

# The ecology of life history evolution

Genes, individuals and populations

**Prof. dr Marcel E. Visser**

Inaugural lecture upon taking up the post of Special Professor of Ecological Genetics at Wageningen University on 7 March 2013



WAGENINGEN UNIVERSITY  
WAGENINGEN **UR**



# The ecology of life history evolution

*Genes, individuals and populations*

Prof. dr Marcel E. Visser

Inaugural lecture upon taking up the post of Special Professor of Ecological Genetics at Wageningen University on 7 March 2013



WAGENINGEN UNIVERSITY  
WAGENINGEN **UR**

ISBN 978-94-6173-597-3

# The ecology of life history evolution

## *Genes, individuals and populations*

*Meneer de rector, professoren, familie en vrienden, dear colleagues from both the Netherlands Institute of Ecology and the Wageningen University, students, ladies and gentlemen.*

The living world is enormously diverse; species differ greatly in their morphology but also in what we call life history traits. Penguins produce a single egg and care for just a single chick but mallards can produce easily up to eight offspring and look after them. Other species differ in their age of first reproduction; small rodents often reproduce in the same year that they are born, while other species, like elephants, may take fifteen years before they start reproducing themselves. And also in other aspects, species differ greatly. Bewick's swans migrate from their wintering areas here in the Netherlands all the way up to the north of Russia to breed but a blue tit may be born, reproduce and die in the same forest.

Also closely related species show these very clear phenotypic patterns. Darwin finches from the Galapagos Islands may have thick bills, such as the ground finches which feed on seeds. But there are also other species, tree finches, which eat insects and have much smaller bills. Although these species are closely related, there are large phenotypic differences between them. And even within species we find phenotypic patterns: In the peppered moth there are two morphs, a dark and a light morph. In the UK at the end of the 1950's there were some places where the dark morph was almost absent, while in other places it dominated the population<sup>1</sup>. So, again, there are clear phenotypic patterns across the geographic range.

Phenotypic patterns not only occur in morphology but also in life history traits. Our long term study on the island of Vlieland is one of the populations where we follow the nest box populations since 1955, more than 50 years now. On Vlieland, there are four smaller forests in the west of the island and there is a larger forest around the village in the east. We find systematic differences in the clutch size of great tits between these two parts of the population. In the west, birds lay on average 9.5 eggs while in the eastern part of the island they lay one egg less, about 8.5 eggs<sup>2</sup>. These kinds of phenotypic patterns are intriguing; why do they occur?

Ultimately it will be the ecological context which determines these phenotypic patterns. In the example of the peppered moth, small, insectivorous birds, like robins, will catch the moths while they are resting on the trunk of a tree. If the tree trunk is light, the light form will be almost invisible and the dark form will be predated. But if the trunks are dark, the light form will be much more conspicuous and will be predated and the dark form will escape predation<sup>3</sup>. It is therefore an ecological process, predation, which shapes the selection pressure on these different coloured morphs.

This brings me to the third component that I want to discuss at this introduction; adaptation by natural selection. This was of course the great idea by Darwin<sup>4</sup>, now over 150 years ago. And there are three components which are necessary for evolution. One is variation within the species, for instance between morphs, furthermore this variation has to be heritable and the third step is that there has to be differential reproduction, differential survival. These three components combined, variation, differences in fitness and heredity leads to micro-evolution (Figure 1).

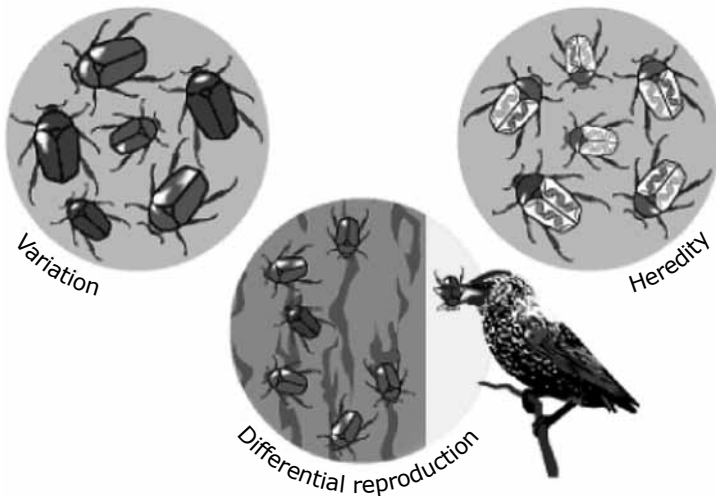


Figure 1. Prerequisites for micro-evolution: variation, differences in fitness and heredity.  
 Credit: University of California Museum of Paleontology's Understanding Evolution  
 (<http://evolution.berkeley.edu>).

Phenotypic patterns, the ecological context and adaptation by natural selection. These three things together form the definition of ecological genetics, the name of the chair that I now hold here at the Wageningen University: ecological genetics. Ecological genetics was pioneered by E.B. Ford, with his book, which was actually called *Ecological genetics*<sup>5</sup> about 50 years ago. It is the study of evolutionary processes,

especially adaptation by natural selection in an ecological context, in order to account for phenotypic patterns observed in nature. So ecological processes lead to differential selection pressures, and thereby to natural selection, that shapes the populations in such a way that we get the phenotypic patterns that I have described at the beginning of the lecture.

Now why is ecological genetics such an important research discipline? There are two reasons for this. First, we live in a changing world. The world is changing in many ways, but one way in which it clearly changes these days is global warming. Since the 1980's temperatures have increased worldwide which changes the ecological context, and if the ecological context changes we also expect the phenotypes to change. Ecological genetics will help us to understand these changes.

One of the clearest changes we see in phenotypic patterns due to climate change is what we call seasonal timing or phenology. Plants and animals are changing the time when they are flowering, the time when they return from the wintering areas and the time when they reproduce<sup>6</sup>. Here, at the Wageningen University, *de Natuurkalender* is run by Arnold van Vliet and his people at the Environmental Systems Analysis Group, and general public can send in their observations about phenology. Phenology is an intriguing field simply because phenology is changing so rapidly. People can observe changes in phenology literally in their back yard and that is one of the reasons why the *Natuurkalender* is such a big success. People send in their data, or call in on a Sunday morning to the *Vroege Vogels* radio show to share their new phenological observations.

Reports on changes in phenology have been around for the last 20 years. In one of the first of such papers, Crick et al.<sup>7</sup> looked at corn bunting, chiffchaff and magpies and a whole range of other species. And in almost all of these species the laying dates got earlier over the last 20 years, probably as a direct consequence of the change in temperature. So, we see that phenotypic patterns are clearly changing.

There must be over thousands and thousands of these records now and a recent review has looked at the extent of the differences in these shifts<sup>8</sup>. They collected published estimates of the mean change in phenology, i.e. the mean change in seasonal timing, in days per decade. Species were split up into three groups: primary producers, primary consumers and the secondary consumers. While the primary producers and the primary consumers shift about four days every ten years, the secondary consumers only shift about two days. As a consequence predators, the species that are high up in the food chain, are actually shifting at a lower rate than their food is. This leads to what we call a phenological mismatch<sup>9, 10</sup>.

One of the key questions is to what extent these observed shifts in seasonal timing are due to plasticity and to what extent they are due to micro-evolution? To what extent is it that different genotypes increase in the population, which perhaps would lead to an earlier phenology. And if you would have asked that question about 25 years ago, the answer would have been quite simple. People would have said: the rate of micro-evolution is very slow and much slower than the rate of ecological change.

But literally at the turn of the millennium, in December 1999, a paper came out that kind of changed that view. Hendry & Kinneson<sup>11</sup> actually demonstrated that micro-evolution can be quite fast, and could play out at the same time scale as ecological changes. Suddenly a whole new discipline was born, the discipline of eco-evolutionary dynamics. It also led to the interesting idea that perhaps populations that are now too slow in their phenological shifts can be rescued by evolution<sup>12</sup>. Evolution might be fast enough for these species to evolve, to change in such a way that they can actually keep up with their changing environment.

The possibility of evolutionary rescue is the second reason why ecological genetics is such an interesting discipline at the moment: not only the world is changing but also there seems to be scope for micro-evolution to play a role in how species cope with that change. One thing that is essential for that is that we understand something about the rate of change. It is not only whether natural selection will actually lead to more adapted populations, but the question really is: at what speed will micro-evolution take place and how does that speed compare to the rate of environmental change<sup>13</sup>? Ecological genetics will thus set the stage for the amount of evolutionary rescue that can happen.

I want to illustrate some of this with our own work with a very simplified food chain: the food chain of oak trees, winter moth caterpillars, and great tits and pied flycatchers as insectivorous birds. I have worked on this food chain over the last 15 years with a whole range of people of which I want to specially mention Christiaan Both, now professor at University of Groningen, with whom I have worked with on the pied flycatchers for many years now. Within this food chain, phenology plays an important role. The winter moths need the freshly emerged leaves from the oak to feed on<sup>14</sup>, and then the great tits and the pied flycatchers feed their offspring with large caterpillars that feed on these oak leaves<sup>15, 16</sup>. The flycatchers are still in Africa at the moment, they will be coming back shortly, while great tits, as you all know from your own back yard, are around all year. The seasonal timing of these three species is interesting because of the strong fitness consequences. For egg hatching date in the winter moths this really depends on the exact timing relative to the bud burst of the



oak trees and the fitness consequences of the laying dates of both bird species depend on the match with the time that large caterpillars are abundant.

The world has changed over the past 20 years and what has happened to the great tits and their food, is that “in the good old days”, in the 1980’s, there was a clear phenological match: there was a short period at the end of May when there were a lot of caterpillars around, and that would coincide exactly with the time that the great tits had their chicks in their nest. This phenological match meant that most of the great tits would have ample food to provide their offspring. After the 1980’s, when the world got warmer, phenologies started to shift. But as we saw already in the example of the review which looked at the trophic levels between primary producers, primary consumers and secondary consumers, rates at which phenology shifted are not the same. In our system the secondary consumers, the great tits, shift at a lesser rate than their food, the primary consumers. Food shifts about eight days every ten years and the great tits only shift about two days every ten years. This has led to the situation where the populations are phenologically mismatched with their food: only the very early birds can now profit from the huge increase of biomass over the course of the season and late birds all breed on the declining slope of the food peak<sup>17</sup>.

The mismatched reproduction in great tits where the birds are too late for their food peak has clear consequences: the early birds do relatively well relative to the late birds, their fitness is higher, and this leads to selection for earlier laying. This can be seen in the temporal pattern of the selection differential, which is a measure of for the strength of selection on laying date. The selection differential is negative when there is selection for early laying date, while when it is around zero there is stabilising selection: early birds and late birds do equally well. At the end of the 1970’s, there was stabilising selection in our population but this has now changed and the selection differential has become negative: the early birds started doing better and better relative to the late birds<sup>10, 18</sup>.

If we go back to the three components of micro-evolution I described earlier, we see that the differential fitness component is met in our great tits, the birds that lay early have a higher fitness than the birds that lay late and therefore you would expect them to be favoured by natural selection. There is, however, one pitfall that I want to point out and that is that all our data on fitness in these analyses are based on a correlation between fitness and laying date. This is what we typically find, early birds have a high fitness and late laying birds have a low fitness. As I said this is a correlation, so we need to do experiments to find out if this correlation is actually causation. For instance, as was pointed out in the 1980’s already by Price<sup>19</sup>, it could well be that both laying date and fitness are affected by nutrient status: animals with

a high nutrient status that live in a good part of the forest or have a good condition might lay early and have a higher fitness while there is no causal relation between fitness and laying date. We therefore need to do experiments where we shift birds on the laying date axis and that is what we have been doing for a decade or so now and it turns out to be very difficult. There's not really time to go through all our endeavours trying to do this, we are still doing experiments on this, but what we see from our results, and what we see from results of other people that have been published on this is that there seems to be a causal relationship between laying date and fitness and therefore our measure of selection is valid<sup>20, 21</sup>.

Now, what else do we need? We need variation for laying date. We can demonstrate this from our long term study at de National Park the Hoge Veluwe, where we have been working now for over 55 years. When we look at this for two random years we see that the earliest birds in 1978 laid at the 20th of April, the latest birds on the 20th of May. So there is ample variation. The same is true in 2010, the variation is still clear but the mean has shifted substantially. So the second box to tick, variation, is also met.

The third component needed is heritability of laying date. Only if a mother and her offspring resemble each other a response to selection on variation is possible. We have shown that there is heritability of laying date, but interestingly enough, this heritability depends on the temperature. In warm springs, heritability for laying date is higher than in cold springs: there is more additive genetic variation to be selected on<sup>22</sup>. This is interesting as in warm years also the selection for early laying is strongest, and thus in warm years there is both strong selection for early laying and a higher heritability of laying date. This is a potential mechanism that will actually speed up evolution. So the third component is also there, heritability of the trait.

If we now return to our scheme on evolutionary rescue there seems to be a scope for rescue in the great tits. But I want to stress again that what is really important is the rate at which things are changing, we need to understand the rate of genetic change. Now, who are the scientists that know a lot about genetic change? Those, of course, are the animal breeders. It is what they have been doing for thousands of years; they have been selectively breeding, within species, for different morphs. This selective breeding used to be called artificial selection and Darwin chose the term natural selection specifically to make the contrast with artificial selection. Darwin himself knew very well about artificial selection. He started his book *On the origin of species*<sup>4</sup> with a long story about pigeons, different forms of the pigeons and how they were bred by humans (Figure 2). This was the way he introduced the whole idea that in the natural world, different forms might be selected. There has been close interaction

between animal breeders and the scientists working on ecological genetics, the people who study evolutionary ecology in the wild. I want to mention a few of these tools evolutionary ecology has borrowed from animal breeders over the course of time.

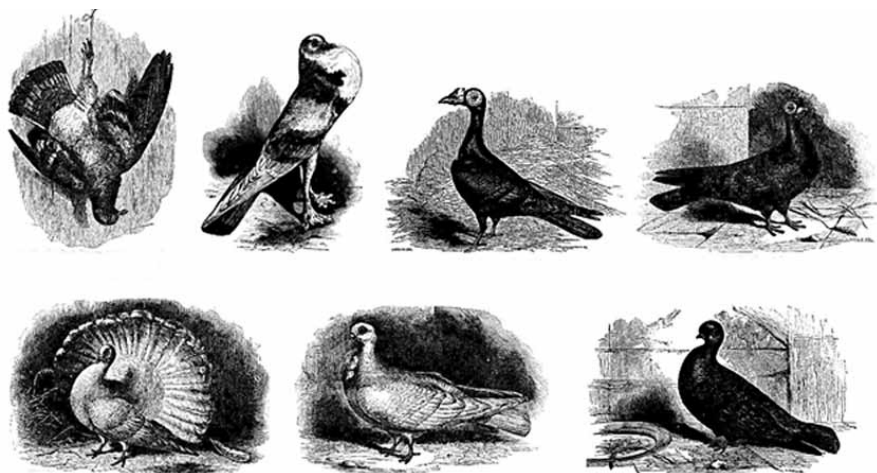


Figure 2. Illustration from Darwin's "Variation in Animals and Plants under Domestication" (1868).

The first tool that was borrowed by the evolutionary ecologists from the animal breeders is what we call the breeder's equation, and this is also how evolutionary ecologists refer to it when they work with wild populations. The breeder's equation describes how the change in the frequency of genotypes depends on the heritability of and the selection on a trait<sup>23</sup>. It is a formula we can use to calculate the response to selection when we can measure both the heritability and the selection in an appropriate way.

The second tool that was borrowed from the animal breeders, at the end of the last century, are animal models. Animal models are being used by animal breeders to calculate something we call a breeding value: the value a specific animal has for a breeding programme<sup>24</sup>. It estimates the genetic part of for instance milk yield. This has been used now also in wild populations and there we happily talk about the breeding value of clutch size or the breeding value of laying date. Not because we are in the process of breeding great tits on their clutch size, but because natural selection acts on that component. To calculate breeding values you need to have a pedigree, and that is what we have. We have a pedigree of many birds in our study area as we have always recorded who is the offspring from who since 1955. For example, we can look up one of our birds from the Hoge Veluwe study area in our database; female

F...411583. We know, for instance, who her father and who her mother is, we also know her grandfather and her grandmother from her father' side. But from her mother' side they are unknown, these are probably immigrants that came in from outside our study area. And we also know that this female has bred four years, every year with a different male, and that she produced in total twenty offspring. Now if we want to know something about the breeding value of this individual, of her clutch size, laying date or tarsus length, we not only use the data on her own phenotype but also that of her mother, of her grandmother, her daughters and her sisters. The entire pedigree from the Hoge Veluwe looks more complex and it contains many individuals for whom we know their parents. And for many other individuals we also know their grandparents, but if we go down in this pedigree of course the numbers get smaller. However, there are individuals where we can go back 17 generations and still know something about their ancestors. And these of course are quite important datasets to look at things like breeding values.

The third tool that I want to mention is, even within animal breeding, quite novel. It is marker-assisted selection, to create selection lines for a trait<sup>25</sup>. Selection lines used to be created by measuring phenotypes, to breed a selection of for instance cows, but then you have to wait until the next generation of cows produces milk to tell which of these cows gives a lot of milk, and thus need to be included in the selection line, and which did not give much milk, and thus should not be included. But if there are known genomic markers that are associated with that milk yield this selection step can already be made at a much earlier stage, while the new generation are still calves and you could genotype them from their DNA. So, marker assisted selection is a very powerful tool to make selection lines for traits that are expressed later in life, and also, similar to milk yields, traits that are only expressed in one of the sexes, in this case the females.

I will come back to marker assisted selection later but first I want to talk about genomics. Again a field that is very strong in animal breeding that evolutionary ecologists have been taking advantage of. We run a project, called the songbird genomics project, together with Martien Groenen and Richard Crooijmans from Wageningen University and Kees van Oers from the NIOO, and two groups from the UK. We have applied state of the art genomics to a non-genomic but an ecological model species, the great tit. A major advantage is that we have ample phenotypic data from this species in the wild. If we can link that to genomic information it will give us the power to do a number of things that I will mention in a moment. What we have done over the past years is to create our genomic toolbox. One of the things we did is to create a SNP chip<sup>26, 27</sup>. A Single Nucleotide Polymorphism, a SNP, can be used as a genetic marker which will tell us something about a position on the

genome. These SNPs are then put on a map. We made such a map for the great tit where 8000 markers have been placed so we know where on the chromosomes the markers are<sup>28</sup>. The other thing that we are working on at the moment is a whole genome sequencing of the great tit. There have been a large number of species sequenced but not that many ecological model species, the great tit will be one of the first.

What are we going to do with our genomic toolbox? There are three things I want to mention. First, we attempt to identify genes that are associated with life history traits. We have genotyped 2000 birds, using a 10 kSNP chip, and for these 2000 birds we have a range of phenotypes so that we can look at the association between genotype and phenotype. Unfortunately up to now we do not find much for seasonal timing. But interestingly enough there is a clear pattern for day-night timing, for circadian rhythms. We measured the so called free running rhythm in great tits<sup>29</sup> by keeping a bird under dim light so that it does not have any information about day-night rhythms from for instance photoperiod. It will still exhibit a certain rhythm: it will go to sleep and get active in its subjective day. Such free running rhythm tells us something about the internal clock. We would expect of course for this internal clock to run at about 24 hours; as I will show you shortly that is not the case in our great tits. We can correlate these free running rhythms with our SNP variation to determine which genes, or at least which SNPs closely associated with genes, account for the variation in free running rhythm between individuals. Two SNPs come up, associated with the genes Tau and CRY1. This is also an interesting example because it links the work I do with the Chronobiology department of the University of Groningen of Domien Beersma with the work I do with Martien Groenen at the Animal Breeding and Genetics department of the Wageningen University. It links, I suspect, two research groups which would otherwise very rarely meet.

Why is it interesting to link phenotypic variation in free running rhythm to genetic variation? As I said, interestingly enough almost all great tits have a free running rhythm shorter than 24 hours. That means that they are all early birds, they become active in the early morning. Why is that, what kind of selection pressures are causing that? Knowledge of genotypes, enables us, ecologists, to take these questions to the field. In the field we have been taking blood samples from the birds for DNA for the past 15 years. Thus for many of the birds we have genotypes and phenotypes and we can start looking at the interaction between the two. How are genes expressed in the wild under different environmental conditions? And even further down the line we could potentially look at micro-evolution, for evolution in terms of shifts in gene frequency. The example I showed you on the free running rhythms allows us to go into the wild, measure the day-night rhythm of birds under entrained conditions (i.e.

their chronotype) and see what the difference is in chronotype of birds with a short and with a long free running rhythm, which we can determine by genotyping them. And even more, we could look at selection operating on that and maybe even look at how frequency of the genes that correlate with free running rhythms are changing over time. Genomics will be more and more about understanding the conditions under which genes are being expressed. And I think, as these genes have evolved under natural conditions, we have to look at them under natural conditions. Thus, at some point, the evolutionary ecologists will start paying back the debt that they have to the animal breeders as they will be able to provide them with many phenotypes from the wild.

I promised you that I would come back to the marker assisted selection. This is one of the ideas we have for the coming 5-10 years. We would like to make selection lines for early and late laying birds, using marker assisted selection. Similar as with the milk yield of the cows, laying date is a very difficult trait for phenotypic selection. It would require breeding a massive number of offspring to determine when they lay their eggs before a selection for the birds for the next generation could be made. And also similar to milk yield in cows, males of course do not express a laying date. The idea would be to use an even higher density SNP marker chip and determine the association between SNP markers and phenotype. Then use those SNP markers to do the selection of the next generation birds. This would mean that every year, after the chicks become independent, we take a blood sample, look at their DNA and make the selection so we do not have to wait an entire year before they express the phenotype themselves.

The title of my inaugural lecture is *the ecology of life history evolution, genes, individuals and populations*. What I have shown you is that genetics and ecology are really intertwined. Especially in a world where the environment is warming, it is crucial to understand that interaction, to understand the rate of evolutionary change compared to the rate of environmental change. This will be important, also, to understand how the living world is going to change in a changing environment. So where are the populations that are mentioned in this title? What we talked about is evolutionary rescue but there might also be ecological rescue. I will show you an example of a recent paper where we have looked at this<sup>30</sup>. I have already showed you that the average phenological mismatch between the birds and their food is increasing. Birds are responding too slow and are getting more and more mismatched with their food. And as a consequence, the number of fledglings that are produced in our population is declining, fewer birds are produced in years when there is more mismatch. But if we then look at the number of these fledglings that return to breed themselves, what we call the recruits, you see that there is no relationship with the number of

fledglings. This is a process which is called density dependence. Independent of the number of fledglings produced, the same number of birds return the next year to breed themselves. And as a consequence there is no change in population numbers over time, despite the increasing mismatch. We can show that it is indeed the density dependence that plays a role. When we use a model in which density dependence is turned on, as observed in our population, we see that population numbers are declining under different climate change scenarios but they are not declining that fast. But if we switch density dependence off, and there is thus a linear relationship between the number of offspring produced and the number of offspring that recruit the next year, there is a much more dramatic decline in population numbers. So does this mean that an ecological process such as density dependence can rescue the great tits? No, not really, because even when there is density dependence population numbers are coming down. But it does mean, however, that ecological processes can buy evolution time. There is more time for evolutionary processes to change, and perhaps rescue, the population.

I am running a number of projects together with members of the Animal Breeding and Genetics department. The project that I already mentioned is the songbird genomics project and I really hope we are going to continue that in the coming 5-10 years because there is still a lot of challenging work to do. Very recently we started another project, what I would call the winter moth genomics project. Together with Hendrik-Jan Megens and Martien Groenen we will be looking at the genomics of the winter moth. Today I talked mainly about the great tits as our experimental system but there are similar stories to be told on winter moth and also on the flycatcher. In the winter moth, the exciting story is that we can show that there are genetic changes occurring in the population<sup>31</sup>. And since we have stored also DNA from the winter moth this will allow us to go back in time and see how these changes have actually led to genomic changes. Another project we just started with Han Mulder and Johan van Arendonk is on great tit fledgling mass and it is nice to see that there are now people at the Animal Breeding and Genetics department that are actually doing calculations on great tits.

There is thus ample scope for scientific interactions but I would also like to mention the teaching that we do at Wageningen University. Together with Kate Lessells, I have been teaching a four-week Master course for the past six years or so. The 26 students from the 2013 edition of the course will actually finish the course tomorrow with the last set of oral exams. The course is always a very intense period, both for the students and for Kate and me but it is also inspiring and it is also our impression that the students learn something too. Yesterday the students presented their final assignments at the NIOO-KNAW and these were on a wide range of organisms. This

closes the circle of this lecture; we are back at the enormous diversity of the living world. A new generation of scientists is in the making and that is the strength of the university: generating knowledge and passing it on to the next generations.

Finally, a few words of thank. I would like to thank Johan van Arendonk and Martien Groenen for initiating this chair in Ecological Genetics and the Rector and the Academic Board of Wageningen University for the installation of this special chair. I am looking forward to a fruitful collaboration over the next years.

*You don't become a scientist on your own:* I was shaped as a young scientist at the University of Leiden, where I did my Master and PhD degree at the Animal Ecology department working with Jacques van Alphen. I then worked at Imperial College, University London, which made me realize that not only the natural world is very diverse but also the scientific world. And of course I have been shaped as a scientist by the people at the Animal Ecology department of the NIOO, and in fact continue to be shaped by these interactions.

*You can't be a scientist on your own:* I have been privileged to work with a large group of talented PhD students and post-docs that together with me have developed the research line I talked about today. The department of Animal Ecology is an excellent department, as was assessed by an international peer-review committee earlier this year, and I am grateful not only to the scientists at the department but also to the support staff, who play an instrumental role in keeping our research at the highest level. Outside the NIOO I am grateful for my pied-a-terre at the Chronobiology department at the University of Groningen of Domien Beersma and now also at the Animal Breeding and Genetics department of the Wageningen University. I hope to build further on our collaborations with both this group, the department of Frank Berendse, with whom we are running a large project, and with many other Wageningen research groups.

*You are not only a scientist:* Although this is true, it does not always seem that way. Science, and all matters that are associated with it, take up a lot of time. But of course I am more than a scientist. It is a great pleasure to see my both parents here on the first row. During my childhood, you have planted the seed of biology and I am grateful for that. Dear Lucie, we have been together since our first year of our biology study in Leiden and you have advised and supported me all the way from my first steps in science up to today. Also in times that it seemed that I was only a scientist. Thank you for that. Dear Yvonne, Nienke and Lilia, three daughters in their three new dresses on the first row, what a sight. You are also the next generation and it is



a great joy seeing you grow up to become young adults. I am sure that you have understood more of this inaugural lecture than the one seven years ago in Groningen. But I am also sure that you are equally happy that it is finished now.

*Ik heb gezegd*



## Literature cited

1. Cook, L. M. The rise and fall of the carbonaria form of the peppered moth. *Q. Rev. Biol* 78, 399-418, (2003).
2. Postma, E. & van Noordwijk, A. J. Gene flow maintains a large genetic difference in clutch size at a small spatial scale. *Nature* 433, 65-68, (2005).
3. Cook, L. M., Grant, B. S., Saccheri, I. J. & Mallet, J. Selective bird predation on the peppered moth: the last experiment of Michael Majerus. *Biology Letters* 8, 609-612, (2012).
4. Darwin, C. On the origin of species by means of natural selection, or the preservation of favoured races in the struggle for life. (John Murray, 1859).
5. Ford, E. B. Ecological genetics. (Chapman & Hall, 1964).
6. Parmesan, C. Influences of species, latitudes and methodologies on estimates of phenological response to global warming. *Global Change Biology* 13, 1860-1872, (2007).
7. Crick, H. Q. P., Dudley, C., Glue, D. E. & Thomson, D. L. UK birds are laying eggs earlier. *Nature* 388, 526, (1997).
8. Thackeray, S. J. et al. Trophic level asynchrony in rates of phenological change for marine, freshwater and terrestrial environments. *Global Change Biology* 16, 3304-3313, (2010).
9. Stenseth, N. C. & Mysterud, A. Climate, changing phenology, and other life history and traits: Nonlinearity and match-mismatch to the environment. *Proceedings of the National Academy of Sciences of the United States of America* 99, 13379-13381, (2002).
10. Visser, M. E., van Noordwijk, A. J., Tinbergen, J. M. & Lessells, C. M. Warmer springs lead to mistimed reproduction in great tits (*Parus major*). *Proceedings of the Royal Society of London Series B-Biological Sciences* 265, 1867-1870, (1998).
11. Hendry, A. P. & Kinnison, M. T. Perspective: The pace of modern life: Measuring rates of contemporary microevolution. *Evolution* 53, 1637-1653, (1999).

12. Gonzalez, A., Ronce, O., Ferriere, R. & Hochberg, M. E. Evolutionary rescue: an emerging focus at the intersection between ecology and evolution. *Phil. Trans. R. Soc. B* 368, 20120404, (2013).
13. Visser, M. E. Keeping up with a warming world; assessing the rate of adaptation to climate change. *Proceedings of the Royal Society of London Series B-Biological Sciences* 275, 649-659, (2008).
14. Visser, M. E. & Holleman, L. J. M. Warmer springs disrupt the synchrony of oak and winter moth phenology. *Proceedings of the Royal Society of London Series B-Biological Sciences* 268, 289-294, (2001).
15. Both, C. & Visser, M. E. Adjustment to climate change is constrained by arrival date in a long-distance migrant bird. *Nature* 411, 296-298, (2001).
16. Visser, M. E., Holleman, L. J. M. & Gienapp, P. Shifts in caterpillar biomass phenology due to climate change and its impact on the breeding biology of an insectivorous bird. *Oecologia* 147, 164-172, (2006).
17. te Marvelde, L., Webber, S. L., Meijer, H. A. J. & Visser, M. E. Mismatched reproduction is energetically costly for chick feeding female great tits. *Functional Ecology* 25, 1302-1308 (2011).
18. Reed, T. E., Jenouvrier, S. & Visser, M. E. Phenological mismatch strongly affects individual fitness but not population demography in a woodland passerine. *Journal of Animal Ecology* 82, 131-144, (2013).
19. Price, T., Kirkpatrick, M. & Arnold, S. J. Directional selection and the evolution of breeding date in birds. *Science* 240, 798-799, (1988).
20. Verhulst, S. & Nilsson, J. A. The timing of birds' breeding seasons: a review of experiments that manipulated timing of breeding. *Philosophical Transactions of The Royal Society B*, 1-12, (2007).
21. Gienapp, P. & Visser, M. E. Possible fitness consequences of experimentally advanced laying dates in Great Tits: differences between populations in different habitats. *Functional Ecology* 20, 180-185, (2006).

22. Husby, A., Visser, M. E. & Kruuk, L. E. B. Speeding up micro-evolution: annual strength of selection and heritability are positively associated in a wild bird population. *PLoS Biology* 9, e1000585, (2011).
23. Lush, J. *Animal breeding plans*. (Iowa State College Press, 1937).
24. Henderson, C. R. Estimation of genetic parameters. *Ann. Math. Stat.* 21, 309-310, (1950).
25. B.C., C. & Mackill, D. J. Marker-assisted selection: an approach for precision plant breeding in the twenty-first century. *Phil Trans R Soc Lond B* 363, 557-572, (2008).
26. van Bers, N. E. M. et al. Genome-wide SNP detection in the great tit *Parus major* using high throughput sequencing. *Molecular Ecology* 19 (Suppl. 1), 89-99, (2010).
27. van Bers, N. E. M. et al. The design and cross-population application of a genome-wide SNP chip for the great tit *Parus major*. *Molecular Ecology Resources* 12, 753-770, (2012).
28. van Oers, K. et al. Replicated high-density genetic maps of two great tit populations reveal new insights into avian genome structure and evolution. *Heredity*, (Submitted).
29. Helm, B. & Visser, M. E. Heritable circadian period length in a wild bird population. *Proceedings of the Royal Society B-Biological Sciences* 277 3335-3342, (2010).
30. Reed, T. E., Grøtan, V., Jenouvrier, S., Sæther, B. E. & Visser, M. E. Population growth in a wild bird is buffered against phenological mismatch. *Science* 340, 488-491 (2013).
31. van Asch, M., Salis, L., Holleman, L. J. M., van Lith, B. & Visser, M. E. Evolutionary response of the egg hatching date of a herbivorous insect under climate change. *Nature Clim. Change* 3, 244-248, (2013).





Prof. dr Marcel E. Visser

*'Natural selection shapes the life histories of organisms. The ecological interactions of these organisms with their biotic and abiotic environment shape the selection pressure on their phenotypes while their genetics determine how fast this selection leads to adaptation to their environment. The field of ecological genetics studies the response to natural selection in the wild and thus plays a key role in our understanding of the adaptive capacity of life, essential to understand how a changing environment affects the natural world.'*