersed greater distances. In Cherry Creek, the median dispersal distance of WPH was significantly less than that of Muskrat ($W = 490$, $P = 0.004$), but no different from SRH, White's, or Ray. The median dispersal distance of Muskrat was also significantly greater than Ray ($W = 1892.5$, $P = 0.002$). No other pairwise comparisons produced significant differences. In Cherry Lake Creek, the median dispersal distance of WPH was significantly less than that of Muskrat ($W = 579$, $P < 0.0001$) and SRH ($W = 412$, $P = 0.020$), but not White's or Ray. The median dispersal distance of Muskrat was significantly greater than that of Ray ($W = 904$, $P = 0.003$) and White's ($W = 222$, $P = 0.039$).

Discussion

This study examined how five populations of juvenile cutthroat trout dispersed after being translocated into five locations in a fishless watershed. We observed that dispersal patterns in the first two years of life varied across introduction sites and across donor populations. Because of the potential impacts of the differences we observed, it is important to understand as much as possible about what caused these differences, and we will discuss each of these notable observations in turn.

First, what caused differences in dispersal distance among introduction sites? Water temperature in the Cherry Creek watershed varied across introduction locations and may have affected how far fish dispersed. Cherry Creek—the site in which individuals displayed the most movement—had the warmest water temperatures, while the site in which individuals dispersed the least, Cherry Lake Creek, had the coldest. Water temperature affects all aspects of life for stream-dwelling salmonids; it strongly governs growth, development, reproductive cycles, migrations and other life history traits concomitant to survival (Liknes and Graham 1988, McIntyre and Rieman 1995, Bear et al. 2005). Water temperature could have directly governed dispersal behavior in this system or the relationship between water temperature and dispersal could have been mediated by another factor, such as growth. Further research, including examining dispersal in additional warm introduction sites, will be necessary to test the hypothesis that water temperature affects dispersal distance. If this hypothesis were supported in future research, it would also be necessary to determine whether this pattern exists primarily because warm water encourages dispersal or because cold water limits dispersal.

Another possible explanation for the increased downstream dispersal we found in Cherry Creek is that there may be less quality of young-of-year (YOY) habitat in this location. Lower quality YOY habitat could encourage individuals to disperse in search of necessary resources. For example, increased lateral habitat (e.g., backwater and eddies at the margin of channels) is associated with increased YOY cutthroat trout densities (Moore and Gregory 1988). We did not survey habitat in this study. However, we anecdotally observed that the habitat in Cherry Creek is distinguished from the other sites because the first several kilometers downstream from the introduction site flow through low gradient meadow, while other sites tend to have steeper gradients and more tree cover. More systematic habitat surveys would be necessary to further test the hypothesis that the availability of YOY habitat influenced dispersal difference among introduction sites.

Population density may also be related to differences in dispersal distance among introduction sites. We tested this hypothesis by comparing the density of fry across introduction sites. We released fry manually and counted the number of fry released in each introduction site. We also measured stream width at most introduction locations. Given this information, we calculated fry density as the number of fry per stream width meter. We found that the unnamed tributary—not Cherry Creek—had the greatest density of fry (results not shown). Cherry Creek had the second greatest fry density, followed by Pika and Cherry Lake Creek, which had similar densities that were approximately half that of the unnamed tributary (results not shown). Therefore, it appears that fry density does not explain differences in dispersal distance among introduction locations.

Our sampling efforts could have contributed to some of the differences in dispersal distance we found among introduction sites. At age 1, we sampled over similar distances in the unnamed tributary and Cherry Lake Creek (Figure 3.2), but sampled more extensively in Cherry Creek, Pika Creek, and South Fork (Figure 3.2). When we completed post-hoc pairwise comparisons, we found that 7 out of 10 comparisons among sites at age 1 were significantly different (Table 3.2). Three of these significant differences feasibly could have been impacted by the differences in sampling effort describe above (Cherry Lake Creek vs. Cherry Creek and vs. South Fork, and Cherry Creek vs. the unnamed tributary), but the other four cannot be explained by our methodology.

At age 2, differences in dispersal distance between introduction sites are unlikely to be due to differences in sampling effort. In Cherry Lake Creek we sampled five fewer sections than in Cherry Creek and we sampled less consistently across space (Figure 3.3). However, our sampling in Cherry Lake Creek was most extensive beyond 3 km downstream of the introduction site (Figure 3.3), so our estimate of dispersal distance in Cherry Lake Creek should be biased toward greater distances. The fact that the median dispersal distance in Cherry Lake Creek was substantially smaller than that in Cherry Creek *despite* sampling biased in the other direction suggests age 2 individuals in Cherry Lake Creek dispersed considerably shorter distances than age 2 individuals in Cherry Creek.

Our second notable observation was that we found marked differences in dispersal distance among donor populations. At age 1, the most striking differences were between WPH and the other populations (Figure 3.2). Individuals from WPH consistently dispersed significantly shorter distances than individuals from Ray, Muskrat, and SRH (Table 3.3). The most obvious difference between WPH and the other populations is that WPH has long been a captive-reared population. Though individuals from both SRH and

WPH technically came from hatchery populations, there are important differences between these populations. The SRH population was created recently from wild WCT populations geographically close to Cherry Creek. In contrast, the WPH was founded almost 30 years ago. Both hatchery populations differ from the wild populations because they are outbred and because the females are larger. However, the SRH population has had one, or maybe two, generations to adapt to captivity, while the WPH population had at least 10 generations for fish to adapt to captivity.

Recent studies have documented adaptation to captivity in salmonid hatchery populations that is detrimental to fitness in the wild. In steelhead trout, each generation of captive rearing reduced reproductive capabilities by 40% (Araki et al. 2007). Christie et al. (2012) attributed this decline to rapid adaptation to captivity. In our system, the population most likely to be adapted to captivity (WPH) dispersed the least. It is not immediately obvious how captivity would select against a tendency to disperse. One potential explanation is that hatchery fish have been selected for rapid growth rate, and fish that grow rapidly outcompete fish from other locations and therefore disperse less (e.g., Nakano 1995, Hughes 2000, Hansen and Closs 2009). To test this hypothesis, we would need to examine growth rates throughout the first couple years of life to see if: (1) individuals from WPH grew more quickly than individuals from other populations, and (2) faster growing individuals dispersed shorter distances than slower-growing individuals.

Another way hatchery populations like WPH differ from wild populations is in embryo size. Differences in embryo size could contribute to the differences in dispersal we found among donor populations because greater embryo weight can confer a growth advantage in habitats with competition (Einum and Fleming 1999). Trout that grow more quickly can outcompete smaller trout for access to food, causing smaller fish to disperse greater distances than larger fish (e.g., Nakano 1995, Hughes 2000, Hansen and Closs 2009). Hence, differences in initial embryo weight could have led to differences in growth, which could have led to differences in dispersal. To test the hypothesis that greater embryo weight led to decreased dispersal, we compared the mean length of females from each population. We compared female length because female size in trout is positively correlated with embryo weight (Beacham and Murray 1985). We compared the lengths of females that donated embryos to Pika Creek and the unnamed tributary in 2008. WPH female length data was not collected in 2007, so we could not compare lengths in Cherry Creek and Cherry Lake Creek.

If embryo size caused the differences in dispersal distance we found among donor populations, we would expect the largest females to come from the population that dispersed the least, namely WPH. When we compared the lengths of females, we found that the largest females were from SRH; the mean ± SD length of females from SRH was 396.8 ± 21.4 mm. The second largest females were from WPH; the mean ± SD length of females from WPH was 276.7 ± 36.9 mm. The females from SRH were significantly longer than the females from WPH, which were significantly longer than the females from the three wild stocks (results not shown). This pattern does not support the hypothesis that differences in embryo weight led to differences in dispersal among populations because both the SRH and the WPH populations had large females that contributed large embryos, yet dispersal behavior was very different in these two populations.

Differences in fry emergence dates could also have contributed to the differences in dispersal distance we observed among populations. Fry from different populations emerged at different times because spawning dates varied across populations. Fry that emerge earlier in the season may have been able to monopolize feeding locations, forcing later-emerging fry to disperse greater distances. To test this explanation for differences in dispersal patterns among donor populations, we compared the introduction dates of embryos from different donor populations. In 2007, embryos from SRH and WPH were introduced on the same days, one week to one month before embryos from White's, Ray, and Muskrat. In 2008, embryos from WPH were introduced at the same time as embryos from every other donor population. In summary, the variation in the timing of embryo introduction and subsequent emergence cannot explain the differences in dispersal among populations.

We observed differences in dispersal among populations at age 1 and age 2. Further research should focus on the duration of these differences. If differences among populations are unpredictable over time, it may not matter which populations contribute individuals to a translocation project, but if differences among populations are consistent the long-term success of translocation projects may depend on which populations contribute individuals. In this study, the fact that the differences in dispersal distance among populations changed slightly from age 1 to age 2 could have resulted from our study design. We had fewer sites in which to compare populations at age 2. Additionally, just 27 individuals represented the WPH population at age 2, while over 65 individuals represented every other population except White's.

This study has a few important management implications. First, dispersal behavior following translocations varied among populations. If we had introduced only fish from WPH into this system, it would have taken much longer to fill habitat than if we had only introduced fish from Muskrat. Second, though most fish tended to fill habitat downstream of the introduction sites, some fish moved through fishless habitat, suggesting some fish had an innate tendency to disperse downstream. The frequency of this trait may vary by populations. An innate tendency to disperse downstream could be a problem in many cutthroat translocation efforts because cutthroat populations are often isolated from non-native trout with barriers to upstream movement. Knowing the dispersal tendencies of donor populations is therefore important to successfully establishing new populations using translocations. Third, there is potential for fish to move long distances downstream as early as age 1. In smaller systems, fish would have been lost over barriers within the first year after this translocation. Harig and Fausch (2002) found that cutthroat trout translocations were most likely to lead to established populations when available stream habitat exceeded 5.7 km. This study supports the suggestion that translocated fish require extensive stream habitat.

Previous research on cutthroat translocations did not prepare us for the differences in dispersal distance we found among populations and among introduction sites. Yet differences like these could seriously impact the effectiveness of translocation projects. Given the cost of these projects and the consequences of failure, it is critical that researchers, managers, and other interested parties continue to collaborate to determine the strategies and factors necessary to maximize the effectiveness of translocation projects.

Tables and Figures

3.1. Number of embryos introduced by donor population and introduction site.

Donor populations	Cherry Creek	Cherry Lake Creek	Pika Creek	Unnamed tributary	South Fork	*Total*
Muskrat	2790	2655	1583	1621	1891	*10540*
Ray	1919	1548	890	810	889	*6056*
White's	351	664	409	565	322	*2311*
SRH	1553	1522	1712	1565	—	*6352*
WPH	498	513	1251	1394	922	*4578*
Total	*7111*	*6902*	*5845*	*5955*	*4024*	*29837*

Table 3.2. Bonferonni adjusted *P*-values for Wilcoxson rank-sum tests comparing median dispersal distance between introduction sites at age 1.

Comparison	*P*-value
Cherry — Pika	**<0.0001**[a]
Cherry — Unnamed tributary	**<0.0001**
Cherry — South Fork	**<0.0001**
Cherry — Cherry Lake Cr.	**<0.0001**
Pika — Unnamed tributary	1.000
Pika — South Fork	**0.007**
Pika — Cherry Lake Cr.	0.196
Unnamed tributary — South Fork	1.000
Unnamed tributary — Cherry Lake Cr.	**<0.0001**
South Fork — Cherry Lake Cr.	**<0.0001**

[a] Bold values indicate significance at alpha level 0.05.

Table 3.3. Bonferonni adjusted *P*-values for Wilcoxson rank-sum tests comparing median dispersal distance between donor populations at age 1.

Comparison	Cherry Creek[a]	Pika Creek	Unnamed tributary	Cherry Lake Creek
Ray — Muskrat	1.000	—	—	1.000
Ray — White's	0.259	—	—	1.000
Ray — SRH	1.000	—	—	0.230
Ray — WPH	**<0.0001**	—	—	**<0.0001**
Muskrat — White's	0.095	**0.010**	**0.022**	1.000
Muskrat — SRH	0.378	1.000	1.000	0.549
Muskrat — WPH	**<0.0001**	**<0.0001**	**0.001**	**<0.0001**
White's — SRH	1.000	0.070	**0.010**	1.000
White's — WPH	**0.034**	1.000	0.754	**<0.0001**
SRH — WPH	**0.022**	**<0.0001**	**<0.0001**	**0.021**

[a] Comparisons are within introduction site; South Fork was excluded because there were no differences among populations (Kruskal-Wallis = 6.15, df = 3, *P* = 0.10). Bold values indicate significance at alpha level 0.05. Missing values reflect poor survival by individuals from Ray introduced in 2008.

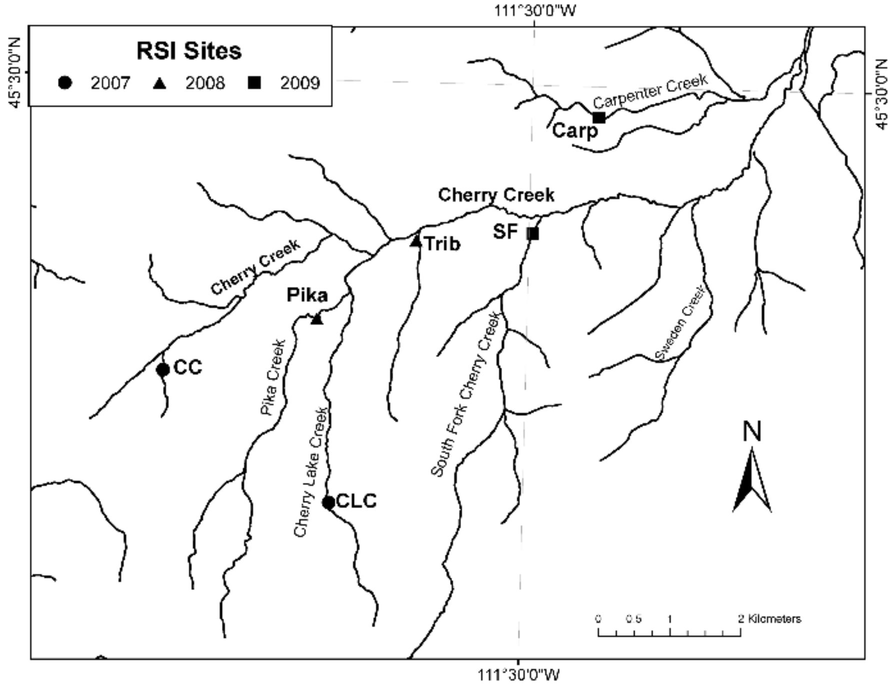

Figure 3.1. Study site showing introduction sites. Fish introduced to Carpenter Creek are not discussed in this paper because no dispersal data was available for this site.

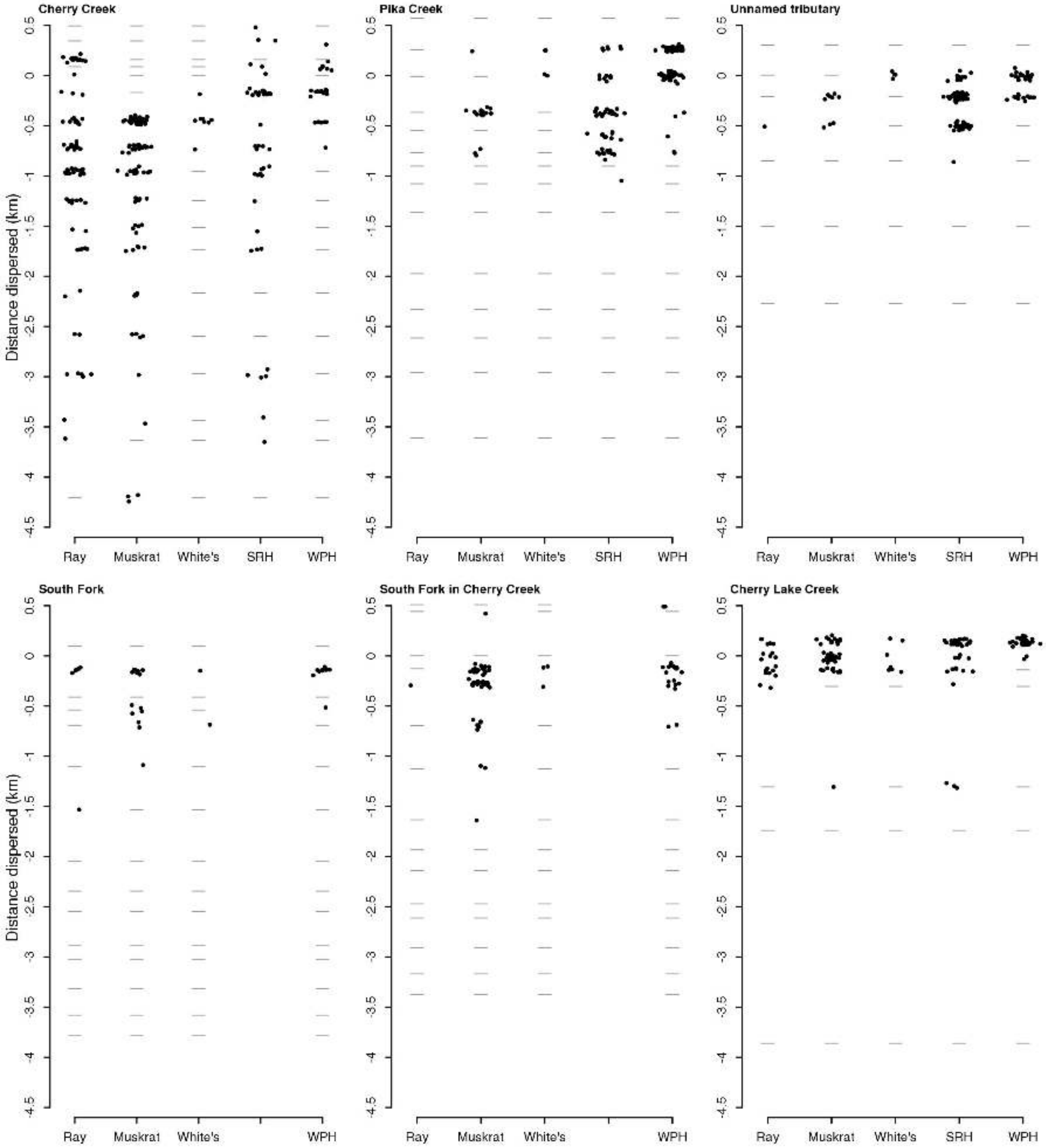

Figure 3.2. Distance between hatching location and capture at age 1 by donor population. Each panel represents one introduction site, except South Fork and South Fork in Cherry Creek. At the South Fork introduction site, hatched fry were released in one of two locations: at the introduction site in South Fork and in Cherry Creek above the mouth of South Fork. Negative dispersal distance values represent downstream movement; positive values represent upstream movement. Each dot represents a captured fish. Dots have been jittered horizontally and vertically to avoid overlap. Each line represents a section sampled in which no fish from that donor population/introduction site combination were found.

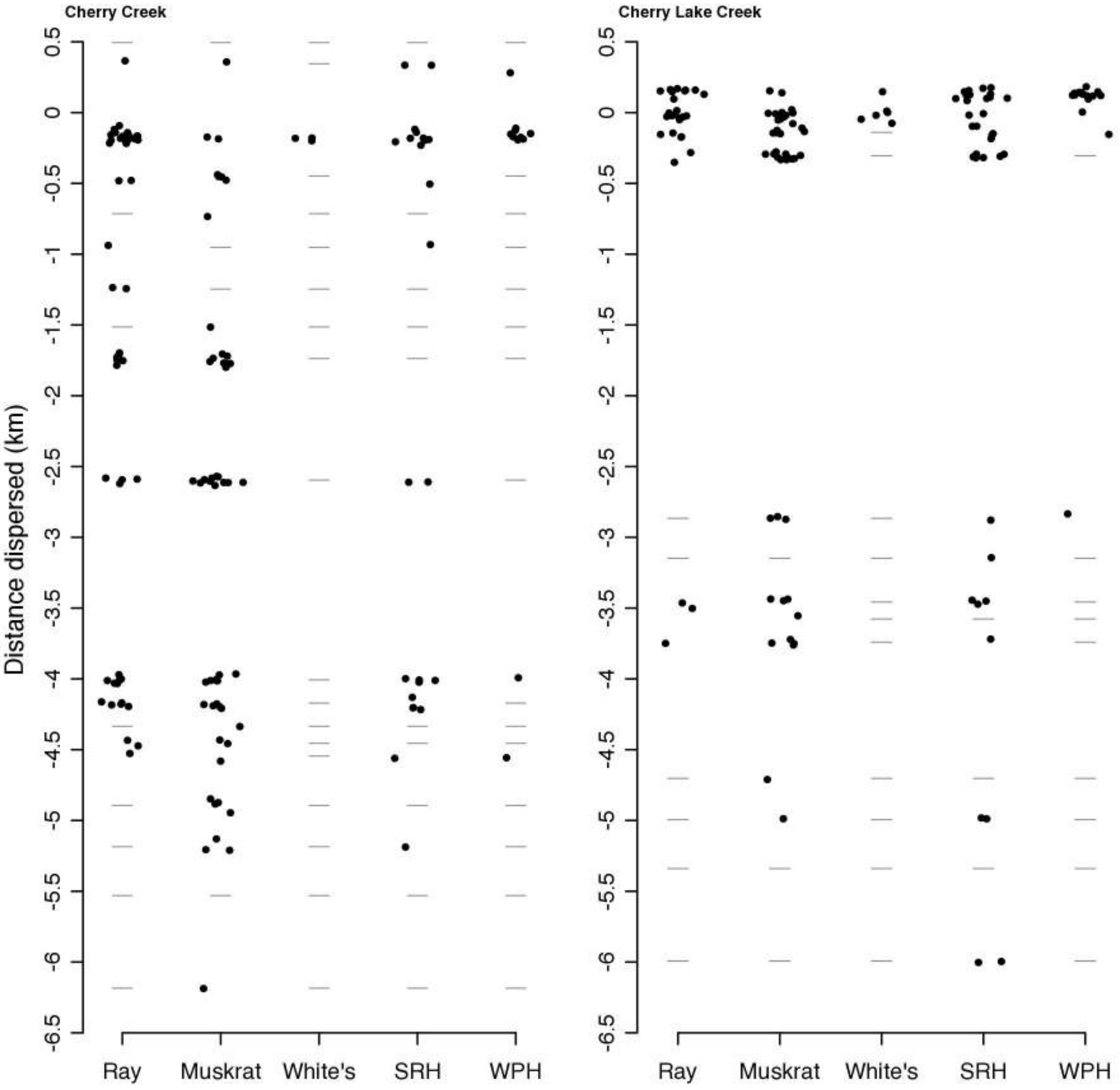

Figure 3.3. Distance between hatching location and capture at age 2 by donor population. Each panel represents one introduction site. Negative dispersal distance values represent downstream movement; positive values represent upstream movement. Each dot represents a captured fish. Dots have been jittered horizontally and vertically to avoid overlap. Each line represents a section sampled in which no fish from that donor population/introduction site combination were found.

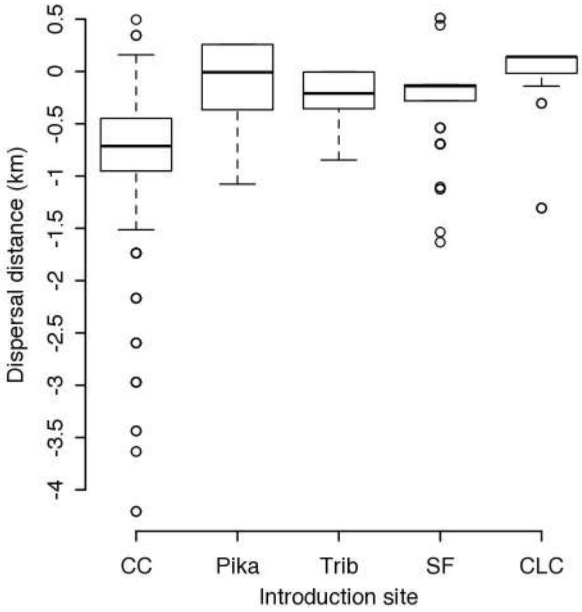

Figure 3.4. Box-and-whisker comparison of dispersal distance at age 1 across introduction site. The darkest line represents the median. The space within the box is called the interquartile range (IQR); the upper and lower bounds of the closed box represent data points in the 75th percentile and the 25th percentile, respectively. Whiskers represent the lowest and highest data points no more than 1.5 times the IQR above and below the box. Data points not included in this range are represented as dots.

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CHAPTER FOUR

ACTIVE LEARNING *NOT* ASSOCIATED WITH STUDENT LEARNING IN A RANDOM SAMPLE OF COLLEGE BIOLOGY COURSES

Contribution of Authors and Co-Authors

Manuscript in Chapter 4

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Abstract

Previous research suggested that adding active learning to traditional college science lectures substantially improves student learning. However, this research predominantly studied courses taught by science education researchers, who are likely to have exceptional teaching expertise. The present study investigated introductory biology courses randomly selected from a list of prominent colleges and universities to include instructors representing a broad population. We examined the relationship between active learning and students learning in the subject area of natural selection. We found no association between student learning gains and the use of active learning instruction. Although active learning has the potential to substantially improve student learning, this research suggests that active learning, as used by typical college biology instructors, is not associated with greater learning gains. We contend that most instructors lack the rich and nuanced understanding of teaching and learning that science education researchers have developed. Therefore, active learning as designed and implemented by typical college biology instructors may superficially resemble active learning used by education researchers, but lacks the constructivist elements necessary for improving learning.

Introduction

Students in introductory science courses often fail to learn fundamental scientific concepts (e.g., Halloun and Hestenes, 1985; McConnell *et al.*, 2006). For example, students leaving introductory biology courses often believe evolution is caused by an animal’s desire to change. Similarly, students often leave introductory physics courses believing heavy objects fall faster than lighter ones. There is a consensus among education researchers that much of the difficulty students have learning science can be attributed to the passive role students play during traditional lectures (e.g., McKeachie *et al.*, 1990; Bonwell and Eison, 1991; Nelson, 2008). Therefore, in the past decade, there has been a growing number of calls to increase the amount of active learning in college science lectures (e.g., National Science Foundation, 1996; National Research Council, 1997, 2003, 2004; Boyer Commission, 1998; Allen and Tanner, 2005; Handelsman *et al.*, 2005).

Active learning is difficult to define, but essentially occurs when an instructor stops lecturing and students work on a question or task designed to help them understand a concept. A classic example of active learning is a think-pair-share discussion, in which students think about a question posed by the instructor, pair up with other students to discuss the question, and share answers with the entire class.

Extensive research shows that lectures using active learning can be much more effective than traditional lectures that use only direct instruction. For example, a seminal survey of introductory physics classes at nine high schools and 13 colleges and universities showed that, on average, students taught using active learning learned twice as much as students taught using direct instruction (Hake, 1998a, 1998b). A host of quasi-experimental studies comparing student learning in a lecture-based course to student learning in an active learning version of the course, found adding active learning increased student learning. These studies established active learning could improve student learning across a wide variety of science disciplines (Ruiz-Primo, 2011), including biology (Jensen and Finley, 1996; Udovic *et al*., 2002; Knight and Wood, 2005; Freeman *et al.*, 2007; Nehm and Reilly, 2007; Haak *et al.*, 2011), physics (Shaffer and McDermott, 1992; Crouch and Mazur, 2001; Deslauriers *et al.*, 2011), and chemistry (Wright, 1996; Naiz *et al.*, 2002). There have been so many papers documenting this trend that it is now widely accepted that students taught with active learning will learn substantially more than students taught the same material with direct instruction.

However, a close review of the literature supporting the effectiveness of active learning reveals a serious limitation: most of the active learning courses studied to date were taught by instructors who had science education research experience (by which we mean they published papers on science education, received funding for education research, or attended conferences on science education research) (e.g., Hake, 1998a, 1998b; Knight and Wood, 2005; Deslauriers *et al.*, 2011). We expect education researchers have a rich and nuanced understanding of their field. This expertise may improve an instructor's effectiveness in many ways, including the ability to use active learning (Pollock and Finkelstein, 2008; Turpen and Finkelstein, 2009). This limitation has been recognized (e.g., Hake, 1998a; Pollock and Finkelstein, 2008), but the implications of this potential problem have not been explored. In particular, we are concerned the impressive learning gains documented in the active learning literature may not be representative of what typical instructors are likely to obtain.

The goal of this research was to address that gap by studying the relationship between the use of active learning instruction and how much students learned about natural selection in a random sample of introductory college biology courses from around the United States.

Methods

Sample

The goal of our sampling design was to infer results to introductory biology courses at major colleges and universities throughout the United States. Thus we began with a list of the two largest public colleges and universities from each of the fifty states, plus a list of the 50 top-ranked colleges and universities from the 2009 “US News & World Report Best Colleges” ranking; some institutions were on both lists. From this combined list of 144 institutions, we randomly selected 77. We then contacted instructors at these institutions to participate during one of three consecutive semesters in 2009 and 2010.

In each school, we sought out introductory biology courses that taught natural selection and were designed for biology majors. To identify appropriate courses and course instructors, we used information gathered on institution websites and from biology department staff. We chose to survey courses teaching natural selection because it is a mechanism of evolution and therefore a core concept in biology (Gregory *et al.*, 2011), because it is conceptually challenging for students to learn (Bishop and Anderson, 1990; Nehm and Reilly, 2007; Gregory, 2009), and because well-developed instruments exist to measure conceptual understanding of natural selection (e.g., Anderson *et al.*, 2002; Nehm and Reilly, 2007; Nehm and Schonfeld, 2008). We contacted a total of 88 introductory biology instructors, sending at least three emails over a month, followed by at least one phone call. We made a final attempt four to six months later to contact instructors who did not respond to our initial queries.

Of the 88 instructors from 77 institutions we invited to participate in our study, 33 (38%) agreed to participate fully; these instructors are hereafter referred to as FULLY PARTICIPATING INSTRUCTORS. These instructors taught 29 different courses at 28 institutions in 22 states. Two of these institutions were private and 26 were public. Seven institutions were on the "US News & World Report Best Colleges" list. If an instructor declined to participate in our study, we asked him or her to complete a survey describing his or her course and teaching methods so we could account for non-response bias. We were able to collect data from an additional 22 instructors, which represents 25% of the entire random sample of instructors and 44% of the instructors who did not agree to fully participate in this study. These instructors are hereafter referred to as PARTIALLY PARTICIPATING INSTRUCTORS. Compared to previous research assessing the relationship between active learning instruction and student learning gains, our sample is the largest sample of instructors and institutions and the only sample that was randomly selected from a broad population of college science instructors.

Assessing Learning

In each fully participating course, we assessed how much students learned about natural selection. We assessed learning by testing students near the beginning (pre-test) and end (post-test) of the term using two instruments that measure conceptual understanding of natural selection. First, we used the Conceptual Inventory of Natural

Selection – Abbreviated (CINS-abbr), a 10-question multiple-choice test (see sample questions in Appendix A; Anderson *et al.*, 2002; Anderson, 2003; Fisher, *et al.*, unpublished data) The questions on this instrument are nearly identical to those on an original concept inventory with well-established reliability (Anderson *et al.*, 2002). Each distractor, or wrong answer, was designed to appeal to students who hold common misconceptions about natural selection. The content and face validity of these questions has been established for both the original CINS and the CINS-abbr (Anderson *et al.*, 2002; Fisher, *et al*., unpublished data*)* Second, students completed one open-ended question from a set of five questions developed by Bishop and Anderson (1990) and later revised by Nehm and Reilly (2007) to measure college biology majors' understanding of natural selection. This set of open-ended questions was designed to assess student understanding across different levels of Bloom's taxonomy (Nehm and Reilly, 2007). We used a question at Bloom's 'application' level, which tests a student's ability to apply knowledge to a novel question. This set of questions tends to be more difficult for students than CINS questions (Nehm and Schonfeld, 2008). The question we used, hereafter called the 'cheetah question' was:

> "Cheetahs (large African cats) are able to run faster than 60 miles per hour when chasing prey. How would a biologist explain how the ability to run fast evolved in cheetahs, assuming their ancestors could run only 20 miles per hour?"

To score student responses to the cheetah question, we developed, piloted, refined, and applied a coding rubric (Appendix B). Biology experts (TMA and STK) designed the rubric after reviewing a rubric previously developed for the cheetah question (Nehm and Reilly, 2007). Our rubric gave more weight to three concepts we felt were core concepts a student must understand in order to understand natural selection: the existence of phenotypic variation within a population, the heritability of that variation, and differential reproductive success among individuals. We gave less weight to three additional concepts we felt were representative of more advanced understanding: the causes of variation, a change in the distribution of individual traits within a population, and change taking place over many generations. We designed this coding rubric to be sensitive to developing understanding, yet allow room for students to demonstrate more advanced understanding. To establish inter-rater reliability (IRR), two researchers (TMA & CAC) independently scored a random sample of 210 responses. IRR was measured using Pearson's correlation. There was a strong correlation between the total essay score awarded by the two researchers ($r = 0.93$, $p < 0.0001$). The researchers then independently scored the remaining responses to the cheetah question using the coding rubric.

Due to the large number of students included in this study (over 8000), we scored a sub-sample of student responses to the cheetah question from each course. We randomly selected approximately 50 students from each course and scored responses from students who completed both pre- and post-test cheetah questions. The mean sub-sample size was 42 students (*SD* = 12). For analyses of learning gains on the cheetah question described below, we excluded three courses whose sub-sample included fewer than 20 students and one course in which pre- and post-test responses could not be matched by student.

Students completed the CINS-abbr and the cheetah question on paper or online. To test for differences between student performance on paper versus online instruments, we used independent samples *t*-tests. We found no significant differences in mean test scores or learning gains between courses using online testing and those using paper testing (see full results in Appendix 4.5).

In some courses, students earned nominal course credit for logging into the online test, but actually completing test questions was voluntary in all classes. To look for differences between test performance in courses in which students earned credit and courses in which students did not, we again used independent samples *t*-tests. We found only one significant difference between courses in which students earned credit and those in which students did not, and it was in the opposite direction than would be expected if awarding credit led to increased participation or performance. Students in courses in which credit was not awarded had significantly higher scores on the post-test CINS-abbr than students in courses that awarded credit ($p = 0.03$) (see full results in Appendix 4.5). Because awarding credit was not associated with improved test performance or learning gains as would be predicted, we did not include this as a variable in further analysis.

Calculating Learning Gains

In order to decide how best to calculate how much students learned about natural selection, we examined the intercorrelations among pre- and post-test scores and four possible calculations of learning gains: effect size (Cohen's *d*), average normalized gain, percent change, and raw change (Table 4.1). The calculations of learning gains were highly intercorrelated (see supplemental online materials), with Pearson's *r* ranging from

0.79 to 0.99 (all *p*-values < 0.001; *p* was calculated using the Holm-Bonferonni method to account for error associated with multiple comparisons). Although average normalized gain is a commonly used estimator of learning gains in research on active learning (e.g., Hake, 1998a; Crouch and Mazur, 2001; Knight and Wood, 2005), it was strongly correlated with mean course pre-test scores on the CINS-abbr ($r = 0.51$, $p = 0.012$, Appendix 4.5). This correlation means that courses with high average pre-test scores receive relatively higher normalized gains than courses with lower average pre-test scores. Additionally, percent change was strongly negatively correlated with pre-test scores on the cheetah question ($r = -0.62$, $p = 0.003$, Appendix 4.5), resulting in a bias in the other direction. We ultimately chose to calculate learning gains using Cohen's *d* for a repeated measures design (Dunlap *et al.*, 1996). No calculation of learning gains is without problems, so we also repeated the analyses described below using each of the four calculations of learning gains. If all analyses produced similar results, we would feel confident that the way we choose to quantify student learning was not impacting our overall results.

Surveying Teaching Methods and Course Details

We gathered details on each course from the instructor and the students. An online survey (Appendix 4.3) was used to gather data from FULLY PARTICIPATING INSTRUCTORS, as well as PARTIALLY PARTICIPATING INSTRUCTORS. The instructor survey solicited information about the course, the instructor's teaching experience and teaching methods, and the students' background. We also surveyed students during the post-test about their instructor's teaching methods and their perceptions of the course (Appendix 4.4).

To corroborate self-report data from instructors, the instructor and his or her students answered an identical question about the instructor's use of active learning (Appendix 4.3, question 8; Appendix 4.4, question 3). Student reports of active learning agreed with instructor reports. Agreement between instructor responses and the most common student response (i.e., the mode) in each course was calculated using Cohen's kappa, which indicated substantial agreement ($K = 0.69$) (Viera and Garrett, 2005). Therefore, we used instructor reports of active learning for all further analyses.

Previous research has typically categorized instructors' methods as either "active learning" or "traditional lectures," but as active learning methods have become more widely used, this categorization no longer adequately captures the variation among instructors' teaching methods. We approached the problem of measuring an instructor's use of active learning by asking several questions and examining the relationships among instructor responses to these questions. We asked instructors three questions about their use of active learning in the lecture portion of their course. First, we asked instructors to report how often they used specific active learning exercises (described in Table 4.2) previously shown to be effective (e.g., Ebert-May *et al.*, 1997; Crouch and Mazur, 2001; Andrews *et al.*, 2011; Deslauriers *et al.*, 2011). We then created a continuous variable describing an instructor's weekly use of these active learning exercises by summing the frequencies they reported for all six categories of exercises. To do so, we assumed each course met three times per week and counted "Once per week" as once per week, "Once per class” as three times per week, and “More than once per class” as six times per week. This variable may underestimate the use of active learning by excluding other exercises an instructor was using to promote active learning and by limiting “More than once per week” to only six exercises per week, so we also asked instructors to report their general use of any active learning by asking how often they used exercises meeting Hake’s (1998a) definition of interactive-engagement (another commonly-used term for active learning):

> "activities designed at least in part to promote conceptual understanding through interactive engagement of students in heads-on (always) and hands-on (usually) activities which yield immediate feedback through discussion with peers and/or instructors.”

Finally, we asked instructors how many active learning exercises they used during the section of the course dedicated to teaching natural selection. For all three questions, we described exercises instead of using common names (e.g., Peer Instruction, think-pair-share) so instructors would not have previous associations with the exercises described.

We found instructors’ reports of using specific active learning exercises during the course were strongly correlated with their reports of using active learning in teaching natural selection ($r = 0.52$, $p = 0.002$). We therefore chose to use instructor reports about active learning use throughout the course for further analyses. In contrast to our expectations, instructors provided more conservative estimates of their general use of any active learning (as defined by Hake, 1998a) than their estimates of their use of specific active learning exercises (Figure 4.1). For example, instructors who reported using general active learning methods just once per week reported a mean of 3.33 specific exercises per week. Ultimately, we decided to quantify an instructor’s use of active learning as the weekly frequency with which they used specific active learning exercises because this quantification allowed us to capture more variability among instructor methods. However, we also conducted statistical analyses with the more general report of active learning to assure results remained the same.

Data Analysis

We used data gathered from the instructor survey to compare FULLY PARTICIPATING INSTRUCTORS to PARTIALLY PARTICIPATING INSTRUCTORS to check for selection bias resulting from non-response. We looked for differences using independent samples *t*-tests and Fisher's exact tests. We found no differences between the two groups of instructors, suggesting non-response did not cause a selection bias. There were no significant differences in the mean number of specific active learning exercises used per week, mean class size, mean teaching experience, mean class time dedicated to teaching natural selection, or mean attendance rates. Neither were there differences in type of institution (public or private), the list their institution came from (large public institutions or most prestigious institutions), the instructor's position, or the frequency with which they used general active learning methods (see full results in supplemental online materials).

To answer our question of interest– is active learning instruction positively associated with student learning gains in typical college biology courses–we used general linear regression models. We used one model with effect size of learning on the CINS-abbr as the response variable and one model with effect size of learning on the cheetah question as the response variable. We used two models because four courses had insufficient data to analyze learning gains on the cheetah question, but had complete CINS-abbr data. Using two models allowed us to avoid unnecessarily excluding these courses from all analyses. Additionally, we examined linear regression models using other calculations of learning gains, as well as a model that replaced the continuous weekly frequency of specific active learning exercises with the more general categorical use of any active learning, to see if results remained the same. We checked assumptions for our models using QQ-plots and plots of fitted values versus residuals. Assumptions were met for all linear regression models.

Many factors affect how much students learn in a course, so we used data gathered from the instructor survey and student survey to control for variation in learning gains due to factors other than the use of active learning. We included several continuous control variables in our linear models, including the number of years an instructor had taught college biology, hours of class time devoted to teaching natural selection, proportion of students who attended class regularly, proportion of students who completed both the pre- and post-test, and class size. Student responses to questions about how difficult they found the course compared to previous science courses and how interesting they found the course were coded numerically and also included as continuous control variables. Students chose from a Likert scale (Appendix 4.4), which we then coded from one to five, where one corresponded to “Very uninteresting” and “Much less difficult” and five corresponded to “Very interesting” and “Much more difficult.” We then calculated means for each course.

We used indicator variables to include categorical control variables in our models. We included a factor accounting for the presence or absence of non-majors in a course. We also included a two-level factor for the instructor's position: tenure track or non-tenure track. Lastly, we included two factors to describe whether the instructor addressed common student misconceptions about natural selection: one for whether or not an instructor reported "explaining to students why misconceptions are incorrect" and a second for whether or not an instructor reported "using active learning exercises and otherwise making a substantial effort toward correcting misconceptions."

We excluded data from one question on the instructor survey because it was strongly intercorrelated with two other control variables. The number of times an instructor had taught the course was correlated with both the number of years an instructor had taught college biology ($r = 0.50$, $p = 0.002$) and class size ($r = 0.49$, $p = 0.004$). Therefore, we excluded the number of times an instructor had taught the course from our models.

Results

Our analysis produced four noteworthy results. First, instructors reported frequently using active learning exercises (Table 4.2). Thirty-nine percent ($n = 13$) of instructors reported using four or more different activities (as described in Table 3.2) on a weekly basis and only 6% ($n = 2$) reported using none of these activities. Instructors reported using a mean of 8.03 ($SD = 6.65$) exercises per week, which would be equivalent to about three clicker questions per class meeting. During the portion of the course dedicated to teaching natural selection, instructors reported using a mean of 2.88 (*SD* = 1.43) active learning exercises. When asked to categorize the frequency with which they used general active learning methods as defined by Hake (1998a), 61% of instructors reported using active learning at least once per class meeting (Table 4.3). Introductory biology instructors' reports of their use of active learning in this study were similar to physics instructors' reports of their use of research-based teaching methods (most of which incorporate active learning); in a national survey of college physics courses, 48.1% of instructors reported they currently used at least one research-based method and 34.4% reported using two or more (Henderson and Dancy, 2009).

Our second noteworthy result was that learning gains in many of the courses were modest (Table 4.4). Effect sizes (Cohen's *d*) on the CINS-abbr ranged from -0.11 to 1.26 and the mean effect size was 0.49 (*SD* = 0.31). Thirty-nine percent (*n* = 13) of courses had an effect size lower than 0.42, which corresponds to students answering only *one* more question (out of 10) correctly on the post-test than on the pre-test[1]. When learning was calculated as average normalized gain, the mean gain was 0.26 (*SD* = 0.17). On the cheetah question, learning gains were even lower. Effect sizes ranged from -0.16 to 0.58. The mean effect size was 0.15 (*SD* = 0.19) and the mean normalized gain for the cheetah question was 0.06 (*SD* = 0.08). These remarkably low learning gains suggest that

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[1] A course average was calculated as the average number of points (out of 10) scored on the pre- or post-test CINS-abbr. An effect size can be calculated as the change in average score (Post-Pre) divided by a pooled standard deviation. The average pooled standard deviation for the CINS-abbr was 2.39. We divided the change in average score that interested us (a one point increase between pre- and post-test course averages) by the average pooled standard deviation for our sample. That calculation produces the effect size that corresponds to students across courses answering, on average, one more question correctly on the post-test CINS-abbr than they answered correctly on the pre-test.

students are not learning to apply evolutionary knowledge to novel questions in introductory biology courses.

Our third and most important result was that we did not find an association between the weekly frequency of active learning exercises used in introductory biology courses and how much students learned about natural selection (Figure 4.2, Table 4.5). An instructor's use of active learning was not associated with learning gains on the CINS-abbr ($p = 0.058$) or the cheetah question ($p = 0.669$), and though not statistically significant the regression coefficients for active learning in both models were negative (Table 4.5). When we calculated learning gains as average normalized gain, percent change, or raw change, we obtained the same result (Figure 4.3, Table 4.6, Appendix 4.5). When we replaced the weekly frequency of specific active learning exercises with an instructor's more general use of any active learning methods, we again obtained the same result. No matter how we quantified these variables, or what control variables we included in the analysis, we obtained the same result: student learning was not positively related to how much active learning instructors used.

Despite the absence of a positive relationship between active learning and student outcomes, our final noteworthy result is that several variables were positively related to student learning measured by the CINS-abbr (Table 4.5). Our analysis revealed the two misconception factors ("explaining why misconceptions are incorrect" and "using active learning exercises to make a substantial effort toward changing misconceptions") were positively associated with learning gains on the CINS-abbr ($p = 0.045$ and $p = 0.048$, respectively). This finding corroborates previous papers suggesting that misconceptions must be confronted in order for students to learn natural selection (Sinatra *et al.*, 2008; Kalinowski *et al.*, 2010). Because common misconceptions are used as distractors in CINS-abbr questions, we would expect courses in which misconceptions were directly targeted to have higher learning gains on this instrument. That said, misconceptions seem to be the largest barrier to understanding students face when learning natural selection (Bishop and Anderson, 1990; Gregory, 2009), so a test that measures the extent to which students reject misconceptions is likely to be a reliable measure of their overall understanding (Nehm and Schonfeld, 2008). Further research will be necessary to determine the relationship between how students learn natural selection and how an instructor addresses common misconceptions about natural selection.

In addition to the misconception factors, how difficult students found a course relative to past science courses and how interesting students found a course were also significantly positively associated with student learning on the CINS-abbr ($p = 0.040$ and $p = 0.021$, respectively). The questions used to gather student perception data provide insufficient detail to understand the complex relationships among instructor behavior, student perceptions, and student learning. Nevertheless, these results suggest research that examines student learning should not overlook the impact of students' experiences in a course.

Discussion

We have shown that even though instructors of introductory college biology courses are using active learning, students in many of their courses have learned very little about natural selection. Notably, students in most courses were no more successful in applying their knowledge of natural selection to a novel question at the end of the course than they were at the beginning of the course. The absence of a relationship between active learning and student learning is in stark contrast with a large body of research supporting the effectiveness of active learning. We attribute this contrast to the fact that we studied a different population of instructors. We randomly sampled college biology faculty from a list of major universities. Therefore, instructors using active learning in our study represent the range of science education expertise among introductory college biology instructors using these methods. In contrast, most of the faculty using active learning in previous studies had backgrounds in science education research. The expertise gained during research likely prepares these instructors to use active learning more effectively (Pollock and Finkelstein, 2008; Turpen and Finkelstein, 2009).

Specifically, it is possible that a thorough understanding of, commitment to, and ability to execute a constructivist approach to teaching are required to successfully use active learning (Bransford *et al.*, 2000). Constructivism–the theory that students construct their own knowledge by incorporating new ideas into an existing framework–likely permeates all aspects of education researchers' instruction, including how they use active learning. Without this expertise, the active learning exercises an instructor uses may have superficial similarities to exercises described in the literature, but may lack constructivist elements necessary for improving learning (Bransford *et al.*, 2000). For example, our results suggest that addressing common student misconceptions may lead to higher learning gains. Constructivist theory argues that individuals construct new understanding based on what they already know and believe (Piaget, 1973; Vygotsky, 1978; Bransford *et al.*, 2000), and what students know and believe at the beginning of a course is often scientifically inaccurate (e.g., Halloun and Hestenes, 1985; Bishop and Anderson, 1990; Gregory, 2009). Therefore, constructivist theory argues that we can expect students to retain serious misconceptions if instruction is not specifically designed to elicit and address the prior knowledge students bring to class.

A failure to address misconceptions is just one example of how active learning instruction may fall short. Instructors may fail to achieve the potential of active learning in the design or implementation of exercises, or both. There are many possible ways that active learning exercises could be poorly designed. For example, questions used in an exercise may only require students to recall information, when higher-order cognitive processing (e.g., application) is required to fully grasp scientific concepts (Crowe *et al.*, 2008). Alternatively, questions posed to students could be poorly connected to other material in the course so that students fail to see important relationships among concepts (Bransford *et al.*, 2000). It is also possible that the active learning exercises used to discuss fundamental theories may not be sufficiently interesting to students to motivate them to participate (Boekaerts, 2001).

On the other hand, regardless of how well an active learning exercise is designed, an instructor must make many implementation decisions that will ultimately affect the success of the exercise. For example, a think-pair-share discussion may not be effective if the instructor does not allow students enough time to think about a question (Allen and

Tanner, 2002). Or, an instructor may solicit only one answer from the class and therefore fail to expose the range of ideas held by students. In addition, an instructor may not ask students to predict the outcome of a demonstration or thought experiment and therefore fail to make students aware of their own erroneous ideas (Crouch *et al*., 2004). Furthermore, instructors may display any number of subtle behaviors or attitudes that influence the extent to which students participate in active learning exercises, and thereby affect how much students learn (Turpen and Finkelstein, 2009; Turpen and Finkelstein, 2010).

Our results corroborate research showing that college science teachers are incorporating active learning methods, but are often doing so ineffectively. A recent study compared college biology instructor's self-reports of teaching with expert observations of the instructor's teaching and found that, while instructors felt they were using reform methods, experts disagreed (Ebert-May et al., 2011). Similarly, a national survey of teaching practices in college physics courses found that 63.5% of instructors reported using think-pair-share discussions, but 83% of the instructors who used this method did not use it as suggested by researchers (Henderson and Dancy, 2009). Mounting evidence suggests that somewhere in the communication between science education researchers and typical college science instructors, elements of evidence-based methods and curricula crucial to student learning are lost.

The results of this study have three implications for education researchers across science disciplines. First, we need to build a better understanding of what makes active learning exercises effective by rigorously exploring which elements are necessary and sufficient to improve learning (for examples, see Crouch *et al.*, 2004; Smith *et al.*, 2009; Perez *et al.*, 2010; Smith *et al.*, 2011). Second, we need to develop active learning exercises useful for a broad population of instructors. Third, we need to identify what training and ongoing support the general population of college science faculty and future faculty need to be able to effectively use active learning, taking into account obstacles instructors will face, including individual, situational, and institutional barriers to reform (Henderson, 2005; Henderson and Dancy, 2007; Henderson and Dancy, 2008).

Our results also have two important implications for instructors. First, no one can assume they are teaching effectively just because they are using active learning. Therefore, instructors need to carefully assess the effectiveness of their instruction to determine whether active learning is reaching its potential. There are a growing number of reliable and valid multiple-choice and essay tests that assess student knowledge (e.g., Anderson *et al.*, 2002; Baum *et al.*, 2005; Nehm and Reilly, 2007; Smith *et al.*, 2008; Nadelson and Southerland, 2009). We recommend using these tests in a pre/post-test design to assess the effectiveness of instruction, as well as using formative assessments to monitor learning throughout instruction (e.g., Angelo and Cross, 1993; Marrs and Novak, 2004). Second, instructors should assume students enter science courses with pre-existing ideas that impede learning and that are unlikely to change without instruction designed specifically for that purpose (Bransford *et al.*, 2000). To replace students' misconceptions with a scientifically accepted view of the world, instructors need to elicit misconceptions, create situations that challenge misconceptions, and emphasize conceptual frameworks rather than isolated facts (Hewson *et al.*, 1998; Allen and Tanner, 2005; Kalinowski *et al.*, 2010).

Our study revealed that active learning was *not* associated with student learning in a broad population of introductory college biology courses. These results imply active learning is not a quick or easy fix for the current deficiencies in undergraduate science education. Simply adding clicker questions or a class discussion to a lecture is unlikely to lead to large learning gains. Effectively using active learning requires skills, expertise, and classroom norms that are fundamentally different from those used in traditional lectures. Appreciably improving student learning in college science courses throughout the United States will likely require reforming the way we prepare and support instructors and the way we assess student learning in our classrooms.

Tables and Figures

Table 4.1. Equations for calculating learning gains

Learning gain calculation	Equation	Variable definitions
Effect size (Cohen's *d* for repeated measures)[1]	$t_p (2(1 - r)/(n))^{1/2}$	t_p= t statistic from Student's paired *t*-test r = correlation between pre/post-test scores n = students completing pre/post-test
Average normalized gain[2]	(Post-Pre)/(10-Pre)*	Post/Pre = mean course post/pre-test score
Percent change	(Post-Pre)/Pre	See above
Raw change	Post-Pre	See above

[1] See Dunlap *et al.*, 1996

[2] See Hake, 1998a

*This is the equation for the CINS-abbr. The cheetah question equation would be (Post-Pre)/(9-Pre)

Table 4.2. Percent of instructors reporting how often they use specific active learning exercises

Exercise	More than once per class (%)	Once per class (%)	Once per week (%)	Never (or almost never) (%)
Activities in which students use data to answer questions while working in small groups	5.7	2.9	34.3	57.1
Student discussions in pairs or small groups to answer a question	17.1	17.1	22.9	42.9
Individual writing activities that require students to evaluate their own thinking[1]	0	3.1	28.1	68.8
Clicker questions that test conceptual understanding	34.3	11.4	5.7	48.6
Classroom-wide interactions that require students to apply principles presented in class to a novel question	8.6	20.0	37.1	34.3
Other small group activities	5.7	8.6	25.7	60.0

[1] N = 32. For the rest N = 33

Table 4.3. Instructor reports of the frequency with which they use active learning exercises as defined by Hake (1998a)

Frequency	Number of instructors	Percent of instructors
More than once per class	12	36.4
Once per class	8	24.2
Once per week	9	27.3
Never (or almost never)	4	12.1

Table 4.4. Descriptive statistics for course pre- and post-test scores on the CINS-abbr and the cheetah question

Test	Min.	Max.	Mean	SD
CINS-abbr pre[a]	3.56	7.57	5.38	0.86
CINS-abbr post	4.29	8.80	6.52	1.20
Cheetah pre[b]	1.08	4.83	2.92	0.83
Cheetah post	1.50	4.90	3.22	0.85

[a] Out of 10
[b] Out of 9

Table 4.5. Results of linear models examining the relationship between student learning gains (Cohen's *d*) and active learning instruction

Linear model variable	Regression coefficient [95% confidence interval]	
	CINS-abbr model	Cheetah question model
Intercept	-1.88 [-2.16, -1.62]*	0.098 [-1.729, 1.924]
Weekly active learning	-0.02 [-0.04, 0.00]	-0.000 [-0.024, 0.016]
Instructor position (tenure track)	-0.10 [-0.33, 0.13]	0.168 [-0.078, 0.414]
Students regularly attending (%)	-0.03 [-0.97, 0.91]	-0.459 [-1.740, 0.821]
Hours spent on natural selection	0.00 [-0.03, 0.03]	-0.011 [-0.036, 0.014]
Class size	0.00 [-0.00, 0.00][e]	0.000 [-0.000, 0.000][e]
Years of teaching experience	0.00 [-0.01, 0.01]	-0.005 [-0.014, 0.003]
Students pre/post-tested (%)	0.06 [-0.47, 0.60]	0.298 [-0.263, 0.860]
Misconceptions (explained)[a]	0.23 [0.01, 0.45]*	0.194 [-0.036, 0.423]
Misconceptions (active leanring & otherwise)[b]	0.25 [0.00, 0.50]*	-0.019 [-0.265, 0.227]
Course difficulty (student-rated)[c]	0.29[0.20, 0.57]*	-0.003 [-0.292, 0.286]
Student interest in course	0.33 [0.06, 0.60]*	0.058 [-0.237, 0.352]
Non-majors (absent)[4]	0.37 [-0.04, 0.77]	0.447 [-0.109, 1.004]

[a] Two-level factor: Instructor did or did not explain why misconceptions are incorrect
[b] Two-level factor: Instructor did or did not use active learning exercises and otherwise make a substantial effort toward correcting misconceptions
[c] Relative to past science courses the student had taken
[d] Two-level factor: Presence of absence of non-biology majors in the course
[e] No results were exactly zero. These numbers are very small and equal zero when rounded.
* $p < 0.05$

Table 4.6. Comparisons between the direction and significance of the association between explanatory variables in the CINS-abbr linear model and different calculations of learning gains as the response variable

Linear model coefficients	Effect size	Average normalized gain	Percent change	Raw change
Intercept	–*	–*	–	–
Weekly active learning	–	–	–	–
Instructor position (tenure track)	–	–	+	–
Students regularly attending (%)	–	+	–	–
Hours spent on natural selection	–	–	+	+
Class size	–	–	+	–
Years of teaching experience	+	+	–	+
Students pre/post-tested (%)	+	+	+	+
Misconceptions (Explained)[a]	+*	+	+*	+
Misconceptions (AL & otherwise)[b]	+*	+	+	+
Course difficulty (student-rated)[c]	+*	+*	+	+
Student interest in course	+*	+	+*	+*
Non-majors (absent)[d]	+	+	+*	+

(–) indicates a negative association with learning in the model and (+) indicates a positive association with learning

[a] Two-level factor: Instructor did or did not explain why misconceptions are incorrect

[b] Two-level factor: Instructor did or did not use active learning exercises and otherwise make a substantial effort toward correcting misconceptions

[c] Relative to past science courses the student had taken

[d] Two-level factor: Presence of absence of non-biology majors in the course

*$p < 0.05$

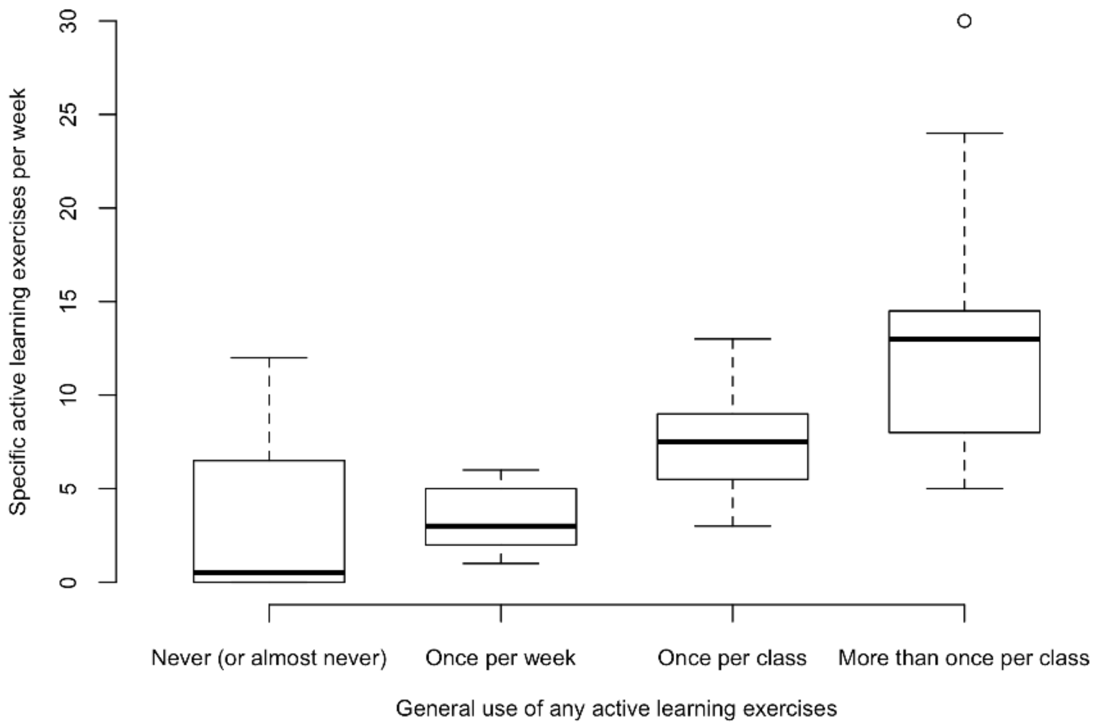

Figure 4.1. Comparison of instructor reports of their weekly use of specific active learning exercises and instructor reports of their general use of active learning exercises as defined by Hake (1998a). The line in the middle of the box represents the median weekly frequency of active learning use for instructors in the group. The top of the box represents data points in the 75th percentile and the bottom of the box represents data points in the 25th percentile. The space within the box is called the interquartile range (IQR). Whiskers represent the lowest and highest data points no more than 1.5 times the IQR above and below the box. Data points not included in this range are represented as dots.

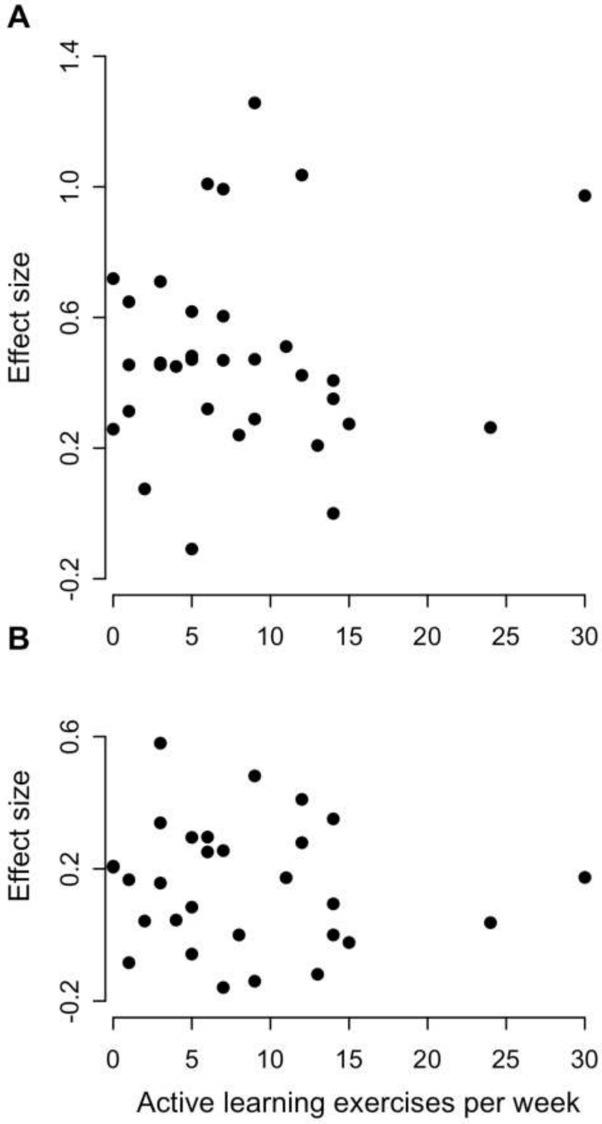

Figure 4.2. Relationship between learning gains (Cohen's *d*) and the number of active learning exercises an instructor used per week. The number of active learning exercises per week was calculated by summing the number of times per week instructors reported using all of the exercises described in Table 4.2. **(A)** Learning gains on the CINS-abbr (N = 33). **(B)** Learning gains on the cheetah question (N = 29).

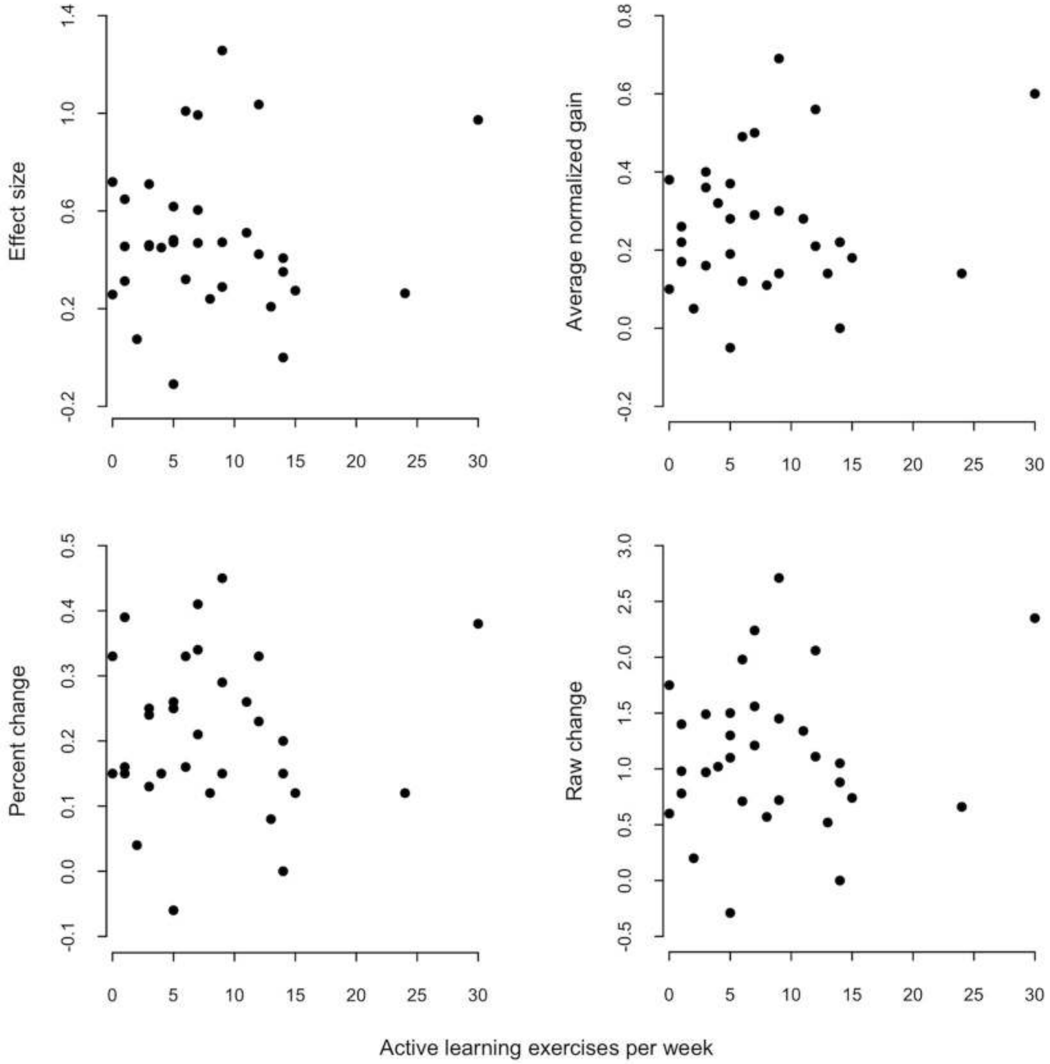

Figure 4.3. Relationship between four different calculations of learning gains on the CINS-abbr and the number of active learning exercises an instructor used per week. The CINS-abbr was scored out of 10 points, so a raw change of one is equivalent to earning one more point on the post-test than on the pre-test. Overall, these graphs are very similar; there is no evidence of a positive relationship between learning gains and the use of active learning instruction no matter how we calculate learning gains.

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CHAPTER FIVE

“ARE HUMANS EVOLVING?” A CLASSROOM DISCUSSION TO CHANGE STUDENT MISCONCEPTIONS REGARDING NATURAL SELECTION

Contribution of Authors and Co-Authors

Manuscript in Chapter 5

Author: Tessa M. Andrews

Contributions: Conceived the study, collected and analyzed output data, and wrote the manuscript.

Co-Author: Steven T. Kalinowski

Contributions: Obtained funding, assisted with study design, discussed the results and implications, and edited the manuscript at all stages.

Co-Author: Mary J. Leonard

Contributions: Obtained funding, assisted with study design, discussed the results and implications, and commented on the manuscript.

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Abstract

Natural selection is an important mechanism in the unifying biological theory of evolution, but many undergraduate students struggle to learn this concept. Students enter introductory biology courses with predictable misconceptions about natural selection and traditional teaching methods, such as lecturing, are unlikely to dispel these misconceptions. Instead, students are more likely to learn natural selection when they are engaged in instructional activities specifically designed to change misconceptions. Three instructional strategies useful for changing student conceptions include: (1) eliciting naïve conceptions from students, (2) challenging non-scientific conceptions, and (3) emphasizing conceptual frameworks throughout instruction. In this paper, we describe a classroom discussion of the question “Are humans evolving?” that employs these three strategies for teaching students how natural selection operates. Our assessment of this activity shows that it successfully elicits students’ misconceptions and improves student understanding of natural selection. Seventy-eight percent of our students who began this exercise with misconceptions were able to partially or completely change their misconceptions by the end of this discussion. The course that this activity was part of also showed significant learning gains (d=1.48) on the short form of the Conceptual Inventory of Natural Selection. This paper includes all the background information, data, and visual aids an instructor will need to implement this activity.

Introduction

In order to learn, students must actively construct knowledge by linking new concepts with prior ideas (Jones and Brader-Araje 2002). Not surprisingly then, students learn more when they analyze, synthesize, and evaluate ideas in the classroom than when they merely listen to lectures (Hake 1998a, Bonwell and Eison 1991). There are many ways to stimulate such thinking during lectures; small group discussions, for example, are particularly effective at increasing learning and motivation (Smith et al. 2009, Springer et al. 1997). Alternatively, instructors can use part of a class period to have students write, analyze data, or solve problems (Bonwell and Eison 1991, Hake 1998b, Crouch and Mazur 2001). A growing body of literature shows that such activities, often called interactive-engagement or active learning (AL), tend to be twice as effective as standard lectures (e.g., Hake 1998a, Crouch and Mazur 2001, Knight and Wood 2005).

Although instruction that employs AL is more effective than lecturing, AL strategies alone are unlikely to help students recognize and replace misconceptions. Natural selection is one of the most important biological processes for introductory biology students to understand, but many students enter introductory biology courses with pre-existing ideas that prevent them from learning how natural selection operates (Mayr 1982, Bishop and Anderson 1990, Greene 1990, Lord and Marino 1993, Gregory 2009). For example, students often believe that evolution occurs as individuals change—either because they need to, because they use or disuse body parts, or because the environment directly changes them (Gregory 2009). Such misconceptions are remarkably resistant to instruction. Simply telling students that these ideas are incorrect is almost completely ineffective, and students are very likely to retain misconceptions after taking traditional, lecture-based courses. Nehm and Reilly (2007) reported that 86% of students completing a traditional introductory biology course had at least one major misconception regarding natural selection. When Nehm and Reilly added active learning to their course, students' understanding of natural selection increased, but 70% of students still retained misconceptions (Nehm and Reilly 2007).

Instruction is much more effective when teachers use active learning strategies *specially designed to change student misconceptions*. There are a variety of instructional approaches available for teaching for conceptual change (TCC). In the approach we describe here, three instructional strategies are useful for helping students replace misconceptions with scientific conceptions: (1) eliciting students' naïve conceptions, (2) challenging non-scientific conceptions, and (3) emphasizing conceptual frameworks (Posner et al. 1982, Vosniadou 2008). Metacognition – or considering one's own thinking, learning, and knowing – is an important component of each of these three strategies of TCC. In order to correct a misconception, a student must continually monitor what she is learning, how it relates to what she already knows, and how her thinking may be changing (Hewson et al. 1998).

Multiple examples of a concept help prepare students to transfer their knowledge to novel questions (Bransford et al. 2000, Catrambone and Holyoak 1989), while facilitating the TCC strategies described above. Experts in biology organize their knowledge around larger concepts, such as natural selection, but students need practice with multiple examples of these concepts in order to be able to recognize when the concept is relevant to a new problem (Bransford et al. 2000). By presenting multiple examples and pointing out similarities and differences between the examples, instructors help students make connections and see meaningful patterns that may seem obvious to the instructor, but may have gone unnoticed by the student (Bransford et al. 2000). Students who learn to recognize these patterns will build more sophisticated conceptual frameworks and will be more likely to transfer their understanding to new questions (Bransford et al. 2000, Catrambone and Holyoak 1989).

Educators and researchers have made many calls for instruction that teaches for conceptual change (Bransford et al. 2000, Alters and Nelson 2002, Hestenes 1979, Kalinowski et al. 2010, Nelson 2008). Biology instructors are beginning to answer this call for classroom and lab activities (Heitz et al. 2010, Kalinowski et al. 2006a, Kalinowski et al. 2006b), but there are still too few TCC activities for introductory biology courses. The purpose of this paper is to describe a classroom activity that uses TCC strategies to teach students how natural selection works. Essentially, the lesson is a class discussion in which students attempt to answer the question "Are humans evolving?" This activity can be used in a class of any size and requires no special materials. We designed this activity to elicit students' conceptions about natural selection, to challenge misconceptions that students have, and to emphasize conceptual frameworks. The activity provides students with detailed examples of natural selection at work. In this paper, we will describe the classroom activity, provide background information an instructor would need to use the activity, and present data that shows that this activity effectively corrects common misconceptions about natural selection.

Activity Description

The fundamental goal of this activity is to improve students' understanding of natural selection. More specifically, this classroom activity had the following objectives:

1) Elicit student misconceptions about natural selection;
2) Facilitate rejection of non-scientific ideas about natural selection; and
3) Engage students in an activity they perceive to be interesting and valuable.

Before using this activity, instructors will need to describe the basic mechanisms of natural selection. In our course, we preceded the human evolution discussion with a lecture that emphasized there are three requirements for natural selection: variation for a trait in a population, heritability of the trait, and differential reproductive success.

The instructor began the discussion of human evolution by asking students: "Are contemporary populations of humans evolving? Please explain how you know." Students wrote their responses to this question, hereafter called the "HUMAN EVOLUTION QUESTION," on index cards. Written responses are important because writing forces students to clarify their thoughts, and the index cards can be collected to provide the instructor with a glimpse of how students in the course are thinking about the question. After students finished writing their individual responses, the instructor asked them to discuss their answers in small groups in order to determine whether they could come to a group consensus. These peer discussions provide students with an opportunity to verbalize, clarify, and defend their ideas, and allow them to "try out" their ideas on peers before they present them to a larger audience. Small group discussions may lead to greater learning than classroom-wide discussions because students are more likely to participate when other students, instead of instructors, lead discussions (Philips and Powers 1979).

The instructor then solicited verbal answers from a wide range of students. He used a class list to randomly call on students and recorded their answers on a PowerPoint slide. This approach ensured that the answers obtained were representative of the class, and helped prevent students from taking a passive role in the activity. Student answers to this question are predictable (Table 5.1, also see Gregory 2009 for more general natural selection misconceptions). For example, students will argue that humans are evolving to "lose" their appendix, to have worse eyesight, to have less hair, to have larger brains, and to be fatter. In contrast, other students will report that human evolution has stopped because "there isn't any sort of predator around that attacks and causes the weak to die."

Next, the instructor proposed to work through the list of student ideas and began by pointing out that there was a wide diversity of answers, and that some of them contradicted each other. He asked students to apply the three requirements of natural selection to assess each idea. For example, students frequently propose that humans are evolving to have less hair (becoming more bald). The instructor would then ask the student to consider each requirement (i.e., Is there variation in baldness? *Yes*.; Is baldness heritable? *Yes, at least for some types*.; and Are bald men having more children then men with full heads of hair*? Probably not.*). We have found that structuring this discussion with the requirements for natural selection quickly dispels some student misconceptions, including the ideas that humans are evolving to be fatter, smarter, and balder. Unlike a misconception such as "individuals evolve" which has likely been built over a lifetime of personal experience with being able to “adapt” to new situations, these ideas are probably not created until we ask this specific question.

After the discussion of student ideas—most of which relate to traits that are probably not evolving— the instructor discussed two traits that likely are favored by natural selection: HIV resistance and height. He began by presenting how HIV may be selecting for specific immune system genes. We suggest presenting the height example second because human height has been affected by both genetic and environmental factors, and students find this combination challenging. The next section of this paper provides instructors with the background information necessary to discuss how natural selection may be affecting HIV resistance and height. (Table 5.2 describes additional resources that can be found in Appendix 5.1).

At the end of the discussion of HIV resistance and human height, the instructor asked students to review and critique their original answers to the HUMAN EVOLUTION QUESTION. On the same index card, he asked students to “Re-read your answer to the question (Are contemporary populations of humans evolving?) and evaluate your reasoning. Is there anything you said that was incorrect? Was there an important part of the answer you were missing?” Hereafter, we call this the “REVISION QUESTION.” Asking students to examine how their ideas have changed encourages metacognition and promotes conceptual change. We knew from past years that our students can be reluctant to criticize their previous answers. To encourage them to think critically about their initial ideas (Hewson et al. 1998), the instructor provided students with five sample student answers and asked them to critique the answers in groups before he asked them to critique their own answers. Each group discussed one sample answer and then the class discussed what was correct and incorrect about each answer. Table 5.1 provides examples of student answers that display common misconceptions; these examples can be used for this part of the activity. At the end of class, the instructor collected both the HUMAN EVOLUTION QUESTION and the REVISION QUESTION and used them to gauge student learning in preparation for the next class period.

Two Examples of Contemporary Human Evolution to Use in the Classroom

As we discussed above, it is important that instructors expose students to multiple examples of a concept (Catrambone and Holyoak 1989). This section of the paper (and Appendix 5.1 described in Table 5.2) provide the background information necessary to present these examples of human evolution to students, as well as numerous citations an instructor could use to find additional information.

HIV Resistance and the *CCR5* Locus

AIDS is a disease of the human immune system caused by the human immunodeficiency virus (HIV) that kills over 2 million people each year (Joint United Nations Programme on HIV/AIDS 2009). Most people in the world are highly susceptible to HIV infection, but individuals who are homozygous for a rare allele at the *CCR5* locus are essentially immune to the disease (Samson et al. 1996). Simply put, HIV enters a white blood cell by binding to the *CCR5* protein. A rare resistant allele, called *CCR5-Δ32*, has a 32 base pair deletion in the DNA sequence of the *CCR5* gene. This deletion causes a frame shift, creating a non-functional receptor and preventing HIV from infecting the cell (Samson et al. 1996).

Is There Variation in the Population? *CCR5-Δ32* has a frequency of around 10% in many European countries and in Russia (Samson et al. 1996, Stephens et al. 1998), but this mutated alleleis essentially absent in Asia and Africa (Samson et al. 1996). Students often believe that mutations occur because they are needed, and if that were true, the *CCR5-Δ32* mutation should be most common in Africa where HIV is more prevalent.

The reason why European populations have high frequencies of the *CCR5-Δ32* allele is not well understood. Mathematical models suggest that random drift of a neutral allele cannot explain the high frequency of *CCR5-Δ32* in European populations (Stephens et al. 1998), meaning that selection was likely responsible. However, debate remains about what may have caused this selection pressure. Some researchers suggest that outbreaks of the bubonic plague, which killed 25-33% of Europeans about 650 years ago, are the most likely source of strong selective pressure for this mutation (Stephens et al. 1998). Other researchers argue that the plague would not have provided sufficient selective pressure to create the current frequency and distribution of the *CCR5-Δ32* allele (Galvani and Slatkin 2003). Studies have also shown that the *CCR5-Δ32* allele does not confer resistance to the plague in mice (Mecsas et al. 2005). Instead, Galvani and Slatkin (2003) suggest it is more likely that the *CCR5-Δ32* allele conferred resistance to small pox and was therefore strongly selected. Finally, one hypothesis proposes that selective pressure from outbreaks of both small pox and haemorrhagic plague explain the current frequency and distribution of the mutated *CCR5* allele (Duncan et al. 2005).

Is This Trait Heritable? The immunity conferred by *CCR5-Δ32* is inherited as a simple Mendelian trait, so it is heritable. We use this example to emphasize to students that the ability of organisms to survive and reproduce is influenced by genotypes present at specific loci. This should help students connect natural selection with Mendelian genetics (two of the most important concepts in biology). We also show students the DNA sequence of *CCR5* and *CCR5-Δ32* alleles, in order to provide a concrete example of how DNA sequences influence phenotypes (Kalinowski et al. 2010). Later, we use *CCR5-Δ32* allele frequencies as an example to illustrate Hardy-Weinberg proportions.

Does Having This Trait Affect the Ability of an Individual to Survive or Reproduce? Two copies of *CCR5-Δ32* (homozygosity) confer a high level of resistance to HIV infection (Samson et al. 1996). Even one copy of *CCR5-Δ32* provides protection from AIDS (Stewart et al. 1997), most likely by prolonging the transition from HIV infection to AIDS. As long as HIV affects an individual's reproductive success in the human population, there will be selection for the *CCR5-Δ32* allele. Globally, only 42% of individuals in need of treatment for AIDS are being treated (Joint United Nations Programme on HIV/AIDS 2009), suggesting that, if *CCR5-Δ32* exists in a population, it will be selected for.

Human Height

Students frequently suggest that humans are evolving to be taller, and human height provides an ideal example to illustrate some of the complexities of natural selection. As students suspect, human height *has* increased substantially over the past three decades (Smith and Norris 2004, Freedman et al. 2000). However, only some of that change in certain populations seems to be due to evolution, rather than improved nutrition and medical care (Mueller and Mazur 2001).

Is There Variation Within the Population? Human height is clearly variable, and a histogram shows human height has a “bell” shaped distribution. We have provided height data collected by Karl Pearson (Table 5.2) to illustrate this point, but a similar figure could be made from students’ heights. Pearson’s data is from the early twentieth century and, as many students will note, people in most countries are taller now. Average adult height has increased about one inch between 1960 and 2002 (Ogden et al. 2004).

Is Height Heritable? Human height is highly heritable, and in fact, the first studies of heritability examined human height. Sir Francis Galton started this work and his younger colleague, Karl Pearson, developed the statistical method of correlation to analyze father-son height data. Current studies estimate heritability of height in humans to be 0.8, meaning that about 80% of the variation in height within populations is due to genetics (Visscher 2008).

Height is a quantitative trait, which means that it is controlled by many genes of small effect. At least twenty genes have been found that contribute 0.2 – 0.6 cm to height per allele (Weedon et al. 2007, Weedon et al. 2008). These genes explain only about 3% of the variation in human height (Weedon et al. 2008), which suggests that many more genes of small effect will be found.

Twin studies are an interesting method of understanding heritability. Studies show that after birth, monozygotic (identical) twins grow to be more similar in height than dizygotic (fraternal) twins. Monozygotic twins reared apart are more different in stature than monozygotic twins reared together, but are still more similar than dizygotic twins who grew up together (Chambers et al. 2001). In dizygotic twins aged 14 to 36 months, 61 - 82% of variation in height can be attributed to genes (Chambers et al. 2001).

Does Being Taller (or Shorter) Affect an Individual's Ability to Survive or Reproduce?

Several studies have shown a positive relationship between height and reproductive success—in particular for men. For example, height was positively related to number of children in a sample of Polish men (after controlling for other factors that affected height in this sample, such as locality of residence) (Pawlowski et al. 2000). A study of West Point Cadets (Class of 1950) also showed that taller men had more children (Mueller and Mazur 2001). This study did not control for potential environmental differences, but used a highly homogeneous sample – mostly middle-class men of European descent who came from rural backgrounds and had parents who had at least a high school degree. Finally, a study of British men born in 1958 found that taller men were less likely to be childless than shorter men, and men who were taller than average were more likely to find a long-term partner *and* to have several long-term partners (Nettle, 2002b). This study controlled for socioeconomic status and serious health problems. Together, this research suggests that – in some populations – men are evolving to be taller, but it is likely that in other populations male height is not evolving; selection could even be moving height in the other direction.

Selection for taller men is likely due to sexual selection, meaning that the increase in reproductive success is mediated by opportunities to mate. Women frequently prefer taller men for dates, sexual partners, or husbands (Buss and Schmitt 1993, Ellis 1992, De Backer et al. 2008). For example, a study of personal ads showed that 80% of women advertised for men six feet or taller, even though the average American male is 5’9”. Interestingly, studies of reproductive success do not show that taller men have more children within any single marriage, but instead are more likely to remarry and have a second family (Mueller and Mazur 2001).

Female preference for tall men is not likely to lead to unconstrained directional selection. Extremely tall men (those in the top decile) are slightly more likely to be childless. They are also more likely to have a work-impairing, long-standing illness, and they have a slightly higher mortality (Nettle 2002b). Additionally, mating partners who are more similar in height are more likely to have non-induced labor and have higher numbers of live-born children (Nettle 2002a, Nettle 2002b).

The relationship between a woman’s height and fitness is more complicated. In developed countries such as America and England, the average woman is 5’4.” In these countries, shorter women have the highest reproductive success and are least likely to be childless (Nettle 2002a). In contrast, in less developed countries such as Guatemala and Gambia, a woman’s height is positively related to reproductive success. In these countries, tall women are more likely to have healthier children. (Sear et al. 2004, Pollet and Nettle 2008). In all studies, the effect of height on reproductive success of women is less drastic than in men.

<u>What Else Affects Human Height?</u> As students are likely to note, human height is strongly affected by nutrition and health care as well as by genes. Because of this, the

average height and weight of children is often used to monitor the health of populations worldwide. For example, several studies have shown that North Koreans are shorter than South Koreans (see Schwekendiek and Pak 2009 for a meta-analysis), and researchers attribute these differences to nutrition. Similarly, height increased in the Japanese population in the generation born after World War II (Ali et al. 2000). Height also tends to vary by socioeconomic status within countries; children from more well off families are taller than children from poorer families (even in developed countries like the US) (Eveleth and Tanner 1990). Both nutrition and childhood illness are oft-cited sources of growth limitations. These two forces can form a positive feedback loop. Infections cause nutritional status to deteriorate, and malnourished children are more susceptible to illness (Eveleth and Tanner 1990).

In summary, height is highly heritable in ideal conditions, but the effects of childhood illness and malnutrition can have large and lasting effects on overall height. This point is both important and challenging for many students. Understandably, they have a hard time imagining the mechanisms through which genes could have some effect but not complete control, and instead often consider a trait a result of *either* nature or nurture, but not both.

Assessment of Activity Goals

We assessed the effectiveness of the human evolution activity described above in an introductory biology course on ecology and evolution. The first half of this course dealt with evolution and was taught by one of us (STK). The course had 58 students, and met for lecture three times per week for 50 minutes and three hours once a week for a laboratory (e.g., Kalinowski et al. 2006a, Kalinowski et al. 2006b). Most students in this course reported planning to pursue a career in medicine (e.g., physician, pharmacist, physician's assistant). In this section of this paper, we present assessments of how well the human evolution paper met its three goals: 1) to elicit misconceptions, 2) to facilitate the rejection of misconceptions, and 3) to engage students in an activity they found interesting and educationally useful.

Goal 1 – To Elicit Student Misconceptions About Natural Selection

We reviewed students' initial responses to the HUMAN EVOLUTION QUESTION and categorized all answers as either: "definitely containing a misconception," "probably containing a misconception," and "not containing a misconception." While scoring answers we defined a misconception as an idea that: 1) is inconsistent with a scientific understanding of natural selection, 2) represents a misunderstanding of one of the major aspects of natural selection and, 3) is commonly held. This meant that we did not necessarily score factually incorrect ideas as misconceptions. Two raters independently coded all students' responses, and disagreements were resolved through discussion.

Table 5.1 displays the variety of misconceptions elicited by this activity. Forty-four percent of our students' answers to the HUMAN EVOLUTION QUESTION definitely exhibited a misconception, and another 10% of their answers suggested they held misconceptions, but their response was too incomplete or unclear to easily classify as a specific misconception.

Goal 2 - To Facilitate Rejection of Non-scientific Ideas About Natural Selection

We measured student rejection of misconceptions using three different tools. First, we compared the misconceptions displayed in the initial HUMAN EVOLUTION QUESTION (categorized as stated above) to misconceptions displayed on the REVISION QUESTION. For the REVISION QUESTION, we measured whether students rejected misconceptions by categorizing their answer as showing signs of "no improvement," "partial improvement," or "complete improvement." Two raters independently coded all students' responses, and disagreements were resolved through discussion.

Twenty-seven (54%) of our students began this activity with misconceptions (i.e., gave responses scored as either "definitely" or "probably" containing a misconception). By the end of this discussion, 78% (*n*=21) of these students had at least partially improved their answers on the REVISION QUESTION. Eleven students had completely improved their answers by correcting all misconceptions and 10 students partially improved their answers by correcting some misconceptions. In total, 68% of our students provided an initial or revised answer that contained no misconceptions and another 20% revised their answers to partially correct misconceptions. Only 12% of students ended this activity unable to at least partially correct misconceptions they had about natural selection.

Next, we used the 10-question version of the Conceptual Inventory of Natural Selection, called the CINS-II Short Form (CINS-II) (Anderson et al. 2002; Anderson 2003; Fisher et al. in prep) to measure student learning gains. Each distractor on the multiple-choice CINS-II questions represents a common student misconception about natural selection. We used the CINS-II because we wanted to see if the activity described in this paper contributed to an improved understanding of natural selection, not just human evolution. We pre-tested students on the first day of the class and post-tested at the end of the 8-week evolution section of the course. The pre/post-test design measured learning over a period that included more activities than the discussion presented here. However, the human evolution activity served as the major lesson on natural selection so we expect it contributed significantly to student learning gains. We compared the percentage of students who displayed misconceptions on the pre- and post-test of the CINS-II. We used a paired-samples *t*-test (one-tailed) to test the null hypothesis that the difference between post-test and pre-test scores was zero and then calculated an effect size using Cohen's *d*. We corrected the pooled standard deviation used to calculate *d* for the correlation between measures (Dunlop et al. 1996).

Forty-six students (79%) completed both the pre- and post-test CINS-II. They scored significantly better on the 10-question CINS-II after instruction (mean=8.83, SD=1.42) than before instruction (mean=6.57, SD=2.08), (t(45)=6.86, p<0.0001 (one-tailed with alpha=0.025)), meaning that they displayed fewer misconceptions and instead selected scientifically-accepted answers. This corresponds to an effect size of Cohen's *d*=1.48 with a 95% confidence interval from 1.07 to 2.08. This indicates that the class average increased by almost 1.5 standard deviations, which is considered a large positive effect.

For our third measure of how students' misconceptions changed during this activity, students filled out an evaluation of the discussion described in this paper during the class period after this activity. We asked students two open-ended questions, including what they thought the instructor hoped they learned from the activity and what *they* felt was the most important thing they learned from the activity. In response to these questions, students commonly wrote down the non-scientific conceptions they had rejected during this activity. Most often, students reported that they had learned that populations, rather than individuals, evolve. Table 5.3 provides descriptions of the concepts students reported learning and the number of students who named these concepts. Interestingly, some of the concepts reported by multiple students were not a main focus of the lesson, but are valuable lessons for how evolution proceeds (e.g., Evolution takes place over a long time, rather than in one generation). In 70% (*n*=35) of student responses to these questions, students reiterated the importance of using the three requirements (i.e., variation, heritability, selection) for natural selection to determine if a trait is evolving, suggesting that the activity successfully emphasized the importance of considering these requirements.

Goal 3 – To Engage Students in an Activity They Found to be Interesting and Valuable

Some instructors have experienced student resistance when they change from lecturing to more interactive classes that include activities like the one described in this paper (Hestenes 1979), so on the evaluation mentioned above we asked students to provide their opinions about this activity. The evaluations were anonymous and voluntary and 93% percent (*n*=54) of our class completed the evaluations. We asked students to indicate on a 6-point Likert scale (strongly disagree, somewhat disagree, slightly disagree, slightly agree, somewhat agree, and strongly agree) how well the activity held their interest and better helped them understand evolution. We also asked students to use the same scale to provide their opinions about specific parts of this classroom exercise, including how helpful they found writing and reexamining their answers and discussing answers with classmates.

When asked if the activity held their interest, 94.4% agreed, and 88.9% agreed that the activity was intellectually challenging (Table 5.4). Overall, students responded positively to writing and re-examining their answers and discussing questions with classmates (Table 5.4).

Discussion

Over 75% of the students in our course who initially displayed misconceptions regarding natural selection recognized and began to change their misconceptions after two hours dedicated to this activity. We could never have achieved this magnitude of learning gains with traditional lecture methods. Regrettably, recent research has shown that it is not unusual for introductory science courses to produce negligible student learning gains (Hake 1998a, Andrews et al. unpublished). Natural selection is particularly challenging to learn, and some studies show targeted instruction produces only modest changes in students' conceptions (Bishop and Anderson 1990, Nehm and Reilly 2007). Our students' learning gains compare favorably to other studies that have tested AL and TCC strategies to teach natural selection (Bishop and Anderson 1990, Nehm and Reilly

2007, Jensen and Finley 1996, Jensen and Finley 1997) and this activity would be relatively easy for an instructor to incorporate into his or her course.

We were interested in how well our students retained what they had learned during this activity, so we included the HUMAN EVOLUTION QUESTION on the final exam, which students took 12 weeks after this activity (8 of those 12 weeks were dedicated to teaching ecology). Only 4% of our students displayed misconceptions on the final exam version of the HUMAN EVOLUTION QUESTION (96% of students who participated in this activity also took the final exam). This is a marked improvement from their answers to the REVISION QUESTION (where 32% of student answers failed to completely correct misconceptions). Because this re-testing took place three months after the activity, we suspect that rather than simply retaining this information, students continued to build their understanding of natural selection (and thereby their ability to answer this question without displaying misconceptions) in the four additional weeks dedicated to evolution. Throughout the evolution section of this course, we consistently embedded AL and TCC strategies into our instruction and our results suggest these methods effectively produce learning gains in undergraduate introductory biology students. In agreement with learning research (Bransford et al. 2000), it also suggests that a holistic and scientifically-accepted understanding of natural selection is not built during a single class activity. Rather, these complex conceptual frameworks are built over time as students are forced to question their ideas, incorporate new ideas, and apply these newly integrated ideas (Posner et al. 1982).

As with any classroom activity, instructors will need to carefully incorporate a discussion of contemporary human evolution into their courses. In a previous implementation of this activity, we did not give students enough practice with natural selection before this activity and, as a result, the question was too difficult and students became frustrated. To answer the HUMAN EVOLUTION QUESTION, students will need to be able to recall the requirements for natural selection and to apply them to humans. In our course, we used the class period before this activity to illustrate these requirements with examples of selection at work. Specifically, students discussed dog breeding (i.e., artificial selection), selection for coat color in old field mice (see Kalinowski et al. 2010), and neck length in giraffes. Student misconceptions regarding natural selection are frequently so persistent that students may be unprepared for the human evolution question unless instructors have previously addressed common student misconceptions regarding inheritance. For example, we used the discussion of dog breeding (see the 'Elaborated example' in Kalinowski et al. 2010) to illustrate for students that evolution does not proceed via the inheritance of acquired traits.

Our human evolution discussion was designed to teach students how natural selection operates. This emphasis does not minimize the importance of other causes of evolution (e.g., mutation, genetic drift, gene flow). Before this exercise, we introduce natural selection as *one* process that causes evolution, and we talk in detail about genetic mutation as a source of variation, but we do not cover other evolutionary processes until after our students understand natural selection. As the class proceeds, we return to the examples in this exercise as we teach gene flow and genetic drift.

Beyond content, the format of this activity (e.g., small group discussions, classroom-wide discussions) may be foreign to students and thus slightly intimidating. First, students accustomed to passively sitting in class may be reluctant to participate in class discussions because they are afraid of providing an incorrect answer. Second, students in the habit of acting as receivers and recorders of facts during class may be uncomfortable allowing for uncertainty while discussing a question. We encourage the incorporation of AL and TCC methods before the human evolution discussion to familiarize students with a more interactive classroom environment.

Formative assessment will be invaluable for incorporating a discussion of human evolution into an introductory biology course. In order to challenge and change student ideas, it is imperative that an instructor know what his or her students are thinking. To do this, instructors will need to obtain responses from a broad sample of the class. This is important, because if only a few students answer the question, their answers may be insufficient to capture the range of misconceptions present in the classroom. This is why we have all students write down an answer and why we randomly call on numerous students. Standardized tests, such as the CINS-II (Anderson et al. 2002; Anderson 2003; Fisher et al. in prep), are also useful for assessment. As we developed this activity over the course of three years, and tested student learning, we were sometimes surprised to learn that our personal assessment of the effectiveness of a discussion was highly inaccurate. We cannot stress enough the importance of knowing students' initial ideas and assessing learning throughout a course; without this testing, an instructor cannot know if he or she has successfully taught the students anything.

Alternative hypotheses to explain our students' significant learning gains include an exceptional instructor, exceptional students, or simply an exceptional amount of time in preparation for teaching. We do not believe any of these hypotheses adequately explain why this activity produced impressive learning gains (and misconception rejection). First, our initial implementation of this activity did not produce the sort of learning gains we eventually produced, suggesting that our instruction was not exceptional, but merely practiced. The suggestions for implementation in this section are the lessons we learned. Most students in our course plan to pursue careers in medicine. These aspirations may correspond to increased motivation to succeed, increased past success with school, and higher than average standardized test scores, but also less positive traits such as a highly competitive attitude that hinders cooperative group work, and a fear of new classroom methods that they perceive as likely to interfere with their proven ability to succeed in traditional classrooms. We acknowledge that these differences may contribute to the learning gains we found, but other studies have found AL and TCC methods more effective than traditional methods in science classes with non-majors and majors from a broader range of science disciplines than our sample (e.g., Hake 1998a, Bonwell and Eison 1991, Crouch and Mazur 2001, Bishop and Anderson 1990, Jensen and Finley 1996), suggesting that these methods produce learning gains for a wide range of students. Finally, though we have obviously dedicated a substantial amount of time to refining this activity, we also know instructors who use only lecture methods often devote equal amounts of time to class preparation. Time and dedication alone do not produce significant learning gains.

As we continue to incorporate AL and TCC methods into our course, we envision a course where most of the learning takes place in activities that use TCC and AL strategies, particularly when covering topics about which students hold many misconceptions. As studies showing the inadequacy of using only lectures continue to accumulate, we believe it is ethically questionable and scientifically irresponsible to continue using predominantly lectures to teach college science. This activity is one step toward a course based on research on the effectiveness of teaching methods and, we hope, a step toward a reformed paradigm of how we teach college biology.

Tables and Figures

Table 5.1. Common misconceptions and example student answers

Category	Description of misconception	Examples from student answers
Teleological/ Intentionality	Student believes change happens as a result of need or desire	“Humans are evolving to be protected against new diseases. This evolution is due more to choice than to natural selection.” “When the human population needs to evolve to change to its surroundings, it will.” “ I doubt that the earth will allow humans to become different species.”
Principle of inertia	Student believes selection has always occurred and so will continue to occur	“Evolution is a process that will never stop, even in the human species.” “I believe humans are still evolving because there is no reason why this process would have gone on for so long without stopping and suddenly come to a halt.” “If we accept the theory of evolution as an explanation for historical data, we must assume that we will continue to evolve.”
Use and disuse	Student believes traits that are used are retained and those that are not used are lost	“I think that the human head will increase in size because as a race, humans are acquiring more and more knowledge.” “Some people are born without wisdom teeth because they are for chewing much tougher things that have long since been lost in the human diet.” “I think that the pinky-toe on our feet will get smaller and smaller until it goes away because it doesn’t seem to have a purpose.” “More and more people are being born without an appendix. Seeing as this is not useful to us, this makes sense, and is evidence of evolution.”
Lack of selection/natural selection as all or nothing	Student believes natural selection no longer occurs in first world countries OR that selection only happens when organisms die	“Medicine has halted natural selection by enabling the defined ‘weaker’ of the species to live longer.” “There is no differential fitness in the modern world for humans.” “There isn’t any sort of predator around that attacks and causes the weak to die.” “There is nothing favoring the survival of only specific people.” “Everyone can survive in our environment.”
Uniform species	Student believes all organisms in a species are essentially alike	“There is a significant amount of recorded human history, and they don’t seem that different from us.” “I am no different from my mom and she isn’t any different from her mom.”
NS as speciation	Student believes evolution equals speciation	“No, because evolving equals change from one species to another.” “I don’t believe we will become a new species.”

Table 5.2. Supplemental material description

Discussion Tools	**Goal of this item:**
Sample student(s)-instructor dialogue	to show the pattern of logic we use to directly address student misconceptions
Relevant cartoon	to provide a visual representation of a common student misconception (humorously)
Example Tools	**Goal of this item:**
CCR5 and HIV interaction diagram	to show students how the *CCR5* protein interacts with HIV on a cell surface
CCR5 DNA sequences	to provide a concrete representation of variation in the population at the *CCR5* locus
Table of allele frequencies	to show students how the frequency of the mutation varies around the world and provide a basis for discussing how evolution is likely to change allele frequencies in parts of the world differentially affected by HIV
Graph of human height change over the last two centuries	to provide a visual representation of the change in human height that students often mention as evidence of evolution
Details about height data	to provide instructors with a large data set that can be used to create graphs and address questions about human height
Histogram of height	to show students how height varies in the human population
Height is heritable graph	to provide a simple visual representation of the evidence that height is heritable by comparing father and son height
Map of chromosome sections associated with human stature	to show students how quantitative traits (traits controlled by multiple genes and the interactions between those genes) can be the result of multiple DNA segments
Reproductive success and height graph	to show students evidence that height can affect reproductive success

Table 5.3. Concepts learned during this activity, as reported by students

Concept learned	# of students
Reproductive success (not just survival) needs to be considered when we think about selection	2
Individuals do not evolve or change their own genes	9
Evolution is a continuous process	1
The environment doesn't directly change DNA sequences	5
The environment doesn't directly cause evolution	4
Evolution takes place over a long time period, not one generation	7
Other students have many different ideas about evolution	2

Table 5.4. Student opinions about the human evolution activity

Statement	% Agreed[a]	% Disagreed[b]
This activity held my interest	94.4	5.6
This activity challenged me intellectually	88.9	11.1
This activity helped me better understand evolution.	98.1	1.9
Writing down my answers and reexamining them later helped me learn.	88.7	11.13
Discussing the questions with my classmates helped me learn.	87.0	13.0

[a] Answers include "slightly agree," "somewhat agree," and "strongly agree"
[b] Answers include "slightly disagree," "somewhat disagree," and "strongly disagree"

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CHAPTER SIX

CONCLUSIONS

Questions about undergraduate evolutionary biology education and questions about evolutionary biology benefit equally from a rigorous scientific approach to building knowledge. While many dissertations in biological sciences have been based on the premise that the scientific process is a supremely effective tool for growing our knowledge of the natural world, few biology dissertations have been based on the premise that the scientific process increases our knowledge of how students learn about the natural world just as effectively. Using a scientific approach, I have addressed questions about differences among populations of westslope cutthroat trout that could affect the success of translocations—an important conservation strategy. I have also addressed questions about what strategies can be used to facilitate student learning about natural selection and the association between student learning and instructor teaching methods.

In particular, that final question benefitted from a rigorous scientific approach. Numerous studies have shown that students taught using active learning strategies learn substantially more than students taught using primarily lectures. These studies have been widely cited in national calls for undergraduate science reform and described as useful strategies for all instructors. Yet there had not yet been a systematic study of the effectiveness of these methods when used by typical faculty. Instead studies primarily examined atypical faculty versed in education research and theory. The study described in Chapter 5 showed strategies effective for education experts are not necessarily effective for typical faculty. This finding suggests the need for a major shift in our approach to education reform. Rather than continuing to develop exercises and strategies that may or may not be effective for most instructors, we need to focus on supporting and training faculty so they too can maximize the effectiveness of their teaching. This is but one example of the strides that can be made in our knowledge of biology education when biologists address these questions using their expertise in scientific methodology and the scientific process.

Chapter 3 illustrates a similarly important advancement in our knowledge of translocations. Few, if any, studies have addressed questions about the populations that should contribute to a fish translocation to maximize its chance of success. I found that populations can behave quite differently when introduced to a common habitat. Differences in dispersal are particularly important for trout because extensive dispersal over barriers will seriously jeopardize a translocation project. Translocations are expensive, labor-intensive, and generally used when less invasive conservation strategies are no longer sufficient. To ensure these projects contribute to species conservation as intended, we need to scientifically approach questions about strategies and factors associated with translocation projects.

In conclusion, biologists have the power, the passion, and the expertise to begin revolutionizing undergraduate biology education. Colleagues with expertise in biology and education can help to harness the energy and skills already present in biology departments across the country. Together, we can enhance the future of biological exploration by investing in biology education.

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APPENDICES

APPENDIX A

SAMPLE QUESTIONS FROM THE CONCEPTUAL INVENTORY OF NATURAL SELECTION-ABBREVIATED

Scientists have long believed that the 14 species of finches on the Galapagos Islands evolved from a single species of finch that migrated to the islands one to five million years ago (Lack, 1940). Recent research (Burns, et al. 2002) suggests that the original finches came from the Caribbean Islands. Different species live on different islands. For example, the medium ground finch and the cactus finch live on one island. The large cactus finch occupies another island. Among the major differences in finch species are their beak sizes and shapes. Evolutionary changes occur by many processes, one of which is natural selection.
Choose the answer that best reflects how an evolutionary biologist would answer the following questions with natural selection in mind.

What is the best way to characterize the evolutionary changes that occur in a finch population over time?
a. The traits of each individual finch in a population change over time.
b. The proportions of finches with different traits in a population change over time.
c. Mutations occur to meet the changing needs of the finches.
d. The environment causes specific mutations in individual finches to help them survive and reproduce.

What caused populations of finches having different beak shapes and sizes to become distinct species distributed on the various islands?
a. The finches were quite variable, and those whose features were best suited to the available food supply on each island reproduced most successfully.
b. All finches are essentially alike and there are not really fourteen different species.
c. Different foods are available on different islands and for that reason, the finches that colonized each island developed the beaks they needed before they reproduced.
d. The environment on each island gradually molded beak shape in the new species because that particular shape was needed to obtain the available food.

APPENDIX B

RUBRIC USED TO SCORE THE CHEETAH QUESTION

Cheetahs (large African cats) are able to run faster than 60 miles per hour when chasing prey. How would a biologist explain how the ability to run fast evolved in cheetahs, assuming their ancestors could run only 20 miles per hour?

	Concept	Full understanding	Partial understanding
1	Phenotypic variation exists in populations; individuals differ	2 points for explicitly mentioning the existence of variation (specifically that some cheetahs run faster than others)	1 point for implicitly mentioning variation OR for mentioning variation caused by development or need OR for a particularly vague description of differences
2	Mutation (or recombination) create variation in individuals.	1 point for mentioning mutation as the source of the “fast” gene or as a source of variation (CANNOT imply a lack of randomness)	
3	Environmental conditions affect the survival and spread of existing traits by creating differential reproduction between individuals.	2 points for explaining that interactions between the trait (speed) and the environment result in fast cheetahs having more offspring	1 point for explaining that the faster cheetahs had higher survival but not directly addressing reproductive success OR for an incomplete or implicit description of the interaction between the trait and the environment
4	Differential reproduction leads to a change in the proportion of individuals that have a trait in the next generation.	1 point for explaining that this process has caused a change in the proportion of fast cheetahs and/or the genetic make-up of the species	
5	The trait is heritable (*i.e.,* a gene passed on to offspring).	2 points for explaining that the variation is due to genes that are passed from parent to offspring, must specifically mention genes, inheritance, etc. and specify that the genes relate to the trait (speed)	1 point for explaining variation is passed on without mention of genes OR for implying inheritance OR for discussion of genes being passed down within the population (but without reference to individuals)
6	Selection over many generations leads to a change in a trait in a pop.	1 point for explaining that this process must continue many generations, a long period of time, etc.	

APPENDIX C

INSTRUCTOR SURVEY

1. How many times have you taught this course before?

2. How many years have you taught college biology?

3. How many hours did you devote to teaching natural selection in lecture this term?

4. Approximately what proportion of the students enrolled in your course attend regularly?

5. Approximately how many students were in each section of your course?

6. What is your position at your institution?

    a. Tenure track
    b. Non-tenure track

7. Does your course include students who are not biology majors?

    a. No, this course is taken primarily by students majoring in biology.
    b. Yes, but over 75% of students in this course are biology majors.
    c. Yes, but 50-75% of students in this course are biology majors.
    d. Yes, and less than 50% of the students in this course are biology majors.
    e. Yes, but I'm unsure what percentage of students are biology majors.

8. Richard Hake (1998) defines interactive engagement methods as "designed at least in part to promote conceptual understanding through interactive engagement of students in heads-on (always) and hands-on (usually) activities which yield immediate feedback through discussion with peers and/or instructors." Examples of these activities include group work, classroom discussions, in-class writing, and clicker questions that require deep thinking. *How often did you use active learning, interactive-engagement, or other student centered teaching activities used in the LECTURE portion of your course?*

    a. Never (or almost never)
    b. Once per week
    c. Once per class
    d. More than once per class

9. How often did you use active learning, interactive-engagement, or other student-centered activities during the portion of the course dedicated to teaching natural selection?

   a. Never

   b. Once

   c. Twice

   d. Three times

   e. Four or more times

10. How often did you employ the following activities in the lecture portion of your introductory biology course? [Instructors replied to each of the following]

- Clicker questions that test conceptual understanding
- Student discussions in pairs or small groups to answer a question
- Activities in which students use data to answer questions while working in small groups
- Individual writing activities that require students to evaluate their own thinking
- Classroom-wise interactions that require students to apply principles presented in class to a novel question
- Other small group activities

   a. Never (or almost never)

   b. Once per week

   c. Once per class

   d. More than once per class

11. Students often enter introductory biology courses with misconceptions about natural selection. Some of the more commonly documented misconceptions include a belief that individuals evolve because they need to, a belief that individuals gain and lose traits due to use and disuse, and a belief that the environment directly causes evolution within an individual's lifetime and that those changes are passed on to offspring. *Within your curriculum, do you directly target misconceptions? Choose all that apply.*

   a. Yes, I explain to students why misconceptions are incorrect.

   b. Yes, I use active learning exercises and otherwise make a substantial effort toward correcting misconceptions.

   c. No, I do not specifically target misconception.

APPENDIX D

STUDENT POSTTEST SURVEY

1. How difficult was this course compared to other science classes you have taken?

    a. much more difficult
    b. more difficult
    c. about the same as other classes
    d. less difficult
    e. much less difficult

2. How interesting was this course?

    a. very interesting
    b. interesting
    c. average
    d. uninteresting
    e. very uninteresting

3. Richard Hake (1998) defines interactive engagement methods as "designed at least in part to promote conceptual understanding through interactive engagement of students in heads-on (always) and hands-on (usually) activities which yield immediate feedback through discussion with peers and/or instructors." Examples of these activities include group work, classroom discussions, in-class writing, and clicker questions that require deep thinking. *How often were active learning, interactive-engagement, or other student centered teaching activities used in the lecture portion of this course?*

    a. Never (or almost never)
    b. Once per week
    c. Once per class
    d. More than once per class

APPENDIX E

SUPPLEMENTAL ONLINE MATERIALS FOR “ACTIVE LEARNING *NOT* ASSOCIATED WITH STUDENT LEARNING IN A RANDOM SAMPLE OF COLLEGE BIOLOGY COURSES”

Table 1. Comparisons between mean test scores and learning gains between courses using paper and online testing

	Means		Welch’s *t*-statistic	*p*-value
	Paper	Online		
CINS-abbr pre	5.54	5.32	-0.91	0.37
CINS-abbr post	6.93	6.37	-1.70	0.10
Cheetah pre	2.77	2.99	0.80	0.43
Cheetah post	3.06	3.35	1.15	0.26
CINS-abbr effect size	0.57	0.46	-1.20	0.24
Cheetah effect size	0.12	0.16	0.58	0.57

Table 2. Comparisons between mean test scores and learning gains between courses offering course credit to log into the tests and courses not offering course credit

	Means		Welch’s *t*-statistic	*p*-value
	Credit	No credit		
CINS-abbr pre	5.28	5.69	1.58	0.12
CINS-abbr post	6.31	7.11	2.33	0.03
Cheetah pre	2.94	3.12	0.52	0.61
Cheetah post	3.30	3.44	0.42	0.68
CINS-abbr effect size	0.44	0.61	1.62	0.12
Cheetah effect size	0.15	0.13	-0.39	0.70

Table 3. Pearson's correlation matrix for learning gains on the CINS-abbr

	Effect size	**Average normalized gain**	**Percent change**	**Raw change**	**CINS-abbr pretest**	**CINS-abbr posttest**
Effect size	–					
Average normalized gain	0.95***	–				
Percent change	0.92***	0.82***	–			
Raw change	0.98***	0.95***	0.95***	–		
CINS-abbr pretest	0.27	0.51*	-0.03	0.25	–	
CINS-abbr posttest	0.73***	0.88***	0.5*	0.73***	0.85***	–

*$p < 0.05$, **$p < 0.01$, ***$p < 0.001$
The Holm-Bonferonni method was used to calculate *p*-values.

Table 4. Pearson's correlation matrix for learning gains on the cheetah question

	Effect size	**Average normalized gain**	**Percent change**	**Raw change**	**Cheetah pre-test**	**Cheetah post-test**
Effect size	–					
Average normalized gain	0.99***	–				
Percent change	0.86***	0.79***	–			
Raw change	0.99***	0.99***	0.87***	–		
Cheetah pre-test	-0.24	-0.14	-0.62**	-0.27	–	
Cheetah post-test	0.27	0.37	-0.17	0.24	0.87***	–

*$p < 0.05$, **$p < 0.01$, ***$p < 0.001$
The Holm-Bonferonni method was used to calculate *p*-values.

Table 5. Comparisons between fully participating instructors and partially participating instructors, using Welch's *t*-tests for continuous data

	Means		Welch's *t*-statistic	*p*-value
	Fully	Partially		
Weekly frequency of specific active learning exercises	8.03	5.14	-1.64	0.11
Class size	233	208	-0.54	0.59
Years of teaching experience	14.56	13.59	-0.28	0.78
Hours of class time dedicated to teaching natural selection	4.77	5.97	0.82	0.42
Proportion of students regularly attending class	0.79	0.78	-0.32	0.76

Table 6. Comparisons between fully participating instructors and partially participating instructors, using Fisher's exact texts for count data

		Counts		*p*-value
		Fully	Partially	
Instructor position	Tenure track	15	16	0.06
	Non-tenure track	18	8	
Institution type	Private	2	5	0.10
	Public	31	17	
Sampling list	Top 50	10	5	0.76
	Large state institution	23	17	
General active learning use	Never (or almost never)	4	6	0.14
	Once per week	9	9	
	Once per class	8	3	
	More than once per class	12	3	

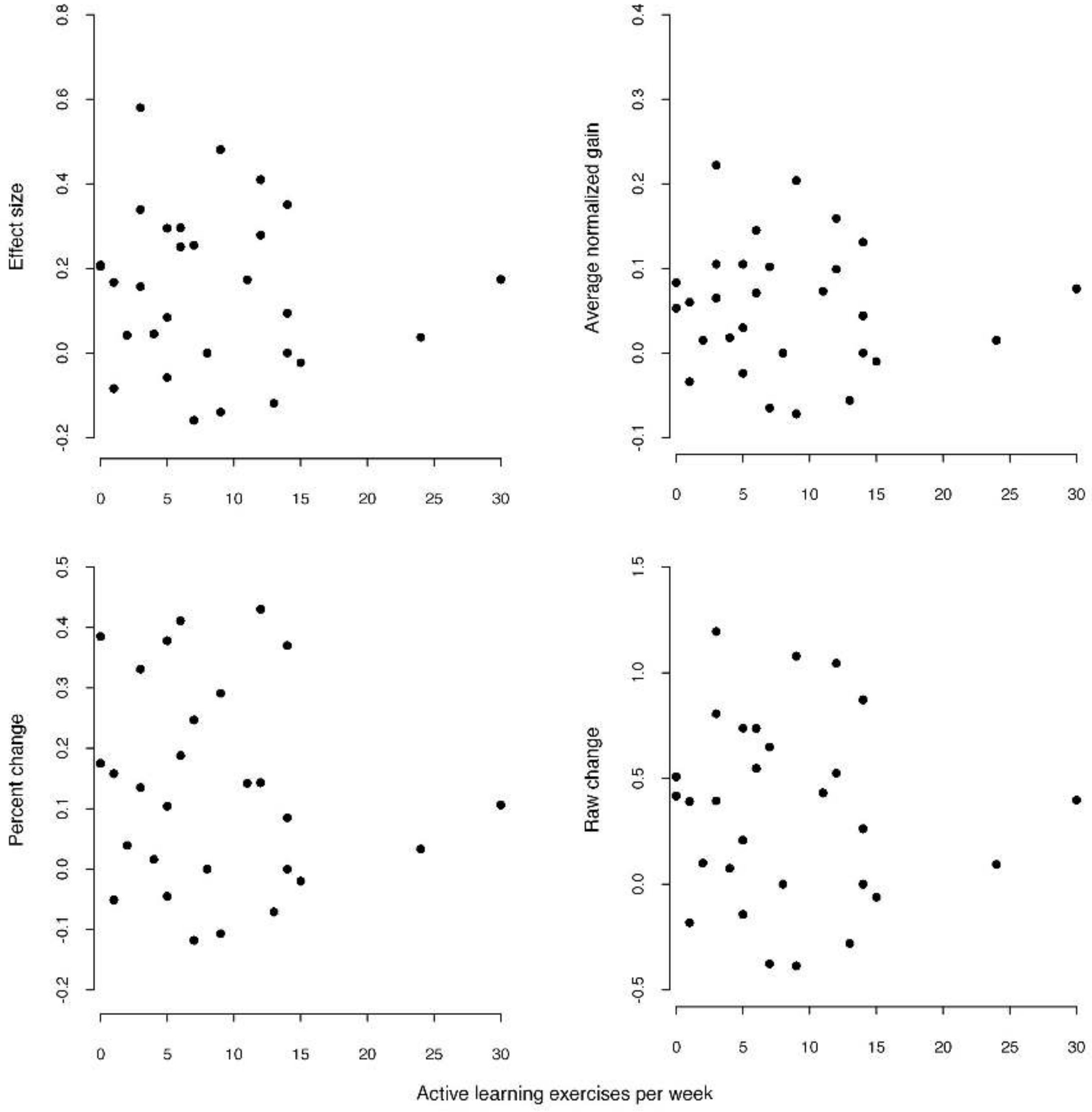


Figure 1. Scatterplots of four calculations of learning gains on the cheetah question and active learning exercises per week.

Relationship between instructor's use of active learning and four different calculations of learning gains on the cheetah question. The cheetah question was scored out of nine points, so a raw change of one is equivalent to earning one more point out of nine on the posttest than on the pretest.

APPENDIX F

SUPPLEMENTAL ONLINE MATERIALS FOR “ARE HUMANS EVOLVING? A CLASSROOM DISCUSSION TO CHANGE STUDENT MISCONCEPTIONS REGARDING NATURAL SELECITON”

1. Tools to discuss common student answers

This section of the supplemental materials includes two items that may be useful for the discussion section of the activity before the instructor presents the two examples of human evolution. Students will likely suggest many traits that they think are evolving in humans. Most commonly, our students mention that wisdom teeth and the appendix are "evolving away" because we don't "need" or "use" them anymore. Students also suggest that our eyesight is getting worse because we "fix" it with glasses and contacts, "allowing the weak to survive." Finally, students will equate change they see in the population as equivalent to evolution. For example, they will suggest that humans are evolving to be fatter, taller, balder, and smarter ("because of computers and technology"). Before presenting traits that are actually evolving in the human population, it is important to use the three requirements to help students reject common and inaccurate ideas. We use the next two items during this portion of the activity.

a. Cartoon

More than once, our students have suggested that humans are evolving to be fatter. When asked if humans are evolving, students often equate *change* they see in the human population with *evolution*. One obvious change they see is that people are more obese than they used to be. Carol Lay, a cartoonist, has created a very apt cartoon for the discussion of whether people are evolving to be fatter. She has graciously agreed to allow us to point you to her website for access to the cartoon, http://www.waylay.com/Store/OrigPages/529.html. We use this cartoon to pose the question, "Are humans evolving to be fatter?" We then ask students to use the three requirements of natural selection to discuss this question. The following dialogue is an example of what this might sound like in a classroom.

b. Sample dialogue

To demonstrate how student ideas are examined during the class discussion, the dialogue below models the instructor's response to student ideas. This dialog begins as a student offers his or her group's idea about how humans are evolving.

Student 1: Humans are much fatter than they were even when our parents were in college, so humans have evolved to be more obese. Maybe we're also evolving to have bigger stomachs and stronger bodies to deal with obesity.

Instructor: OK. One suggestion is that humans are evolving to be fatter and evolving other body characteristics to go along with the increased body fat. Let's consider the three requirements of natural selection. Is there variation in the population with regard to weight?

Student 2: Yes, obviously some people are fatter than others.

Student 3: And some people get fat more easily, even when they are pretty healthy.

Instructor: So there is variation in the population. Is weight or tendency to put on extra weight heritable?

Student 1: Probably, but I don't know. I mean you see whole fat families, so probably it's genetic.

Student 4: Yeah, but families also all eat unhealthy or sit around all day, so maybe they just got fat because of that and not because of their genes.

Instructor: How would we test whether this trait was heritable or not?

Student 5: We could compare parents and their children and see if there is a relationship between them, but, like, take into account what they eat and how much they exercise.

Instructor: So we would create a graph with the child's weight on the x-axis and parent weight on the y-axis, like we've seen before. Assuming it is heritable, do you think fat people are having more children than thinner people?

Student 1: Umm…no, I guess not.

Instructor: So, if we could show that obese people were having more children than thin people, we could agree that humans are evolving to be fatter. However, we don't think that obese people are having more children. This cartoon shows that other people have noticed the fact that people are becoming more obese and that this might be related to evolution. What are some other explanations for why more people are obese?

2. Background information - HIV Resistance and the CCR5 Locus

AIDS is a disease of the human immune system caused by the human immunodeficiency virus (HIV) that kills over 2 million people each year (Joint United Nations Programme on HIV/AIDS 2009). Most people in the world are highly susceptible to HIV infection, but individuals who are homozygous for a rare allele at the *CCR5* locus are essentially immune to the disease (Samson et al. 1996). Simply put, HIV enters a white blood cell by binding to the *CCR5* protein. A rare resistant allele, called *CCR5-Δ32*, has a 32 base pair deletion in the DNA sequence of the *CCR5* gene. This deletion causes a frame shift, creating a non-functional receptor and preventing HIV from infecting the cell (Samson et al. 1996).

Is there variation in the population? CCR5-Δ32 has a frequency of around 10% in many European countries and in Russia (Samson et al. 1996, Stephens et al. 1998), but this mutated alleleis essentially absent in Asia and Africa (Samson et al. 1996). Students often believe that mutations occur because they are needed, and if that were true, the *CCR5-Δ32* mutation should be most common in Africa where HIV is more prevalent.

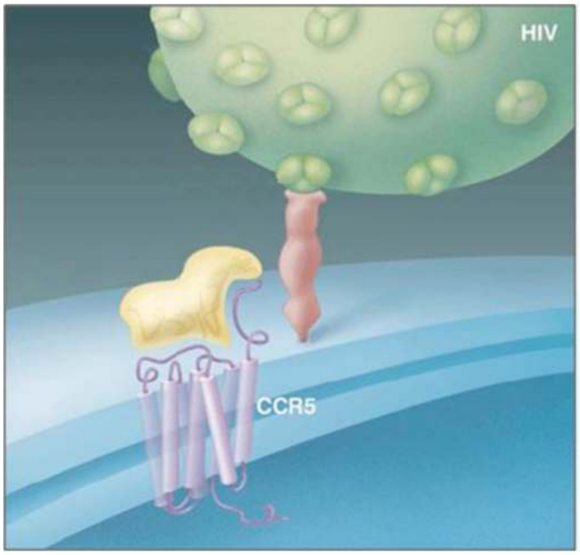
The reason why European populations have high frequencies of the *CCR5-Δ32* allele is not well understood. Mathematical models suggest that random drift of a neutral allele cannot explain the high frequency of *CCR5-Δ32* in European populations (Stephens et al. 1998), meaning that selection was likely responsible. However, debate remains about what may have caused this selection pressure. Some researchers suggest that outbreaks of the bubonic plague, which killed 25-33% of Europeans about 650 years ago, are the most likely source of strong selective pressure for this mutation (Stephens et al. 1998). Other researchers argue that the plague would not have provided sufficient selective pressure to create the current frequency and distribution of the *CCR5-Δ32* allele (Galvani and Slatkin 2003). Studies have also shown that the *CCR5-Δ32* allele does not confer resistance to the plague in mice (Mecsas et al. 2005). Instead, Galvani and Slatkin (2003) suggest it is more likely that the *CCR5-Δ32* allele conferred resistance to small pox and was therefore strongly selected. Finally, one hypothesis proposes that selective pressure from outbreaks of both small pox and haemorrhagic plague explain the current frequency and distribution of the mutated *CCR5* allele (Duncan et al. 2005).

Is this trait heritable? The immunity conferred by *CCR5-Δ32* is inherited as a simple Mendelian trait, so it is heritable. We use this example to emphasize to students that the ability of organisms to survive and reproduce is influenced by genotypes present at specific loci. This should help students connect natural selection with Mendelian genetics (two of the most important concepts in biology). We also show students the DNA sequence of *CCR5* and *CCR5-Δ32* alleles, in order to provide a concrete example of how DNA sequences influence phenotypes (Kalinowski et al. 2010). Later, we use *CCR5-Δ32* allele frequencies as an example to illustrate Hardy-Weinberg proportions.

Does having this trait affect the ability of an individual to survive or reproduce? Two copies of *CCR5-Δ32* (homozygosity) confer a high level of resistance to HIV infection (Samson et al. 1996). Even one copy of *CCR5-Δ32* provides protection from AIDS (Stewart et al. 1997), most likely by prolonging the transition from HIV infection to AIDS. As long as HIV affects an individual's reproductive success in the human population, there will be selection for the *CCR5-Δ32* allele. Globally, only 42% of individuals in need of treatment for AIDS are being treated (Joint United Nations Programme on HIV/AIDS 2009), suggesting that, if *CCR5-Δ32* exists in a population, it will be selected for.

3. Diagram of CCR5 and HIV interaction

We use this diagram to show students the system we are discussing. The following figure shows a cell wall, including the surface proteins, and the HIV virus. The virus is binding to another receptor, but will also need to bind to the *CCR5* receptor to successfully enter the cell. The *CCR5-Δ32* mutation changes the external structure of this receptor and it will no longer bind to HIV. This diagram actually shows a *CCR5* inhibitor (yellow blob) binding to the *CCR5* receptor, but we have found it to be the most useful diagram of the overall structure. A person with the *CCR5-Δ32* allele would have an altered receptor, which in this diagram would mean an altered purple structure.



Modified from SCIENCE 306:387 (2004). Illustration: K. Sutliff/SCIENCE

4. DNA sequence of CCR5 alleles

We present students with the DNA sequence of the *CCR5* protein and the *CCR5-Δ32* sequence so that have a concrete image of the genetic difference. We found these sequences on GenBank; the accession number for *CCR5* is NG_012637. We truncated this and include base pairs 7762-8820. *CCR5-Δ32* can be found with the accession number X99393. In addition to the sequence below, there are text files of these sequences included in the supplemental materials. The wild type *CCR5* sequence is included in a text file called "CCR5-WT.txt" and the *CCR5-Δ32* sequence is included in a text file called "CCR5-delta 32.txt".

CCR5 receptor

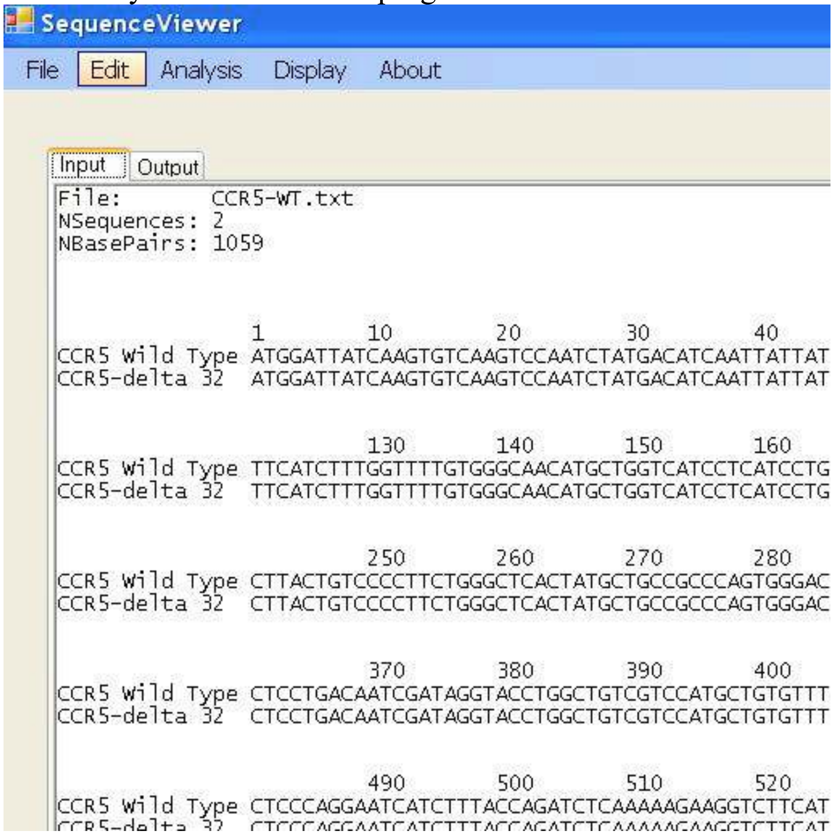
```
atggattatcaagtgtcaagtccaatctatgacatcaattattatacatcggagccctgccaaaaaatcaa
tgtgaagcaaatcgcagcccgcctcctgcctccgctctactcactggtgttcatctttggttttgtgggca
acatgctggtcatcctcatcctgataaactgcaaaaggctgaagagcatgactgacatctacctgctcaac
ctggccatctctgacctgtttttccttcttactgtcccctctgggctcactatgctgccgcccagtggga
ctttggaaatacaatgtgtcaactcttgacagggctctattttataggcttcttctctggaatcttcttca
tcatcctcctgacaatcgataggtacctggctgtcgtccatgctgtgtttgctttaaaagccaggacggtc
acctttggggtggtgacaagtgtgatcacttgggtggtggctgtgtttgcgtctctcccaggaatcatctt
taccagatctcaaaaagaaggtcttcattacacctgcagctctcattttccatacagtcagtatcaattct
ggaagaatttccagacattaagatagtcatcttggggctggtcctgccgctgcttgtcatggtcatctgct
actcgggaatcctaaaaactctgcttcggtgtcgaaatgagaagaagaggcacagggctgtgaggcttatc
ttcaccatcatgattgtttattttctcttctgggctccctacaacattgtccttctcctgaacaccttcca
ggaattctttggcctgaataattgcagtagctctaacaggttggaccaagctatgcaggtgacagagactc
ttgggatgacgcactgctgcatcaaccccatcatctatgcctttgtcggggagaagttcagaaactacctc
ttagtcttcttccaaaagcacattgccaaacgcttctgcaaatgctgttctattttccagcaagaggctcc
cgagcgagcaagctcagtttacacccgatccactggggagcaggaaatatctgtgggcttgtga
```

CCR5-Δ32 "-" represents deleted base pairs

```
atggattatcaagtgtcaagtccaatctatgacatcaattattatacatcggagccctgccaaaaaatcaa
tgtgaagcaaatcgcagcccgcctcctgcctccgctctactcactggtgttcatctttggttttgtgggca
acatgctggtcatcctcatcctgataaactgcaaaaggctgaagagcatgactgacatctacctgctcaac
ctggccatctctgacctgtttttccttcttactgtcccctctgggctcactatgctgccgcccagtggga
ctttggaaatacaatgtgtcaactcttgacagggctctattttataggcttcttctctggaatcttcttca
tcatcctcctgacaatcgataggtacctggctgtcgtccatgctgtgtttgctttaaaagccaggacggtc
acctttggggtggtgacaagtgtgatcacttgggtggtggctgtgtttgcgtctctcccaggaatcatctt
taccagatctcaaaaagaaggtcttcattacacctgcagctctcat------------------------
-------tttccatacattaaagatagtcatcttggggctggtcctgccgctgcttgtcatggtcatctgc
tactcgggaatcctaaaaactctgcttcggtgtcgaaatgagaagaagaggcacagggctgtgaggcttat
cttcaccatcatgattgtttattttctcttctgggctccctacaacattgtccttctcctgaacaccttcc
aggaattctttggcctgaataattgcagtagctctaacaggttggaccaagctatgcaggtgacagagact
cttgggatgacgcactgctgcatcaaccccatcatctatgcctttgtcggggagaagttcagaaactacct
cttagtcttcttccaaaagcacattgccaaacgcttctgcaaatgctgttctattttccagcaagaggctc
ccgagcgagcaagctcagtttacacccgatccactggggagcaggaaatatctgtgggcttgtga
```

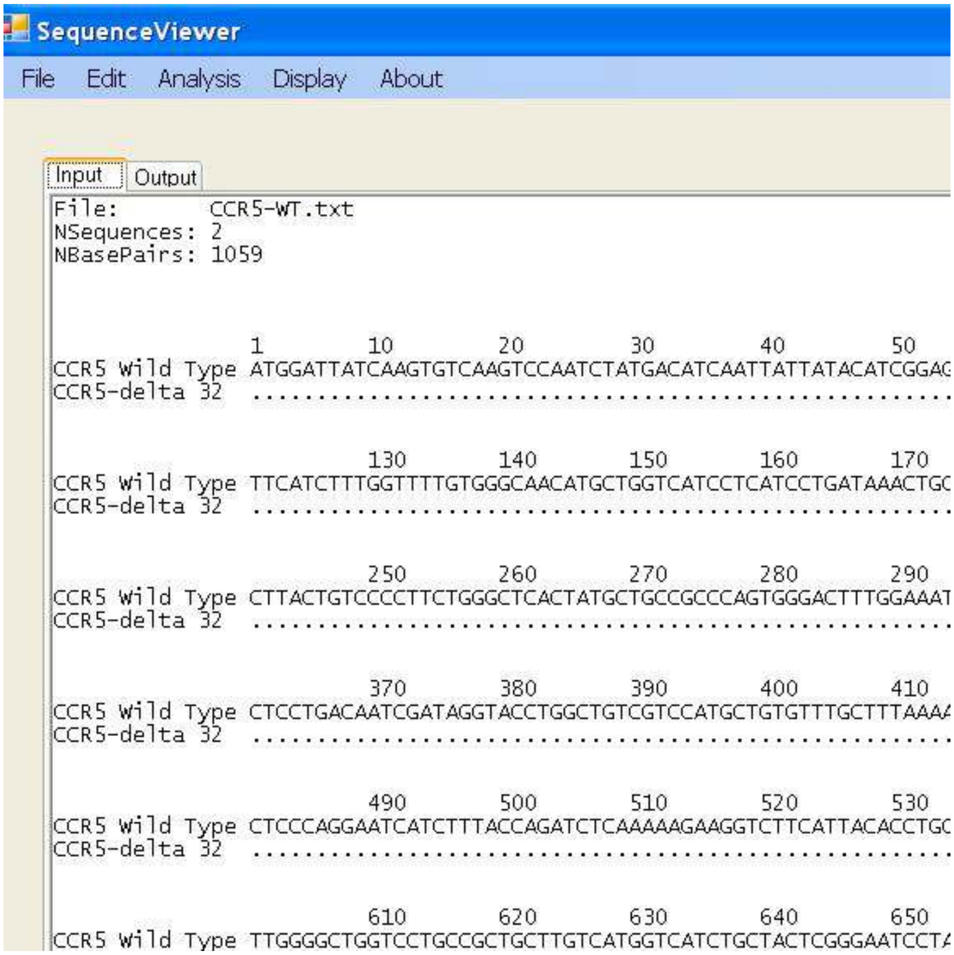
5. Viewing the DNA sequences

We use DNA sequences to concretely illustrate genetic concepts throughout our course (Kalinowski et al. 2010) so we created a simple program so that students can view and line-up different DNA sequences. To show the above DNA sequences in class, you can create a simple PowerPoint slide with one sequence after the other (as shown above) or you can use a more sophisticated program. The next two pictures show how the Sequence Viewer program shows sequences lined up. In the first (Figure 1), the program lines up letters representing the base pairs and uses dashes to show deletions. In the second picture (Figure 2) the program uses dots to represent base pairs that are the same and letters to show differences. This program can be downloaded at http://www.montana.edu/kalinowski/Software/SequenceViewer.htm. The website includes instructions and sample files. The files included in the supplemental materials are already formatted for the program.



```
File:        CCR5-WT.txt
NSequences:  2
NBasePairs:  1059


                  1        10        20        30        40
CCR5 Wild Type ATGGATTATCAAGTGTCAAGTCCAATCTATGACATCAATTATTAT
CCR5-delta 32  ATGGATTATCAAGTGTCAAGTCCAATCTATGACATCAATTATTAT


                          130       140       150       160
CCR5 Wild Type TTCATCTTTGGTTTTGTGGGCAACATGCTGGTCATCCTCATCCTG
CCR5-delta 32  TTCATCTTTGGTTTTGTGGGCAACATGCTGGTCATCCTCATCCTG


                          250       260       270       280
CCR5 Wild Type CTTACTGTCCCCTTCTGGGCTCACTATGCTGCCGCCCAGTGGGAC
CCR5-delta 32  CTTACTGTCCCCTTCTGGGCTCACTATGCTGCCGCCCAGTGGGAC


                          370       380       390       400
CCR5 Wild Type CTCCTGACAATCGATAGGTACCTGGCTGTCGTCCATGCTGTGTTT
CCR5-delta 32  CTCCTGACAATCGATAGGTACCTGGCTGTCGTCCATGCTGTGTTT


                          490       500       510       520
CCR5 Wild Type CTCCCAGGAATCATCTTTACCAGATCTCAAAAAGAAGGTCTTCAT
CCR5-delta 32  CTCCCAGGAATCATCTTTACCAGATCTCAAAAAGAAGGTCTTCAT
```

This photo shows a screen shot of the Sequence Viewer being used to view *CCR5* and *CCR5-Δ32*. All base pairs are represented by letters (i.e. A, C, T, G).



```
File:        CCR5-WT.txt
NSequences: 2
NBasePairs: 1059



               1       10        20        30        40        50
CCR5 Wild Type ATGGATTATCAAGTGTCAAGTCCAATCTATGACATCAATTATTATACATCGGA
CCR5-delta 32  ......................................................


                      130       140       150       160       170
CCR5 Wild Type TTCATCTTTGGTTTTGTGGGCAACATGCTGGTCATCCTCATCCTGATAAACTG
CCR5-delta 32  ......................................................


                      250       260       270       280       290
CCR5 Wild Type CTTACTGTCCCCTTCTGGGCTCACTATGCTGCCGCCCAGTGGACTTTGGAAAT
CCR5-delta 32  ......................................................


                      370       380       390       400       410
CCR5 Wild Type CTCCTGACAATCGATAGGTACCTGGCTGTCGTCCATGCTGTGTTTGCTTTAAA
CCR5-delta 32  ......................................................


                      490       500       510       520       530
CCR5 Wild Type CTCCCAGGAATCATCTTTACCAGATCTCAAAAAGAAGGTCTTCATTACACCTG
CCR5-delta 32  ......................................................


                      610       620       630       640       650
CCR5 Wild Type TTGGGGCTGGTCCTGCCGCTGCTTGTCATGGTCATCTGCTACTCGGAATCCT
```

This photo shows a screenshot of the Sequence Viewer being used to compare *CCR5* and *CCR5-Δ32*. This time matching base pairs are represented by dots. The deleted section is not visible in this photo.

6. Table of CCR5-Δ32 allele frequencies around the world

We use this table first to discuss variability. The following table shows frequencies of the *CCR5-Δ32* allele in different populations around the world.

Ethnic group	Frequency of CCR5-Δ32 allele	Reference
Chinese	0.00	Stephens et al., 1998
French	0.089	Stephens et al., 1998
German	0.108	Stephens et al., 1998
Italian	0.055	Stephens et al., 1998
Japanese	0.000	Samson et al., 1996
Korean	0.00	Stephens et al., 1998
Mexican	0.024	Stephens et al., 1998
Pima Indian	0.00	Stephens et al., 1998
Russian	0.136	Stephens et al., 1998
Saudi	0.00	Stephens et al., 1998
Swedish	0.137	Stephens et al., 1998
Western and Central Africans	0.00	Samson et al., 1996

Some of this data was reproduced from The American Journal of Human Genetics, 62(6), Stephens, J.C. et al., Dating the Origin of the CCR5-Δ32 AIDS-Resistance Allele by the Coalescence of Haplotypes, 1507-1515, Copyright (1998), with permission from Elsevier.

Samson, M., Libert, F. Doranz, B.J., Farber, C., Saragosti, S., Lapoumeroulie, C., et al. (1996). Resistance to HIV-1 infection in caucasian individuals bearing mutant alleles of the CCR-5 chemokine receptor gene, Nature, 382, 722-725.

7. Background information – Human height

Students frequently suggest that humans are evolving to be taller, and human height provides an ideal example to illustrate some of the complexities of natural selection. As students suspect, human height *has* increased substantially over the past three decades (Smith and Norris 2004, Freedman et al. 2000). However, only some of that change in certain populations seems to be due to evolution, rather than improved nutrition and medical care (Mueller and Mazur 2001).

Is there variation within the population? Human height is clearly variable, and a histogram shows human height has a "bell" shaped distribution. We have provided height data collected by Karl Pearson (Table 2) to illustrate this point, but a similar figure could be made from students' heights. Pearson's data is from the early twentieth century and, as many students will note, people in most countries are taller now. Average adult height has increased about one inch between 1960 and 2002 (Ogden et al. 2004).

Is height heritable? Human height is highly heritable, and in fact, the first studies of heritability examined human height. Sir Francis Galton started this work and his younger colleague, Karl Pearson, developed the statistical method of correlation to analyze father-son height data. Current studies estimate heritability of height in humans to be 0.8, meaning that about 80% of the variation in height within populations is due to genetics (Visscher 2008).

Height is a quantitative trait, which means that it is controlled by many genes of small effect. At least twenty genes have been found that contribute 0.2 – 0.6 cm to height per allele (Weedon et al. 2007, Weedon et al. 2008). These genes explain only about 3% of the variation in human height (Weedon et al. 2008), which suggests that many more genes of small effect will be found.

Twin studies are an interesting method of understanding heritability. Studies show that after birth, monozygotic (identical) twins grow to be more similar in height than dizygotic (fraternal) twins. Monozygotic twins reared apart are more different in stature than monozygotic twins reared together, but are still more similar than dizygotic twins who grew up together (Chambers et al. 2001). In dizygotic twins aged 14 to 36 months, 61 - 82% of variation in height can be attributed to genes (Chambers et al. 2001).

Does being taller (or shorter) affect an individual's ability to survive or reproduce? Several studies have shown a positive relationship between height and reproductive success—in particular for men. For example, height was positively related to number of children in a sample of Polish men (after controlling for other factors that affected height in this sample, such as locality of residence) (Pawlowski et al. 2000). A study of West Point Cadets (Class of 1950) also showed that taller men had more children (Mueller and Mazur 2001). This study did not control for potential environmental differences, but used a highly homogeneous sample – mostly middle-class men of European descent who came from rural backgrounds and had parents who had at least a high school degree. Finally, a study of British men born in 1958 found that taller men were less likely to be childless than shorter men, and men who were taller than average were more likely to find a long-term partner *and* to have several long-term partners (Nettle, 2002b). This study controlled for socioeconomic status and serious health problems. Together, this research suggests that – in some populations – men are evolving to be taller, but it is likely that in other populations male height is not evolving; selection could even be moving height in the other direction.

Selection for taller men is likely due to sexual selection, meaning that the increase in reproductive success is mediated by opportunities to mate. Women frequently prefer taller men for dates, sexual partners, or husbands (Buss and Schmitt 1993, Ellis 1992, De Backer et al. 2008). For example, a study of personal ads showed that 80% of women advertised for men six feet or taller, even though the average American male is 5'9". Interestingly, studies of reproductive success do not show that taller men have more children within any single marriage, but instead are more likely to remarry and have a second family (Mueller and Mazur 2001).

Female preference for tall men is not likely to lead to unconstrained directional selection. Extremely tall men (those in the top decile) are slightly more likely to be childless. They are also more likely to have a work-impairing, long-standing illness, and they have a slightly higher mortality (Nettle 2002b). Additionally, mating partners who are more similar in height are more likely to have non-induced labor and have higher numbers of live-born children (Nettle 2002a, Nettle 2002b).

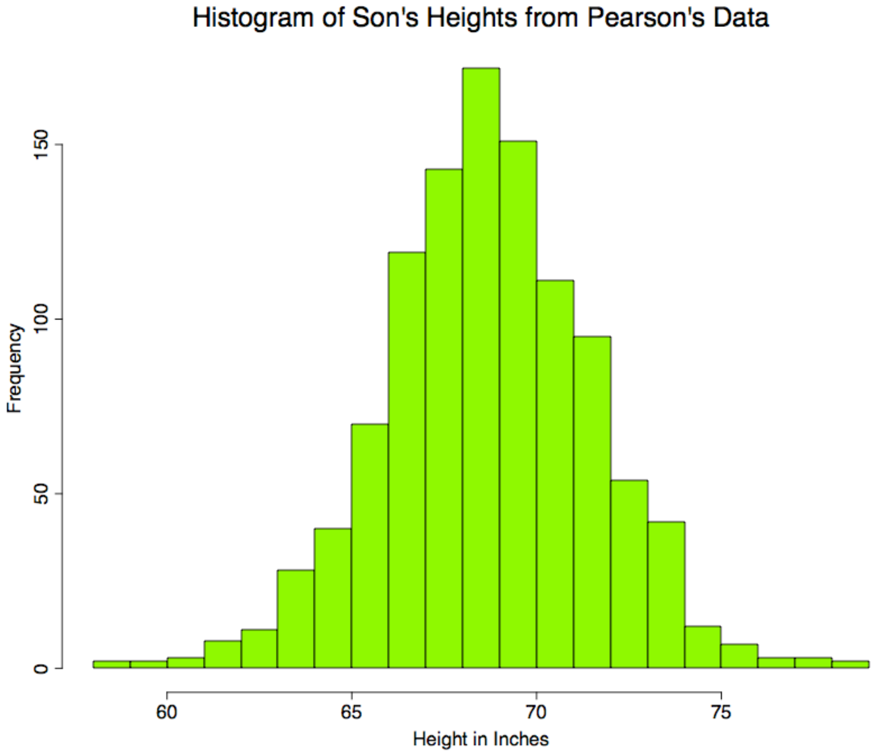
The relationship between a woman's height and fitness is more complicated. In developed countries such as America and England, the average woman is 5'4." In these countries, shorter women have the highest reproductive success and are least likely to be childless (Nettle 2002a). In contrast, in less developed countries such as Guatemala and Gambia, a woman's height is positively related to reproductive success. In these countries, tall women are more likely to have healthier children. (Sear et al. 2004, Pollet and Nettle 2008). In all studies, the effect of height on reproductive success of women is less drastic than in men.

What else affects human height? As students are likely to note, human height is strongly affected by nutrition and health care as well as by genes. Because of this, the average height and weight of children is often used to monitor the health of populations worldwide. For example, several studies have shown that North Koreans are shorter than South Koreans (see Schwekendiek and Pak 2009 for a meta-analysis), and researchers attribute these differences to nutrition. Similarly, height increased in the Japanese population in the generation born after World War II (Ali et al. 2000). Height also tends to vary by socioeconomic status within countries; children from more well off families are taller than children from poorer families (even in developed countries like the US) (Eveleth and Tanner 1990). Both nutrition and childhood illness are oft-cited sources of growth limitations. These two forces can form a positive feedback loop. Infections cause nutritional status to deteriorate, and malnoursished children are more susceptible to illness (Eveleth and Tanner 1990).

In summary, height is highly heritable in ideal conditions, but the effects of childhood illness and malnutrition can have large and lasting effects on overall height. This point is both important and challenging for many students. Understandably, they have a hard time imagining the mechanisms through which genes could have some effect but not complete control, and instead often consider a trait a result of *either* nature or nurture, but not both.

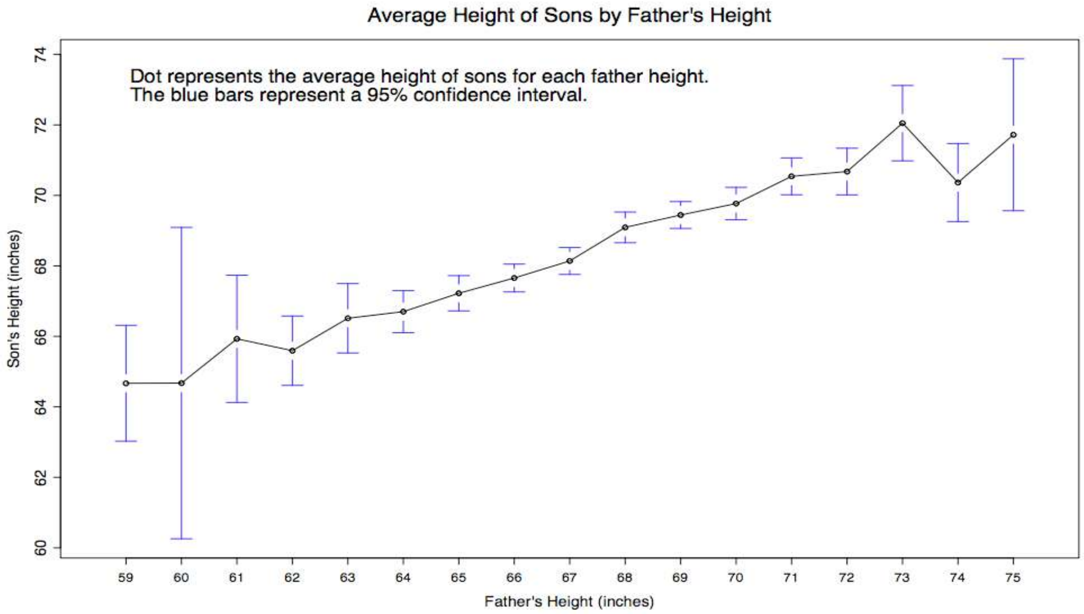
8. Histogram of height data

We use a simple histogram of the sons' heights to remind our class that height is variable in the human population. This graph has height along the x-axis and frequency of that height within Pearson's sample of sons' heights along the y-axis. It shows that at the time this data was collected (around the turn of the 20th century), the average man was about 68 inches tall.



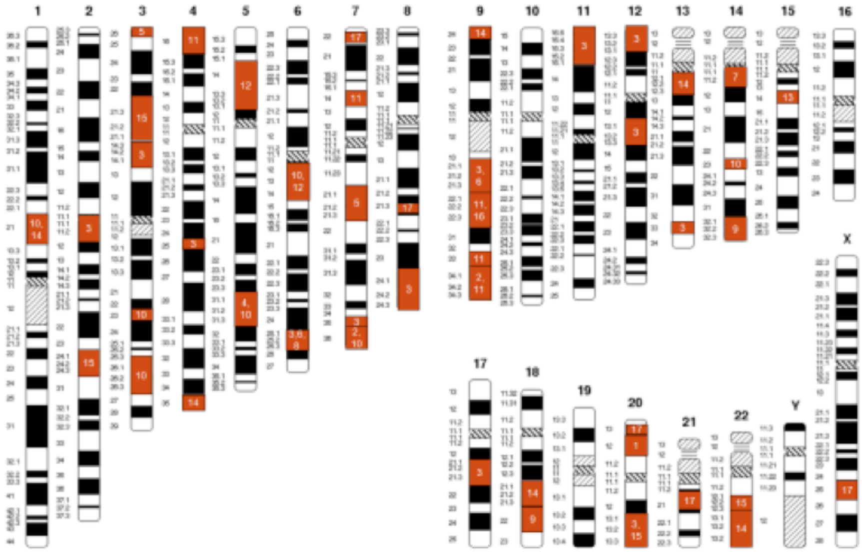
9. Height is heritable

We discuss how as father height increases, the average height of their sons also increases. We also discuss the fact that the confidence bars are wider at the ends of the distribution because there are fewer fathers in these samples.



10. Visual representation of the many genes potentially associated with human height.

The figure below can be found at http://www.genomeutwin.org/stature_gene_map.htm. Each orange section represents an area where researchers have found sequences associated with human stature. The website sites all of the specific studies, if you would like more information. We use this figure to show our students how many genes are potentially related to adult height. This concept is very different from the simple Mendelian genetics of the *CCR5* mutation and we suspect students often do not understand how a trait can be simultaneously affected by do many different parts of the genome.



Last updated 25.6.2007

Reprinted from http://www.genomeutwin.org/stature_gene_map.htm on September, 15, 2010.

Perola M, Sammalisto S, Hiekkalinna T, Martin NG, Visscher PM, et al. (2007) Combined genome scans for body stature in 6,602 European twins: Evidence for common Caucasian loci. PLoS Genet 3(6): e97. doi:10.1371/journal.pgen.0030097

11. Height change over time

We use the graph below to illustrate for student how human height has changed over the last two centuries. After you have discussed the fact that height changes are likely to be affected both by evolution and by the environment, this graph can be discussed again in the context of the differences in change in height between different parts of the world. This graph shows that though height has increased over time on average, it has increased much more quickly in industrial countries, most likely due to better medical care and nutrition (Baten, 2010).

Baten, J. (2010). Global height trends in industrial and developing countries, 1810-1984: An overview, Working paper Tuebingen, Retrieved September 15, 2010, from http://www.wiwi.uni-tuebingen.de/cms/lehrstuhl-homepages/wirtschaftsgeschichte/research/downloads.html.

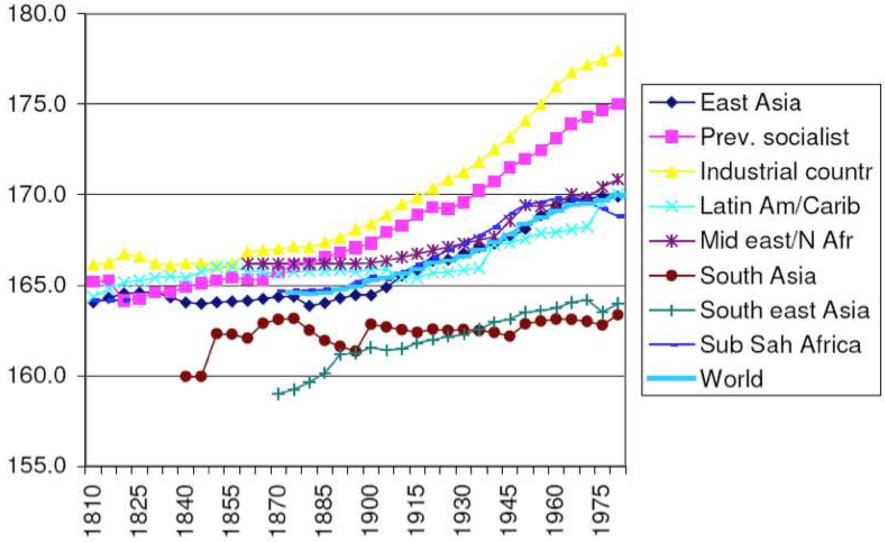
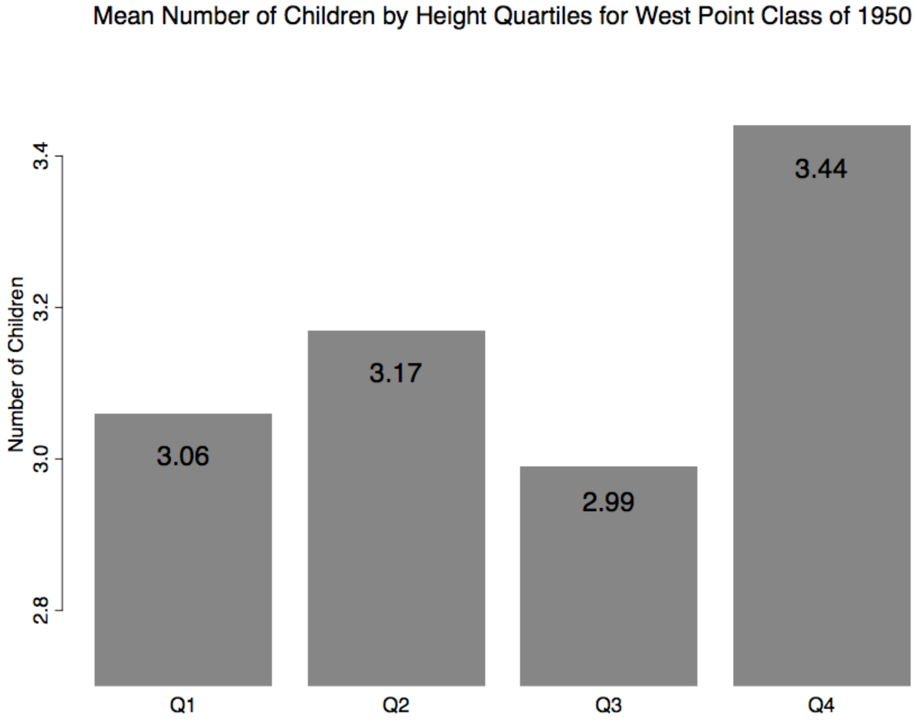


Figure reprinted (with slight alterations) with permission from J. Baten, granted September 16, 2010.

7. Height and reproductive success graph

We use the following graph to simply illustrate how height can affect reproductive success. This data comes from a study of the men of the Class of 1950 from West Point. It shows that the tallest men in that sample also had the most children.



This graph was reproduced (with slight alterations) with permission from Springer Science + Business Media and the authors: Behavioral Ecology and Sociobiology, Evidence of unconstrained directional selection for male tallness, 50, 2001, 302-311, Mueller, U. & Mazur, A., Figure 1b.