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Effects of Multilevel Selection on the Evolution of Homo neandertalensis

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Abstract

In this article, a model is used based on a paper by E. O. Wilson et al. (2007) to examine how multilevel selection has affected the evolution of Neandertals. Multilevel selection theory states natural selection occurs in multiple levels of the biological hierarchy. This model has never been applied to a hominid species to date. By synthesizing this research by Wilson et al. and genetic studies by Green et al. (2010) revealing that Neandertals and humans interbred in the Middle East 80,000 years ago, it is shown that multilevel selection may have affected Neandertal evolution. Further, it is argued that group level selection may not have had as drastic an effect on Neandertal evolution as it did on human populations. This article concludes by recommending ways this model may be applied to other species in the human evolutionary tree to help understand how multilevel selection has affected hominids throughout time.

Key Terms: Biological Anthropology, Evolution, Genetic Studies, Multilevel Selection Theory, Neandertals.

Introduction

Multilevel selection is a theory that has received a great deal of attention in recent years. D.S. Wilson and E. O. Wilson (2007) have shown that group level selection is not only theoretically possible, but that group level selection does actually occur in natural settings. In this article, how multilevel selection may have affected various adaptations of Neandertals is examined. A set of empirical claims was discovered while conducting research for this article regarding multilevel selection created by Wilson and Wilson (2007) that is in turn used as a model for determining which Neandertal adaptations or traits have been selected upon in various levels of the biological hierarchy. By applying various adaptations to the model, it is determined that individual level selection occurred throughout Neandertal evolution and group level selection occurred but less frequently than individual level selection.

Many researchers have looked at Neandertal mitochondrial DNA (mtDNA) (Krings et al. 1997, Ovchinnikov 2000, Krings et al. 2000, Marota et al. 2002, Serre et al. 2006) to determine the relationship between Neandertals and modern humans. All mtDNA studies have concluded that Neandertals and modern humans do not share similar mtDNA sequences. Therefore, if interbreeding between the two species did occur, Neandertals did not contribute mtDNA to the modern human gene pool. Another study looked at membrane-bound fossil DNA (fDNA) of Neandertals and modern humans to examine genetic variations in a different fashion (Scholtz et al. 2000). These researchers also concluded that Neandertals and modern human populations differ in their DNA sequences.

The turning point in the understanding of the relationship between Neandertals and modern humans has come with a study by Green et al. (2010). The researchers completed the draft of the Neandertal genome and determined that Neandertals and modern humans did interbreed in the Middle East about 80,000 years ago. This means that the DNA of all modern humans of non-African descent has anywhere from 1-4% of the Neandertal genome. This is the first study to confirm that interbreeding did occur between Neandertal and modern human populations. All previous studies have been unable to find this evidence. Because the Green et al. study is the first to prove a relationship between Neandertals and modern humans, and because past mtDNA and fDNA studies, including those mentioned above, have been unable to prove that Neandertals and modern humans interbred at any point in history, the scientific community has been cautious when accepting this study.

The Model

Four empirical claims are used by Wilson and Wilson (2007) to create a model to test various Neandertal adaptations. Wilson and Wilson's four empirical claims are: first, there is a problem with biological theory when group level selection is categorically ignored that can be seen in altruistic adaptations throughout nature; second, traits that are disadvantageous to individuals can only arise if the adaptation is beneficial to the whole of a population; third, each adaptation needs to be evaluated for group level selection on an individual basis; fourth, it can no longer be considered a valid argument when scientists claim group level selection did not occur simply because the adaptation occurs in the whole population.

Based upon these four claims, a model was created to test various Neandertal adaptations to see multilevel selection's effect on Neandertal evolution. First, each adaptation must be tested individually and separate from any other adaptations that have previously or will in the future be tested. Second, traits are selected upon at higher levels of the biological hierarchy only when lower levels have been surpassed. Third, traits that arise that are disadvantageous to the individual can only arise if the trait is advantageous to the population as a whole. Fourth, how the trait affects each level of the biological hierarchy must be thoroughly studied, examining each level such as individuals within the same species, between groups of a species and other groups of the same species, and between groups of one species and groups of a different species.

Three adaptations and three genes or sets of genes associated with those adaptations are evaluated with this model. The adaptations are the cold adapted body type, large-mammal based diet, and tool kit. The genes are THADA, DYRKIA, CADPS2, AUTS2, and RUNX2. These three adaptations were chosen because these seemed to be the most important and overarching adaptations that Neandertals had that have been proven. Additionally, the adaptations chosen seem to have affected almost every aspect of Neandertal life, and there was an abundance of published research of varying opinions about each of these three adaptations. The three genes or sets of genes were chosen because they are identified in the draft of the Neandertal genome (Green et al. 2010) as genes that show positive selection in human evolution.

Adaptation #1: Cold Adapted Body

The first adaptation examined is the cold adapted body type. This includes the barrel-shaped chest and short limbs. Their short, stocky bodies helped to conserve heat, something that is known due to ethnographic comparisons of cold adapted modern human populations. Following the first step of the model, one must be sure that this adaptation is tested separately from any other adaptations. Second, one must examine which level of the biological hierarchy may have been at work, remembering that in order for a higher level of natural selection to occur, a lower level of natural selection must first be surpassed. When examining this adaptation, it is seen that this is an adaptation that is beneficial to the individual. A body shape that conserves the most heat was especially important for Neandertals throughout their existence. They lived in glacial areas of Europe and western Asia. This means that Neandertals chosen environment was an extremely cold climate. Therefore, it would have been a very beneficial adaptation to be selected for, since it would have improved the longevity and the health of those individuals who had this adaptation to the cold. Those individuals whose bodies were less able to conserve heat would have been at an increased risk of death from hypothermia. It is probable that this adaptation was selected upon at the individual level of the biological hierarchy since it is an adaptation that is beneficial to the individual. There is no need to look for answers at higher levels of the biological hierarchy, since natural selection always occurs at the lowest levels of the biological hierarchy unless the lowest levels are surpassed.

Using the third step of the model, one must see if the trait was disadvantageous to the individual or if the trait is beneficial to the individual. Because the trait will increase the longevity of an individual due to a decreased risk of cold-related diseases, it was determined that this trait was advantageous to the individual Neandertal. It is also a trait that may be seen as advantageous to a group because a group of Neandertals with this cold related body compared to a group without would be more reproductively successful than the group that is not cold adapted. However, because the trait is first advantageous to the individual and the lower levels of the biological hierarchy are the ones that are selected upon first, it still must be concluded that the adaptation is first advantageous at the individual level.

Using the fourth step of the model, one must compare how the adaptation may have arisen between the various levels of the biological hierarchy. At the level between individuals in a group of the same species, it can be seen that the cold-adapted body would have arisen through natural selection selecting for those individual Neandertals who lived through severe cold conditions. Those individuals that did not have the cold adapted body would perish during times of extreme cold, making them ultimately less likely to reproduction. Because of this, natural selection would be using the individual level of selection to create the distinctive body shape that Neandertal fossils display. After examining all of this evidence, it was ultimately concluded that it was individual selection that was being selected for the cold adapted body.

Adaptation #2: Large-mammal based diet

Neandertal diets consisted mainly of large mammals that were hunted at close range, information that is known from the spears that are found in the archaeological record (Kuhn et al. 2006). The spears that Neandertals created were for thrusting and stabbing, in contrast to modern human spears that were created to be thrown. Recent comparative analysis of Neandertal and modern human shoulders has also shown that modern humans threw on a regular basis and Neandertals did not (Rhodes et al. 2009). Neandertal shoulder regions lack distinctive asymmetry that commonly occurs from habitual throwing. It is also known that large mammals were hunted at close distances because Neandertal fossils have similar injuries to modern day rodeo clowns and cowboys.

Using the model, one must evaluate the diet separate from any other previous adaptations evaluated. According to the second step of the model, one must examine what level of the biological hierarchy may have been at work, remembering that in order for a higher level of the biological hierarchy to be selected upon the lower levels of the biological hierarchy must first be unsettled. The Neandertal diet is a diet well suited to a cold environment. When looking at the diet in terms of benefit to the individual or the group, there is a high risk to the individual who does the hunting because of the close proximity to the large mammals. However, there is also a high benefit to the individual because successfully hunting the large mammals without injury will provide an abundance of necessary food and nutrients for the individual. If all of the members of the particular group participated in the hunt, then all of the members would have access to the food. If all of the members of the group did not participate, it is likely that the hunters shared with the rest of the group in an altruistic manner, similar to modern humans.

Others (Kuhn et al. 2006) say they have found evidence that Neandertals did not divide their labor according to age or gender. This would mean that men, women, and children participated in some way with the large mammal hunts. If this is true, a large mammal rich diet may be considered an individual level adaptation because since each individual participates in the hunt, each individual expects to see a return (i.e., food) from the time that the individual put into the hunt. If the other case is correct where not all Neandertals participated in a large mammal hunt, this may be an example of group level selection. In this case, an individual is at a disadvantage because he or she did not go on the hunt. This does not necessarily guarantee that individual a steady supply of food. If the individual is to be guaranteed food, there needs to be altruism among the members.

Altruism is a trait that does not evolve at the individual level. It is selected upon at the group level because it is disadvantageous for an individual to give another part of the hunt. By giving away part of the hunt for no immediate return, the individual is unsettling the individual level of natural selection. It is in this way that group selection may be able to work between different groups of Neandertal populations. Hill (2002) states that humans have evolved the mentality to share food with other members of one's group. It is likely that Neandertals shared this mentality as well. As an example of how this trait could have evolved at a group level, consider two groups of Neandertals. In one group, the food from the hunt is shared among the members of the group. In the other group, only the hunter or hunters eat what they have killed. Natural selection will at first favor those who do not share, increasing the fitness of the selfish Neandertals. However, natural selection at a group level will counteract the selfish Neandertals, selecting the group whose total combined fitness is greatest. This would be the group that shares its food among all of its members because all of the members of the group would have relatively equal access to food resources.

Using the third step of the model, one needs to check if traits have arisen that are disadvantageous to the individual but beneficial to the population as a whole. In the case where all Neandertals regardless of age or gender participate in the large mammal hunt, the outcome can be viewed two separate ways. First, there is a disadvantage to the individual because the individual is on the hunt and could be in danger of being severely hurt. Second, however, there is an advantage to the individual because the individual is on the hunt and is therefore guaranteed access to the kill. In the case where only certain Neandertals participate in the large mammal hunt, there is again the disadvantage to the individual because the close proximity to the mammal threatens the safety of the individual. There is, however, an advantage to the individual because he or she is guaranteed access to the kill. The major disadvantage to the individual comes into play in the scenario when the Neandertal that participated in the hunt shares the meat with a Neandertal that did not participate. This altruism is ultimately disadvantageous to the individual but is beneficial to the group as a whole. When more Neandertals share their food with other Neandertals, it creates a buffer against harder times when the one who hunted the first time is unable to obtain food but the one who did not hunt the first time does have food to share.

According to the fourth step of the model, one must examine how the large mammal diet adaptation may have occurred compared to the various levels of the biological hierarchy. When examining individuals within a group, it is seen a large mammal diet is a highly nutritious diet, one that when consistent would give an individual a reproductive advantage. While it would have given Neandertals a reproductive advantage, it is hard to imagine a large mammal dependent diet arising without group participation and cooperation. For group cooperation to occur, there needs to be reciprocal trust. Each Neandertal involved in the hunt would need to understand that in order to catch the prey, there had to be cooperation. As Wilson and Wilson (2007) state, "it is simply a fact of social life that individuals must do things for each other to function successfully as a group, and that these actions usually do not maximize their relative fitness" (334). Neandertals cooperation during large mammal hunts exemplifies this remark. Perhaps one individual could hunt on his or her own or could take advantage of the group effort and sit back while the others labored. In these situations, the individual and the group's relative fitness is decreased because there are either less individuals to help with the hunt or the one who went off individually has a smaller probability of killing a large mammal on his or her own. Through this thorough analysis with the model, it was ultimately concluded that group selection was at work on the large-mammal based diet.

Adaptation #3: Tool Kit

In the Middle Paleolithic, Neandertals had a tool culture called the Mousterian. Points, elongated points, and scrappers exemplify this tool culture. The Mousterian shows that Neandertals had the advanced cognitive ability to visualize the size and shape of a tool that can be formed from a particular core (Larsen 2008). The Mousterian was not as varied and complex as modern human tool culture of the same period, the Aurignacian; however, Neandertals still needed to be able to visualize the shape and size of the end product simply by looking at the core.

According to the first step of the model, one must be sure that this adaptation is evaluated separate from any previous adaptations. Continuing on to the second step of the model, one must evaluate which level of the biological hierarchy may have been at work on this adaptation, remembering that in order for a higher level of the biological hierarchy to be selected upon the lower levels of the biological hierarchy must first have been unsettled. This adaptation was trickier to evaluate because this could have been an example of biological natural selection or it could have been an example of cultural selection. Hill et al. (2011) argue that the ability to learn cultural traits from other group members evolved “at least as early as the middle Pleistocene” (108). This means that Neandertals and modern humans share social learning mechanisms that compel group members to conform to and learn from one another. Assuming that the adaptation had a base in biology, it was first examined how the stone tool culture may have been selected upon at the individual level. At the individual level, this stone tool adaptation was extremely beneficial to the individual because the improved tool kit helped the individual complete tasks more quickly and efficiently when compared to the tool kits of earlier hominids. Additionally, Neandertals hunting ability was helped greatly by this tool kit. The stone tools were extremely important for an individual's survival, since the Neandertal diet was heavily dependent upon hunting large mammals.

On the other hand, assuming that the tool kit was based on cultural evolution only, the tool kit is still beneficial to the individual. The individual's ability to hunt and therefore survive is improved, thus adding to the individual's reproductive success. Selection can still work in basically the same ways on cultural evolution, although when culture is involved there is a conscious choice made.

Next one must examine how group level selection may have affected the tool kit if the tool kit had a base in Neandertal biology. A group of Neandertals with a more successful tool kit will be selected upon over a group of Neandertals with a less successful tool kit. If the tool kit had a purely cultural basis, group level selection may have still been at work for similar reasons. In this case, it would be the individual Neandertals that were making the choice to make the tools, but the tools that are more successful at hunting will spread to others in the community. A group of Neandertals with a more successful tool kit will still be selected upon over a group of Neandertals with a less successful tool kit.

According to the third step of the model, one must determine if the trait is disadvantageous to the individual or not. The tool kit, while it could be advantageous to the group as a whole because it improves the quality and quantity of the hunt, is also advantageous to the individual because it improves the individual's quality of life and access to food.

Following the fourth and final step of the model, one must compare how the adaptation may have arisen when comparing individuals within groups, between groups of the same species, and between groups of different species. Between individuals within a group, the reasoning is similar to that which has already mentioned. An individual's success is greatly improved by the addition of an advanced tool kit that helps improve the success of the hunt. For group selection among groups of the same species, the tool kit could arise from selection among the most successful of the groups of Neandertals. For selection between groups of different species, the answer is complicated because this involves the addition of modern human populations. Both had tool kits at this time, but each was different from the other. It is possible that group selection between species eventually helped modern humans become more successful, populating the entire world and leading to the disappearance of Neandertals.

The newest genetic studies (Green et al. 2010) show that Neandertals and modern humans did a limited amount of interbreeding. Perhaps that is one of the many reasons why toward the end of the Neandertals' span of existence, Neandertals created a new tool kit. This new tool kit is known as the Châtelperronian. It is distinctive from the Aurignacian tool kit, which archaeologists know was created by contemporaneous modern humans, because the techniques used to make the Châtelperronian tool kits were completely different from the modern human tool kit. The Châtelperronian tool kit consists of side scrappers and blades that have been retouched (Bar-Yosef et al. 2010). There is no direct evidence at this time that a small amount of gene flow between modern humans and Neandertals may have resulted in some of the changes in Neandertal behavior that are found near the end of Neandertals' span of existence, but it is an interesting hypothesis for future genetic and archaeological research.

An interesting area of study for the future will be close examination of individual genes in both modern human and Neandertal genomes to determine if specific genes can be identified that may have passed between the populations as a result of interbreeding. Perhaps this new research will help to answer questions about Neandertals changing behaviors toward the end of their span of existence. Green et al. (2010) have begun this process with their draft of the

Neandertal genome. They identified various genes that during the evolution of humans have been selected. Some of the functions of the genes are unknown; others are associated with various abilities or diseases. As the genes were examined, it was important to remember that if the function that the gene is believed to have now turns out to be incorrect upon further research, the conclusions will be incorrect.

Gene #1: THADA

The first gene examined was THADA. This is one of the many genes that have been under selection throughout human evolution and has been associated with type II diabetes (Green et al. 2010). Scientists have concluded, therefore that this gene is involved in energy and metabolism. Following the first step of the model, one must examine this adaptation separate from any other adaptations previously examined.

Next, one must examine which levels of the biological hierarchy may have been at work, remembering that in order for a higher level of the biological hierarchy to be selected the lower levels must first be unsettled in some way. When examining this gene, analysis became difficult because the extent the gene may have shown in Neandertals or even modern humans is unclear. Genes are not always turned on or may appear with differing functions when combined with other genes. It is known, however, that this gene is involved in energy and metabolism. It is also known that because of Neandertals stocky build they required more energy and calories per day than modern human populations. If individual selection had occurred in Neandertals, perhaps this gene in combination with others was responsible for their high-energy needs. The body type of Neandertals was advantageous to the individual because it helped to keep the core of the body warm in severe cold, but needing a high caloric intake every day can be disadvantageous to the individual because the individual needs to exert more energy every day finding food. In lean times, the individual Neandertal suffers greatly from needing many calories.

If group selection did occur, it is possible that group selection between Neandertals and modern humans, despite the interbreeding, may have selected modern humans over Neandertals. Modern humans needed fewer calories per day; therefore, in lean times it is probable that groups of modern humans would have a greater advantage over Neandertals. Modern humans needed less food to stay alive, so when food became scarce fewer modern humans would die of hunger than Neandertals.

Using the third step of the model, one must determine if there was a disadvantage of this adaptation at a lower level that could be overcome by an advantage at a higher level. As stated previously, there was a disadvantage to the individual because there was an increased risk of death from starvation or malnutrition. At the group level, there still seems to be a disadvantage especially when compared to modern human populations who needed fewer calories per day and therefore were more likely to be selected for by group level selection. However, it is possible that despite the disadvantage at the group level, other adaptations such as the tool kit and the large mammal diet helped to offset the disadvantages, at least for a period of time. A diet rich in large mammals would give Neandertals many calories and a sophisticated tool kit helped them to hunt more effectively. It is when Neandertals are unable to catch large mammals that the THADA gene adaptation may become a disadvantage at a group level.

Finally, one must compare how the THADA gene may have arisen when compared to various levels of the biological hierarchy. When examining individuals within a group, the THADA gene may have arisen by selection upon the individuals whose body types were most able to cope with cold weather. Despite the requirement for more calories, perhaps the large mammal rich diet was consistent enough and the tool kit effective enough that this branch on the evolutionary tree was successful, at least for a time. When examining groups of Neandertals compared to other groups of Neandertals, it seems that groups will be selected that are the most efficient at staying alive. It may be that the THADA gene was effective at this due to the cold and relatively harsh climate that Neandertals evolved in. When examining Neandertals compared to other species such as modern humans, it seems that natural selection was working at a group level and selecting modern human populations who also possessed this gene but who also required fewer calories per day. Modern humans seemed to have a bigger buffer against lean times because of this. As a result, group level selection acting between species may have been at work. The culmination of this information leads to the conclusion that ultimately, it was individual selection at work on the THADA gene.

Gene #2: DYRKIA, CADPS2, and AUTS2

DYRKIA is a gene known to be associated with cognitive abilities, and CADPS2 and AUTS2 are known to be associated with autism. These three genes are lumped together because they are genes that have been selected upon in human evolution and all involve cognitive abilities. There is not enough information about the genes individually to examine each gene separately.

Researchers are increasingly becoming aware that Neandertals and modern humans differed much less in cognitive abilities than has been previously believed (Coolidge et al. 2004). These genes may have been selected upon at the individual level to improve cognitive abilities throughout the evolution of Neandertals. According to Coolidge et al. (2004) there is not a big difference between Neandertal and modern human cognitive ability. Modern human have enhanced working memory, something that allows modern humans to do on the spot problem solving. Neandertals had expert knowledge, meaning Neandertals knew how to create tools and do other activities one way and were very effective at it. The differences in cognitive abilities may have been selected for at the individual level. Neandertals who were most able to communicate complex ideas with one another were more likely to be successful. Large mammal hunting required Neandertals to complete complex group work, something that requires high-level cognitive abilities. At the group level, groups of Neandertals whose members had the most complex cognitive abilities would be selected over those with less complex cognitive abilities. These groups would be able to successfully complete more difficult activities, including cooperative large mammal hunts.

After following the first step of the model, one must examine these genes separate from all previous genes examine. Then, one must determine which level of the biological hierarchy may have been at work. Certainly, advanced cognitive abilities would be advantageous to the individual because it would increase one's ability to complete complex tasks that were necessary in Neandertal life. These activities include survival in cold climates and large mammal hunting. In order for these advanced cognitive abilities to be most effective, Neandertals needed to be part of a functioning group. Therefore, groups of Neandertals with advanced cognitive abilities working together on complex tasks would increase that group of Neandertals fitness relative to other groups of Neandertals who did not have as advanced cognitive abilities.

Finally, how the cognitive genes may have arisen as a result of natural selection on various levels of the biological hierarchy was examined. For individuals within a group, these advanced cognitive genes would help the individual complete more complicated tasks. For groups of Neandertals compared to other groups of Neandertals, groups with members having these genes would be selected over those without because the group with the genes would have been able to work cooperatively and more effectively on these complex tasks. Finally, for groups of Neandertals compared to groups of other species such as modern human, natural selection would probably select those groups with the highest levels of cognitive abilities. Because Neandertals did not have enhanced working memory and were unable to do complex problem solving on the spot, modern human groups that had these abilities would be selected at a group level over the Neandertals. Because of this careful examination of the data from the model, it was concluded that the genes were selected upon at the individual level.

Gene #3: RUNX2

The last gene examined is RUNX2, a gene on which mutations are known to cause cleidocranial dysplasia. This disease is known to cause various physical characteristics that resemble Neandertal traits. A mutation of this gene will cause a protruding frontal lobe and a barrel-shaped rib cage.

This gene may have been a factor for selecting the cold adapted Neandertal body type. Therefore, it seems this gene could be selected upon at the individual level because a cold adapted body would be beneficial to the individual. It would increase the individual's relative fitness because the individual would be more protected from cold related diseases. At the group level, this gene may have been selected upon because groups of Neandertals with this cold adapted body would have been more successful at reproduction because they could live through times of severe cold. Groups with members who were most successful at survival in a cold climate would have been selected at a group level over those groups with members who were less adapted to the cold climate.

Next, it was determined if this gene could be disadvantageous to the individual. Assuming that this gene helped select a cold adapted body, there would be an advantage to the individual because it would protect the individual from cold related diseases. Finally, how the trait may have arisen at the various levels of the biological hierarchy was examined. If the gene helps to improve the cold adapted body, it might have arisen by individual selection because individuals with this gene would be less likely to die from cold related factors, such as hypothermia. Thus, the individual's reproductive fitness would be greatly improved if the individual had this gene. Since there is no disadvantage at the individual level and the gene may have been selected upon at the individual level, there was no need to examine the group level and other higher levels because the lowest level of the biological hierarchy was not unsettled. Due to the previous analysis with the model, it was concluded that this gene was selected upon at the individual level.

Table 1

The results of the study with step one being a yes or no completion and the other cells showing the conclusion from each step.

	Cold adapted body	Large-mammal based diet	Tool kit	THADA	DYRKIA, CADPS2, and AUTS2	RUNX2
Step 1: Evaluate separate and on a case-by-case basis	Yes	Yes	Yes	Yes	Yes	Yes
Step 2: Traits are selected upon at higher levels only when lower levels have been surpassed	Individual	Individual questionable	Individual/ group	Individual/ group	Group	Individual
Step 3: Traits that are disadvantageous to individuals only arise by higher levels	Individual	Group	Individual/ group	Individual	Individual/ group	Individual
Step 4: Compare how trait may have arisen between different levels of biological hierarchy	Individual	Group	Individual/ group	Individual	Individual	Individual

Discussion

Natural selection has worked at multiple levels of the biological hierarchy through the evolution of Neandertals. In this article, Neandertal adaptations and genes (Table 1) were examined including the cold adapted body structure, the large mammal dependent diet, the tool kits, and the presence of genes such as THADA, DYRKIA, CADPS2, AUTS2, and RUNX2. After analysis of each of these adaptations or genes according to the model created based on four empirical claims by Wilson and Wilson (2007), the level of the biological hierarchy that has been selected upon became apparent.

The cold adapted body structure was selected upon at the individual level. This is because it is first and foremost beneficial and advantageous to the individual who possesses the adaptation. Therefore, because individual selection has not been surpassed in any way, the lowest level of the biological hierarchy is at work. In this case, that means that it was the individual level of selection at work.

The large mammal dependent diet was selected upon by group level selection. This adaptation has disadvantages to the individual because of the high-risk elements of the diet. Hunters needed to get within close range in order to kill the large mammals. This increased a hunter's risk of death or serious injury. Also, large mammal hunting was a cooperative group activity. Because of this, group level selection was at work on the Neandertal diet. Groups of Neandertals that functioned more cooperatively and efficiently than other groups of Neandertals on the large mammals hunts would have higher reproductive success. Also, Neandertal altruism could only have arisen through group level selection because altruism is disadvantageous to the individual but groups of Neandertals that are more altruistic than others will be selected over groups of selfish Neandertals.

Neandertals tool kit was selected upon at the individual level. Having the most effective and efficient tool kit would have been more advantageous to the individual. Groups with the most effective and efficient tool kits would have had an advantage over other groups as well, but since it is beneficial to the individual there is no disruption of the lower levels of the biological hierarchy.

The THADA gene was selected upon at the individual level. This gene is involved in energy and metabolism. This gene may have been involved in creating Neandertals cold adapted body. The cold adapted bodies required more energy and calories per day than modern humans. The advantage at the individual level was because the gene helped to create a body that insulated the individual from cold related diseases, therefore improving the individual's relative fitness. There are disadvantages from needing more energy and calories because Neandertals were more vulnerable in lean times from death by starvation and malnutrition. However, these disadvantages were probably overshadowed by Neandertals need for a cold adapted body. Also, other adaptations such as Neandertals diet and tool kit may have helped to negate the effects of requiring a high caloric intake, at least for the amount of time that large mammal hunting remained effective.

The genes DYRKIA, CADPS2, and AUTS2 were selected upon at the individual level. These genes are all involved in some way in cognitive abilities. It was concluded that these genes were selected at the individual level because advanced cognitive abilities are beneficial to the individual. More advanced cognitive abilities would allow the individual Neandertal to complete more complex tasks, thus increasing the individual's relative fitness. Because Neandertals were social creatures like modern humans and lived in social groups, there is the possibility that group selection could have been working on the social groups. Due to limitations in research, this author will leave the conclusion at individual level selection, but it would be interesting for further research to look into how natural selection may have been working on these social groups.

The last gene evaluated, RUNX2, was selected upon at the individual level. This gene is involved in selecting the cold adapted body. It is selected at the individual level because an individual who possesses this adaptation will be more protected from cold related diseases than those without the adaptation. Because there is no disadvantage to the individual, the lower levels of the biological hierarchy have not been surpassed so it is unlikely that group selection was involved in this adaptation.

Based on the sample of three adaptations and three genes or sets of genes that show positive selection in human evolution, it seems that individual selection was working more often than group selection in Neandertal evolution. This makes biological sense because the lower levels of the biological hierarchy must first be surpassed before group level or other higher levels of the biological hierarchy can be acted upon. There are adaptations that may have involved group level selection. The one adaptation evaluated where this seems likely is the large mammal based diet. As a general rule it seems group level selection was involved in Neandertal evolution, but it seems to occur less often than individual level selection. This is consistent with biological theory.

Conclusion

Using a model based on four empirical claims by Wilson and Wilson (2007), various Neandertal adaptations and genes were tested to determine the level of the biological hierarchy that was being selected for during Neandertal evolution. Overall, it seems that most adaptations were selected at the individual level, but at least one adaptation was selected at the group level.

This is logically consistent with biological theory that individual level selection will occur more often than group level selection.

Various genes that Green et al. (2010) conclude show evidence of evolutionary selection were evaluated. These genes are in the Neandertal genome. Further research is needed to explore more closely the relationship that these genes may show. Future research should be concerned with finding specific genes that were passed between Neandertals and modern humans during the interbreeding that occurred 80,000 years ago. This will be complicated because Neandertals and modern humans share a recent common ancestor, thus the two species share many genes due to other factors. However, researchers may be able to find the genes passed between Neandertals and modern humans during interbreeding by looking specifically for genes that are in the Neandertal genome and in all modern human populations except African populations. This would be evidence of specific genes that Neandertals passed to modern human as a result of the interbreeding. In order to find genes that modern humans may have passed to Neandertals, future research should be concerned with mapping early Neandertal genomes (pre-interbreeding) and comparing that genome to late Neandertal genomes (post-interbreeding). If there are any genes that may appear after 80,000 years ago, those genes may have been the result of the interbreeding.

Future research should also be concerned with evaluating how multilevel selection has affected other branches of the human evolutionary tree. Research in this area will shed light on how strong or weak a force group and other levels of natural selection have been throughout the whole of human evolution.

After conducting this research, it became apparent that group level selection was likely working throughout most of human evolution on an interspecies level. It seems reasonable that group level selection may have ultimately selected modern human populations over Neandertal populations. While the two species were similar, there were differences that natural selection would have been acting upon. The environment at the time of Neandertals was one of constant flux, especially toward the end of their span of existence. It is possible that natural selection working at a group level ultimately chose the population that was most suitable for the new and changing environment. Despite the interbreeding of the two population, the extent to which gene flow may have affected Neandertal or modern human adaptations is unclear at this time because there has only been one study so far that has found evidence of gene flow between Neandertals and modern humans. It is plausible theorize that group selection working between the two species may have led to the domination of modern human over the entire world.

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