Evolutionary Biology

Directional selection

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Contents

Introduction

Directional selection occurs when individuals with traits on one side of the mean in their population survive better or reproduce more than those on the other. It has been demonstrated many times in natural populations using both observational and experimental approaches. Directional selection does the 'heavy lifting' of evolution, by tending to move the trait mean towards the optimum for the environment. It results in increased adaptedness of organisms. It is the principle process that Darwin (1859) envisaged as driving evolution. Two of his own examples were faster wolves being more successful at hunting deer and flowers that produce more nectar being more successful in attracting pollinating insects. These both suggest directional rather than other forms ('modes') of selection. Directional selection is the process that comes most easily to mind when thinking about natural selection, and is the form of selection that has taken place in the best known examples of evolution (eg peppered moth, antibiotic resistance, finch beaks). However, directional selection does not always result in evolution, because it can be constrained in many ways.

If directional selection acts in different directions in different populations or species, because of variation in environmental circumstances, then it is described as divergent. This results in populations becoming different, and can contribute to speciation.

Directional selection can also be artificially imposed, and has been commonly used by animal and plant breeders to improve traits (such as yield) in domesticated organisms, as well as to understand evolution better. I deal first with natural directional selection, before returning to artificial selection at the end.

Darwin, C. 1859. On the Origin of Species by Means of Natural Selection. London: John Murray. Without doubt the most famous book about natural selection, and in the whole of evolutionary biology. Still a very useful and entertaining read that is astonishing for the care with which its enormous evidence base was garnered and organised. Darwin understood the operation of directional selection better than most biologists that followed him for a century afterwards.

General Overviews

Most undergraduate textbooks on evolution, such as Futuyma (2009) and Barton et al(2007), contain basic definitions, descriptions and examples of directional selection, as well as of natural selection more broadly. There are several excellent texts that deal with more advanced topics in natural selection, including directional selection. These include George William's (1966) seminal book that emphasised that selection acts predominantly on individuals and John Endler's (1986) classic Natural Selection in the Wild which reviewed and synthesised evidence of the importance of natural selection in wild populations. More recent and thorough descriptions of the workings of natural selection are found in Mitton's (1997) "Selection in Natural Populations" and Bell's (2008) "Selection".

Futuyma, D. J. 2009. Evolution. 633. Sunderland, MA: Sinauer Associates.
The latest edition of the standard undergraduate textbook for evolution. Contains introductory material on directional selection.

Barton, N. H. et al. 2007. Evolution. 833. New York: Cold Spring Harbor Laboratory Press.
Well illustrated undergraduate text book with good basic introduction to directional selection. Lack of referencing makes it difficult to follow up on examples in detail. Very useful glossary.

Williams, G. C. 1966. Adaptation and Natural Selection: a Critique of Some Current Evolutionary Thought.**,** 307. Princeton, NJ: Princeton University Press.

An enormously influential book. A reaction to the group selectionist and teleological thinking that was common at the time of its writing, Williams was the first clearly and explicitly to advocate, in an accessible style, that the explanation for evolutionary adaptations should be sought mainly in the simple operation of natural selection at the level of the individual and the gene.

Endler, J. A. 1986. Natural Selection in the Wild. 336. Princeton, NJ: Princeton University Press. The first review and synthesis of studies and concepts relating to natural selection in wild populations. It contains detailed consideration of the philosophy and methods for the study of natural selection. A seminal work.

Mitton, J. B. 1997. Selection in natural populations. 240. Oxford: Oxford University Press.
A review and synthesis of studies of selection on genetic variation and protein polymorphisms in natural populations, and why this comes about. The approaches described have been outdated by the modern march to use genomic methods, but the book documents many classic and easily understood examples.

Bell, G. 2008. Selection: the Mechanism of Evolution. 2nd ed. Oxford: Oxford University Press.
A very useful advanced textbook providing thorough and detailed consideration of the operation of selection in the evolution of adaptation. Examples are biased to microbial systems. Concentrates on the evolutionary consequences, rather than the ecological context, of selection, although it includes interesting material on the latter.

Journals

American Naturalist, the journal of the American Society of Naturalists. An old and very well respected journal containing studies of ecology, population biology and evolution. As such it contains much material that is directly or tangentially relevant to the study of natural, including directional, selection. It is well known for promoting studies that combine theoretical and empirical novelty.

Evolution, the journal of the Society for the Study of Evolution, and richer in examples that document natural selection than any other journal. Contains many classic papers going back to the 1940s.

Journal of Evolutionary Biology, the journal of the European Society for Evolutionary Biology, and a comparatively recent addition to the stable of evolutionary journals. Contains much work of relevance to the study of natural selection.

Molecular Ecology, a journal dedicated to papers that incorporate genetic data to answer ecological and evolutionary questions.

Trends in Ecology and Evolution A review journal covering the fields of ecology and evolution, and often containing articles and opinion pieces of relevance to the study of selection. Authors are explicitly encouraged to write in a concise and accessible style.

Definitions and terminology

<u>Verbal definitions of directional selection on phenotypes</u>

In directional selection individuals on one side of the population mean for a trait do better than those on the other, in terms of survival or reproductive success (Schluter 1988). In other words, individuals towards one end of the trait distribution are more successful (Endler 1986). Endler provides the most careful verbal definition of natural selection, one that is in line with Darwin's (1859) initial intention. Endler's definition (and Darwin's) suggests that a trait must have a heritable (genetic) basis for it to be shaped by natural selection, implying that selection must lead to evolution. Many evolutionary biologists disagree with this, including the fathers of the modern synthesis who emphasised that natural selection acts on phenotypes. J.B.S. Haldane (1954) wrote “Natural selection is the differential survival or reproductive success of phenotypes” and “Natural selection acts on phenotypes. It is ineffective unless it favours one genotype over another, but it can occur without doing so”. “Natural selection is not evolution” are the first words of Ronald Fisher in his seminal book “The Genetical Theory of Natural Selection” in which he emphasised that natural selection is a process independent of evolution. Arnold & Wade 1984 is one more recent paper to re-emphasise this point.

Schluter, D. 1988. Estimating the form of natural selection on a quantitative trait. *Evolution.* 42**,** 849-861. . Aside from giving a clear, simple and general definition of directional selection, this paper provides a method (the ‘cubic spline’) for describing the relationship between fitness and a trait (fitness function) that is not dependent on a priori assumptions.

Endler, J. A. 1986. Natural Selection in the Wild. 336. Princeton, NJ: Princeton University Press.
The first review and synthesis of studies and concepts relating to natural selection in wild populations. It contains detailed consideration of the philosophy and methods for the study of natural selection. A seminal work.

Darwin, C. 1859. The Origin of Species by Means of Natural Selection. London: John Murray. Without doubt the most famous book about natural selection, and in the whole of evolutionary biology. Still a very useful and entertaining read that is astonishing for the care with which its enormous evidence base was garnered and organised. Darwin understood the operation of directional selection better than most biologists that followed him for a century afterwards.

Haldane, J. B. S. 1954. The measurement of natural selection. *Proceedings of the 9th International Congress of Genetics.* 1953**,** 480-487. .
Notable for Haldane’s very explicit statements that selection acts on phenotypes.

Fisher, R. A. 1930. The Genetical Theory of Natural Selection. 272. Oxford: Oxford University Press.
A foundation of the 1930s’ ‘modern synthesis’ of population genetics and evolution. Notable because Fisher saw that selection was an important process in its own right, independent of its relevance in evolution. His fundamental theorem of natural selection explicitly recognises that improvements in the performance of organisms brought about by directional selection are continually eroded by changes in the environment.

Arnold, S. J. and M. J. Wade 1984. On the measurement of natural and sexual selection - theory. *Evolution.* 38**,** 709-719. .
Describes the relationship between different measures of selection, and evolutionary change as the outcome. They also discuss the concept of the opportunity for selection, a measure which describes variation in fitness among individuals and which sets an upper boundary on the strength of directional selection.

<u>Mathematical definitions of selection</u>
The most robust formal statement of selection is George Price’s (1970) mathematical formulation that was presaged by Alan Robertson (1966). It equates the rate of change in the mean of a phenotypic character to the association (strictly the genetic covariance) between that character and fitness. The unusual simplicity and power of this equation is dwelt on by Frank (1995) and Gardner (2008). The equation suggests the easiest way to visualise natural selection as a plot of the relationship between fitness and trait value for individual organisms. In such a figure, an overall positive or negative relationship depicts directional selection. The

operation of directional selection thus depends on their being variation in both fitness and traits among individuals.

Price 1970 Price, G. R. 1970. Selection and covariance. *Nature.* 227**,** 520-512. .
Short, mathematical paper presenting the 'Price equation' and its derivation.

Robertson 1966 Robertson, A. 1966. A mathematical model of the culling process in dairy cattle. *Animal Production.* 8**,** 95-108. .
A seemingly obscure paper in which Robertson arrives at a specific case of Price's result, without fanfare, four years earlier

Frank, S. A. 1995. George Price's contributions to evolutionary genetics. *Journal of Theoretical Biology.* 175**,** 373-388. .
A review of the contributions of George Price to the study of selection, with clear explanation of their significance.

2008 Gardner, A. 2008. The Price equation. *Current Biology.* 18**,** R198-R202. .
A primer on the importance of Price's equation, which is still being developed.

<u>Traits and phenotypic variation</u>
A phenotypic trait is a measurement or character of an individual, such as height, weight or eye colour. Trait and phenotype are sometimes used interchangeably, although phenotype is also used to describe a collection of traits that comprise a single individual. Darwin himself was very concerned with documenting the extent of phenotypic variation in both domesticated and wild species, because he understood that such variation was a necessary prerequisite for selection to occur (Darwin, 1859). Variation in phenotypic traits is completely ubiquitous in all populations of organisms, and its demonstration is implicit in just about any empirical study in evolutionary biology. It is found in morphological, physiological, behavioural and life history traits (e.g. Mousseau & Roff, 1987). Variation can be continuous (e.g. Capy et al 1994, Alonso-Blanco & Koornneef 2000) or discontinuous (Skulason & Smith 1995). Variation can be due to the environment (Lively 1986, Scheiner, 1993) or may have a genetic basis (Mousseau & Roff, 1987). Phenotypic variation must have a genetic basis if selection is to result in evolution. There is certainly abundant genetic variation (e.g. Hubby & Lewontin 1966, Glazier et al 2002) in most organisms, but the link between that and phenotypic variation is still a topic of active research (Glazier et al 2002, Barton & Keightley 2002 Nat Rev genet)

Capy, P. et al. 1994. Phenotypic and genetic variability of morphometrical traits in natural populations of Drosophila melanogaster and Drosphila simulans. 2. Within-population variability. *Genetics Selection Evolution.* 26**,** 15-28. .
A thorough demonstration of individual variability in wild populations of Drosophila

Alonso-Blanco, C. and M. Koornneef 2000. Naturally occurring variation in Arabidopsis: an underexploited resource for plant genetics. *Trends in Plant Science.* 5**,** 22-29. .
Documents the extent of phenotypic variation in wild populations of the model plant Arabidopsis

Skulason, S. and T. B. Smith 1995. Resource polymorphisms in vertebrates. *Trends In Ecology & Evolution.* 10**,** 366-370. .
A review of polymorphic (discontinuous) variation in traits associated with resource use in wild populations

Scheiner, S. M. 1993. Genetics and Evolution of Phenotypic Plasticity. *Annual Review of Ecology and Systematics.* 24**,** 35-68. .
A review of the extent of the relationship between traits and the environment in which they developed (phenotypic plasticity) in natural populations

Lively, C. M. 1986. Predator-induced shell dimorphism in the acorn barnacle Chthamalus anisopoma. *Evolution.* 40**,** 232-242. .
Shows how polymorphic variation in the shell shape of a mollusc depends on the presence of a predator during development, rather than having a genetic basis.

Mousseau, T. A. and D. A. Roff 1987. Natural selection and the heritability of fitness components. *Heredity.* 59**,** 181-197. .
An early synthesis of the extent of heritable variation in different kinds of traits in wild populations.

Barton, N. H. and P. D. Keightley 2002. Understanding quantitative genetic variation. *Nature Reviews Genetics.* 3**,** 11-21. .
A review of approaches and ideas relevant to understanding the genetic basis of phenotypic variation, from an evolutionary perspective.

Hubby, J. L. and R. C. Lewontin 1966. A molecular approach to the study of genic heterozygosity in natural populations. 1. The number of alleles at different loci in Drosophila pseudoobscura. *Genetics.* 54**,** 577-594. .
The original demonstration of genetic variation in natural populations using gel electrophoresis, a foundation of the science of molecular genetics.

Glazier, A. M. et al. 2002. Finding genes that underlie complex traits. *Science.* 298**,** 2345-2349. .
A description of methods for identifying the genetic basis of complex phenotypic traits.

<u>Fitness</u>
Probably the most slippery concept in the whole of evolutionary biology, its discussion has been a recurring theme, see for example Fisher (1930), Williams (1966) and Endler (1986). In fact, there is no absolute definition of fitness, and different measures are appropriate in different contexts. Stearns (1992) is a good place to start for a discussion of this while Caswell (2001) gives further detail from the demographic perspective. De Jong (1994) provides a more philosophical consideration. The biggest schism in fitness definitions is between theoreticians and empiricists. The measures used by theoreticians, although most relevant to the prediction of evolutionary change, are essentially impossible to estimate in most natural populations, and empiricists have instead resorted to many others. Lifetime reproductive success (LRS) is generally agreed on as the best of these (see Clutton-Brock, 1988), although the idea of individual fitness (see Caswell 2001) has been developed more recently. Even LRS can take decades of work to estimate in the wild, and empiricists have used a wealth of short-term measures related to survival (e.g. Boag & Grant, 1981) and reproductive success (Kruuk et al, 2002). Even more short-term assessments of performance that may (or may not) be related to these 'components of fitness' have also been used, such as mating success (Andersson, 1982) and mate choice (Houde, 1987).

Stearns, S. C. 1992. The Evolution of Life Histories. 249. Oxford: Oxford University Press.
A textbook introducing basic and more advanced concepts in the study of life-history evolution. The study of life histories focusses on traits that are closely related to fitness, such as size at maturity and litter size.

Caswell, H. 2001. Matrix Population Models. 2nd ed. Sunderland, Mass.: Sinauer associates.
A research text containing an almost exhaustive consideration of the use of matrix population models in the study of evolutionary biology and population demography.

De Jong, G. 1994. The fitness of fitness concepts and the description of natural selection. *Quarterly Review of Biology.* 69**,** 3-29. .
A very thorough exploration of the concepts and definitions of fitness, and the consequences of these for the study of natural selection.

Clutton-Brock, T. 1988. Reproductive Success. Chicago: University of Chicago Press.
An edited volume giving a very good introduction to the estimation of lifetime reproductive success in natural populations. Chapters describe individual long-term studies, as well as general issues, approaches and problems that arise.

Boag, P. T. and P. R. Grant 1981. Intense natural selection in a population of Darwin's finches (Geospizinae) in the Galapagos. *Science.* 214**,** 82-85. .
One the earliest, and the most celebrated, examples of directional natural selection being observed in the wild. A drought in the Galapagos lead to food shortage in which finches with bigger beaks survived because only they could eat the large seeds that remained.

Kruuk, L. E. B. et al. 2002. Antler size in red deer: Heritability and selection but no evolution. *Evolution.* 56**,** 1683-1695. .
In a long-term study of red deer, directional selection due to differences in lifetime reproductive success favours stags with larger antlers.

Andersson, M. 1982. Female choice selects for extreme tail length in a widowbird. *Nature.* 299**,** 818-820. .
An experimental manipulation of demonstration of tail length in male widowbirds was used to demonstrate directional selection on the trait due to differences in reproductive success.

Houde, A. E. 1987. Mate choice based upon naturally occurring color-pattern variation in a guppy population. *Evolution.* 41**,** 1-10. .
Female choice of male guppies with more extensive orange colouration suggests directional selection on the trait in the wild.

<u>Directional selection at the genetic level</u>
Although selection acts on phenotypes, it can be inferred from patterns at a genetic level, especially when a genetic locus is polymorphic and the different alleles give rise to different traits. Population geneticists call directional selection that favours a particular allele ‘positive’ selection, and directional selection that removes alleles ‘purifying’ selection (in fact these are different sides of the same coin). Walsh and Lynch provide an overview of these approaches, while Sabeti give examples from studies of the human genome.

Walsh, B. and M. Lynch Evolution and Selection of Quantitative Traits: I. Foundations. Sinauer. http://nitro.biosci.arizona.edu/zbook/NewVolume_2/newvol2.html#2A
This monumental, encyclopaedic volume, which is not yet published, but available online, contains an astonishing wealth of material on the theoretical and empirical study of selection and evolution. Chapters 9 to 11 contain a thorough description of the many methods for the detection of selection using molecular genetic data.

Sabeti, P. C. et al. 2006. Positive natural selection in the human lineage. *Science.* 312**,** 1614-1620. .
Provides a review of methods for the detection of positive (directional) selection using genetic markers, summary of evidence from older studies of humans using single markers and new data from the whole human genome.

Modes of selection
Directional selection is one form (or 'mode') of natural selection. Brodie et al (1995) make clear the differences (and similarities) between directional, stabilizing and disruptive selection. An older (and now outdated) but interesting perspective comes from Simpson (1944), who talks instead of linear, centripetal and centrifugal selection. Selection can also act on more than one trait at a time, favouring particular combinations of traits (e.g. Brodie 1992; Schluter & Nychka, 1994) or selection on one trait can affect the distribution and evolution of another (Lande and Arnold, 1983).

Brodie, E. D. et al. 1995. Visualizing and quantifying natural selection. *Trends In Ecology & Evolution.* 10**,** 313-318. .
An explicit description of the different ways ('modes') in which natural selection can shape trait distributions.

Simpson, G. G. 1944. Tempo and Mode in Evolution. 237. New York: Hafner.
A important contribution to the modern synthesis. As a palaeontologist, Simpson was predominantly concerned with setting the link between selection, genetics and macroevolution on a firm footing. He was the first to apply the concept of adaptive landscapes to phenotypic characters. He saw directional selection (which he called 'linear selection') as instrumental in the gradual accrual of change in lineages.

Brodie 1992 Brodie, E. D. 1992. Correlational selection for color pattern and antipredator behavior in the garter snake *Thamnophis ordinoides*. *Evolution.* 46**,** 1284-1298. .
A classic example of the way in which selection can favour particular combinations of pairs of traits.

Schluter, D. and D. Nychka 1994. Exploring fitness surfaces. *American Naturalist.* 143**,** 597-616. . Develops a method to visualise selection acting on more than one trait at a time by constructing 'selection surfaces'. Uses the technique to demonstrate the operation of different kids of selection in real data sets.

Lande, R. and S. J. Arnold 1983. The measurement of selection on correlated characters. *Evolution.* 37**,** 1210-1226. .
The original development of the standard mathematical methodology for estimating the strength of selection on individual traits, when several correlated traits have been measured. An enormously influential paper.

Visualising directional selection
<u>Selection is a surface</u>
In reality the different modes of selection cannot be clearly separated. For single traits they may act together or differently on the same population at different times because of changes in the environment. This can be understood by visualising selection as a function or line which relates the value of a trait to fitness. The shape of this function may be complex, implying the operation of different modes of selection at the same time (Schluter, 1988), or across the possible range of variation in the trait (Endler, 1986). Extending the depiction of selection to more than one trait, envisaging selection as a surface becomes very useful especially when the selection regime is complex. Specific pairs of trait values correspond to position on this surface, while its height indicates the fitness of that combination (Schluter & Nychka, 1994). The idea can be extended into

more trait dimensions, although this becomes difficult to visualise (Phillips & Arnold, 1989). Modes of selection on different traits trait may be independent of each other, or favour particular trait combinations. The strength of directional selection for a trait combination is equal to the slope of the surface at that point (Lande & Arnold, 1983)

Schluter, D. 1988. Estimating the form of natural selection on a quantitative trait. *Evolution.* 42**,** 849-861. .
Aside from giving a clear, simple and general definition of directional selection, this paper provides a method (the 'cubic spline') for describing the relationship between fitness and a trait (fitness function) that is not dependent on a priori assumptions.

Endler, J. A. 1986. Natural Selection in the Wild. 336. Princeton, NJ: Princeton University Press. The first review and synthesis of studies and concepts relating to natural selection in natural populations. It contains detailed consideration of the philosophy and methods for the study of natural selection. A seminal work.

Schluter, D. and D. Nychka 1994. Exploring fitness surfaces. *American Naturalist.* 143**,** 597-616. .
Develops a method to visualise selection acting on more than one trait at a time by constructing 'selection surfaces'. Uses the technique to demonstrate the operation of different kids of selection in real data sets.

Phillips, P. C. and S. J. Arnold 1989. Visualizing multivariate selection. *Evolution.* 43**,** 1209-1222. .
Builds on the mathematicalarguments of Lande and Arnold 1983 to show how those abstractions can be used to visualise selection acting on more than one trait at a time.

Lande, R. and S. J. Arnold 1983. The measurement of selection on correlated characters. *Evolution.* 37**,** 1210-1226. .
The original development of the standard mathematical methodology for estimating the strength of selection on individual traits, when several correlated traits have been measured. An enormously influential paper.

<u>Selection surfaces and adaptive landscapes</u>
The utility of fitness surfaces can be extended by combining the information that they contain about the operation of selection at the individual level with information on the distribution of phenotypic traits to construct an 'adaptive landscape': a surface that represents the relationship between the mean phenotypic values in a population and population mean fitness. Simpson (1953) was the first to use this idea, which he developed from a similar concept for genotypes due to Wright (1932). Lande (1976) formalised the idea mathematically, and its significance and usefulness as a bridge between selection, micro- and macroevolution has been expounded by Arnold et al (2001). Many ideas about the adaptive landscape concept are brought together by Svensson and Calsbeek (2012).

Simpson, G. G. 1953. The Major Features of Evolution. New York: Columbia University Press.
A follow up work to Tempo and Mode in Evolution, in which Simpson develops the idea of the phenotypic adaptive landscape.

Wright, S. 1932. The roles of mutation, inbreeding, crossbreeding and selection in evolution. *Proceedings of the Sixth Annual Congress of Genetics.* 1**,** 356-366. .
Paper containing the clearest exposition of Wright's formulation of the adaptive landscape.

Lande, R. 1976. Natural selection and random genetic drift in phenotypic evolution. *Evolution.* 30**,** 314-334. .
A mathematical formalisation of Simpson's idea of the adaptive landscape.

Arnold, S. J. et al. 2001. The adaptive landscape as a conceptual bridge between micro- and macroevolution. *Genetica.* 112**,** 9-32. .
A very clear review of the relevance of the adaptive landscape concept to thinking about the link between micro- and macroevolution.

Svensson, E. and R. Calsbeek 2012. The Adaptive Landscape in Evolutionary Biology. Oxford: Oxford University Press.
An edited book with many chapters by different authors describing the use of the adaptive landscape concept in the study of natural selection and evolution.

Estimating the strength of directional selection

Episodes of selection

Selection can be particularly marked at certain times of an organisms lifecycle (e.g. among juveniles, because of variation in mortality or among mature individuals, because of variation in reproductive success, Schluter & Smith 86; Howard 1979) or because of environmental variation over time (Gibbs & Grant 87, Milner et al 1999). Such bouts of selection are often called 'episodes' (Arnold & Wade 1984 a,b) and selection is often (usually) measured over an episode, rather than over organisms whole lives

Schluter, D. and J. N. M. Smith 1986. Natural selection on beak and body size in the song sparrow. *Evolution.* 40**,** 221-231. .
Demonstrate contrasting patterns of selection on morphological traits due to variation in over-winter survival and springtime reproduction.

Howard, R. D. 1979. Estimating reproductive success in natural populations. *American Naturalist.* 114**,** 221-231. .
An examination of selection through variation in reproductive success in bullfrogs.

Gibbs, H. L. and P. R. Grant 1987. Oscillating selection on Darwin's finches. *Nature.* 327**,** 511-513. .
Selection on beak size in Galapagos finches can change direction as a result of changes in environmental conditions.

Milner, J. M. et al. 1999. Repeated selection of morphometric traits in the Soay sheep on St Kilda. *Journal of Animal Ecology.* 68**,** 472-488. .
Uses data from a long-term study of wild sheep to demonstrate directional selection on body size operating through differences in winter survival. The strength of selection varied according to the population density.

Arnold, S. J. and M. J. Wade 1984. On the measurement of natural and sexual selection - theory. *Evolution.* 38**,** 709-719, Arnold, S. J. and M. J. Wade 1984. On the measurement of natural and sexual selection - applications. *Evolution.* 38**,** 720-734. .
A pair of papers containing the theory for dealing with episodes of selection and its application to several examples

Selection metrics

The strength of selection can be estimated using different metrics. Endler (1986) contains a useful chapter on these, with some consideration of relative strengths and weaknesses of different approaches. Selection on quantitative traits is most often measured as the selection differential (difference in the trait mean before and after selection) and the selection gradient (the regression coefficient of the trait on fitness, when variation in other measured traits has been controlled). Lande and Arnold 1983 is the standard reference when data on individuals are available. There is useful explanation and interpretation in Mitchell-Olds & Shaw, 1987. Manly (1985) and Endler (1986) describe methods for estimating selection when individual data are not available. An example of such an approach using likelihood is given by Munch et al 2003. Easy to read descriptions of approaches to estimating directional selection from molecular data are given by Nielsen 2005 and Hedrick 2005. A useful overview and more detailed technical considerations can be found in Walsh and Lynch.

Endler, J. A. 1986. Natural Selection in the Wild. 336. Princeton, NJ: Princeton University Press.
The first review and synthesis of studies and concepts relating to natural selection in natural populations. It contains detailed consideration of the philosophy and methods for the study of natural selection. A seminal work.

Lande, R. and S. J. Arnold 1983. The measurement of selection on correlated characters. *Evolution.* 37**,** 1210-1226. .
The original development of the standard mathematical methodology for estimating the strength of selection on individual traits, when several correlated traits have been measured. An enormously influential paper.

Mitchell-Olds, T. and R. G. Shaw 1987. Regression analysis of natural selection: statistical inference and biological interpretation. *Evolution.* 41**,** 1149-1161. .
Deals with some of the strengths, weaknesses and underlying assumptions of Lande & Arnold’s approach.

Manly, B. F. J. 1985. The Statistics of Natural Selection. 484. London: Chapman & Hall.
A research text covering a wide range of approaches to the measurement of selection using both quantitative and genetic data.

Munch, S. B. et al. 2003. Quantifying natural selection on body size from field data: winter mortality in *Menidia menidia*. *Ecology.* 84**,** 2168-2177. .
A good example of estimating the strength of selection from sequential population samples rather than individual data.

Nielsen, R. 2005. Molecular signatures of natural selection. *Annual Review of Genetics.* 39**,** 197-218. .
A review of the use of molecular data to detect selection. An excellent place to start for people with limited, or no, knowledge of population genetics.

Hedrick, P. W. 2005. Genetics of Populations. 737 3rd ed. Boston, MA: Jones and Bartlett.
One of the standard textbooks on population genetics, containing the theory and clear examples of using genetic data to estimate directional selection.

Walsh, B. and M. Lynch Evolution and Selection of Quantitative Traits: I. Foundations. Sinauer.
A comprehensive research text for the field of evolutionary genetics, containing excellent material on the measurement of selection.

Examples of directional selection

<u>Selection on quantitative characters</u>

Anthropogenic selection

Directional selection has been inferred by a number of different methods. The best known examples of evolution, which often result from anthropogenic environmental changes, include several where strong directional selection can be inferred, although selection may not have been directly observed. These include the evolution of industrial melanism, most famously in peppered moths in response to pollution from coal burning which is described by Kettlewell (1973) and reviewed in Cook (2003). Levy (1998) reviews the evolution of antibiotic resistance in an accessible article in Scientific American, and in a more technical and up to date article, Levy & Marshall (2004). The evolution of resistance to insecticide provides another example of where strong directional selection can be inferred. Lenormand et al (1999) and Tabashnik (1994) describe and review two of the best documented examples.

Kettlewell, B. 1973. The Evolution of Melanism: the Study of a Recurring Necessity. 1st ed. Oxford: Clarendon Press.
Detailed review of all the early work on industrial melanism.

Cook, L. M. 2003. The rise and fall of the Carbonaria form of the peppered moth. *Quarterly Review of Biology.* 78**,** 399-417. .
Review of more recent studies of industrial melanism, demonstrating how the direction of selection reversed when industrial pollution declined.

Levy, S. B. 1998. The challenge of antibiotic resistance. *Scientific American.* 278**,** 46-53. .
An accessible popular article documenting the rise in antimicrobial resistance in bacteria as a result of antibiotic use.

Levy, S. B. and B. Marshall 2004. Antibacterial resistance worldwide: causes, challenges and responses. *Nature Medicine.* 10**,** S122-S129. .
An updated and more technical version of Levy 98

Lenormand, T. et al. 1999. Tracking the evolution of insecticide resistance in the mosquito Culex pipiens. *Nature.* 400**,** 861-864. .
Draws on an extensive body of work to demonstrate the evolution of insecticide resistance in mosquitoes caused by anthropogenic directional selection, and how this can be countered by migration.

Tabashnik, B. E. 1994. Evolution of resistance to Bacillus thuringiensis. *Annual Review of Entomology.* 39**,** 47-79. .
A review of the emergence of resistance to 'Bt' toxin among agricultural pest species.

Selection in the fossil record

Directional selection can also be inferred from analysis of patterns of evolution in the fossil record. Vermeij (1987) and Bakker (1983) provide examples.

Vermeij, G. J. 1987. Evolution and Escalation: an Ecological History of Life. Princeton, NJ: Princeton University Press.
Documents a number of examples from the fossil record which suggest that predators have caused directional selectionon defensive aspects of morphology in marine organisms

Bakker, R. T. 1983. The deer flies, the wolf pursues: incongruencies in the fossil record. . *In:* SLATKIN, D. J. F. A. M. (ed.) *Coevolution.* 350-382. Sunderland, Mass.: Sinauer.

Uses evidence from the fossil record to show that predators may have driven the evolution of running speed in ungulates but also highlights problems with this interpretation.

Direct observations of natural selection

Perhaps the most satisfying examples of directional selection come from studies in which it has been directly observed in natural or manipulated wild populations. It is only comparatively recently that good examples of directional selection in natural populatins have been described. The best known stems from the long term research of Peter and Rosemary Grant on Geospiza finches in the Galapagos islands, e.g. Boag & Grant (1981). Other examples include selection on trophic morphology in sticklebacks (Hagen & Gilbertson, 1973), and on nestling weight in flycatchers (Linden et al, 1992). The foregoing examples involve selection as a result of variation in survival, but selection can also result from variations in aspects of reproductive success, including on body size in bullfrogs (Howard, 1979), on colouration in guppies and on height in a cohort of military officers (Mueller & Mazur, 2001).

Boag, P. T. and P. R. Grant 1981. Intense natural selection in a population of Darwin's finches (Geospizinae) in the Galapagos. *Science.* 214**,** 82-85. .

One the earliest, and the most celebrated, examples of directional natural selection being observed in the wild. A drought in the Galapagos lead to food shortage in which finches with bigger beaks survived because only they could eat the large seeds that remained.

Hagen, D. W. and L. G. Gilbertson 1973. Selective predation and intensity of selection acting upon lateral plates of threespine sticklebacks. *Heredity.* 30**,** 273-287. .

An early demonstration of selection in the wild, demonstrating contrasting modes of selection on different traits: directional selectional on gill rakers that are involved in obtaining food, and stabilising selection on bony plate number that is involved in antipredator defence.

Linden, M. et al. 1992. Selection on fledging mass in the collared flycatcher and the great tit. *Ecology.* 73**,** 336-343. .

Shows that heavier fledglings generally have better survival in a wild bird population.

Howard, R. D. 1979. Estimating reproductive success in natural populations. *American Naturalist.* 114**,** 221-231. .

Estimates reproductive success from different components of mating in bullfrogs, and documents directional selection on body size.

Houde, A. E. 1987. Mate choice based upon naturally occurring color-pattern variation in a guppy population. *Evolution.* 41**,** 1-10. .

A good example of using mate choice experiments to examine selection, in this case on orange colour in male guppies.

Mueller, U. and A. Mazur 2001. Evidence of unconstrained directional selection for male tallness. *Behavioral Ecology and Sociobiology.* 50**,** 302-311. .

A fascinatinating paper showing ongoing directional selection on height in human males: tall men have more children.

Experimental demonstrations

In observational studies of directional selection it is often difficult to be certain which traits are under selection. One approach to this is to manipulate candidate traits. There are particularly good examples from studies of plants, especially involving selection on floral traits, e.g. Nilsson (1988). Such experiments are more difficult with animals, but Andersson (1982) provides an excellent example. See also Sinervo et al (1992) for a particularly innovative approach to phenotypic manipulation, although in that case the outcome was predominantly stabilising selection.

Nilsson, L. A. 1988. The evolution of flowers with deep corolla tubes. *Nature.* 334**,** 147-149. .
An elegant experiment examining the role of plant-pollinator coevolution in the exxageration of floral traits by directional selectional.

Andersson, M. 1982. Female choice selects for extreme tail length in a widowbird. *Nature.* 299**,** 818-820. .
An experimental manipulation of demonstration of tail length in male widowbirds was used to demonstrate directional selection on the trait due to differences in reproductive success. One of the most important papers in the empirical study of sexual selection.

Sinervo, B. et al. 1992. Allometric engineering - a causal analysis of natural selection on offspring size. *Science.* 258**,** 1927-1930. .
The authors manipulated the size of hatchling lizards by removing yolk from eggs early in development, then followed the survival of hatchlings to estimate the strength of selection on body size.

<u>Selection on genes</u>
The analysis of genetic data provides a potentially powerful way to infer the action of directional selection. In the early days of molecular biology, following the discovery of large amounts of genetic variation in natural populations, there was substantial debate about the extent to which such variation was exposed to selection. Ayala & Anderson (1973) is an elegant experimental study demonstrating directional selection on allelic variants in Drosophila. There are many such similar studies, some reviewed by Hedrick et al (1976) and more cently by Mitton (1997). More recently genomic methods have been brought to bear on the question of the extent of selection at the genetic level. This is a rapidly developing field. Some of the best examples come from studies of human genomic data (e.g. Sabeti et al, 2006; Pickrell 2009), but the methods are being increasingly applied to non-model organisms (e.g. Albertson et al, 2003). Although powerful, these methods are not without difficulty, because it is possible to confuse the signature of directional selection with effects that arise from population structure (Przeworski, 2002).

Ayala & Anderson 1973 Ayala, F. J. and W. W. Anderson 1973. Evidence of natural selection in molecular evolution. *Nature-New Biology.* 241**,** 274-276. .
An elegant experimental study demonstrating directional selection on allelic variants in Drosophila

Hedrick, P. W. et al. 1976. Genetic polymorphism in heterogeneous environments. *Annual Review of Ecology and Systematics.* 7**,** 1-32. .
A review of the evidence of selection on genetic polymorphisms from early studies of both phenotypic and allozyme variation.

Mitton, J. B. 1997. Selection in natural populations. 240. Oxford: Oxford University Press.
A review and synthesis of studies of selection on genetic variation and protein polymorphisms in natural populations, and why this comes about. The approaches described have been outdated by the modern march to use genomic methods, but the book documents many classic and easily understood examples.

Sabeti, P. C. et al. 2006. Positive natural selection in the human lineage. *Science.* 312**,** 1614-1620. .
Provides a review of methods for the detection of positive (directional) selection using genetic markers, summary of evidence from older studies of humans using single markers and new data from the whole human genome.

Pickrell, J. K. et al. 2009. Signals of recent positive selection in a worldwide sample of human populations. *Genome Research.* 19**,** 826-837. .
Further evidence of positive selection in the human lineage from a very wide geographical sample.

Albertson, R. C. et al. 2003. Directional selection has shaped the oral jaws of Lake Malawi cichlid fishes. *Proceedings Of The National Academy Of Sciences Of The United States Of America.* 100**,** 5252-5257. .
An interesting paper that uses evidence from the analysis of quantitative genetic variation to infer the operation of directional selection in shaping the jaws of cichlid fish.

Przeworski, M. 2002. The signature of positive selection at randomly chosen loci. *Genetics.* 160**,** 1179-1189. .
A warning about detection of positive selection and its possible confusion with population structure

<u>Selection on correlated characters</u>
If phenotypic traits are correlated with each other (such as height and weight in humans), then directional selection on one trait can change the mean of the other. This can make it difficult to estimate the true strength of selection acting on any individual trait. Lande and Arnold (1983) provided a solution to this using multiple regression, which correctly estimates the strength of selection on individual traits, as long as other correlated traits under selection are also included in the analysis. Walsh & Lynch, give a useful graphical representation of this. A good example of the approach in predicting the course of microevolution is found in Grant & Grant (1995). Targets of selection can also be discovered by the experimental manipulation of traits. A good example is provided by Boberg & Agren (2009).

Lande, R. and S. J. Arnold 1983. The measurement of selection on correlated characters. *Evolution.* 37**,** 1210-1226. .
The original development of the standard mathematical methodology for estimating the strength of selection on individual traits, when several correlated traits have been measured. An enormously influential paper.

Walsh, B. and M. Lynch Evolution and Selection of Quantitative Traits: I. Foundations. Sinauer. http://nitro.biosci.arizona.edu/zbook/NewVolume_2/newvol2.html#2A
This monumental, encyclopaedic volume, which is not yet published, but available online, contains an astonishing wealth of material on the theoretical and empirical study of selection and evolution. Chapter 27 contains a useful consideration and graphical depiction of the problems inherent in studying correlated characters.

Grant, P. R. and B. R. Grant 1995. Predicting microevolutionary responses to directional selection on heritable variation. *Evolution.* 49**,** 241-251. .
Provides an example of estimating the strength of selection on correlated morphological characters in Galapagos finches, and the use of such estimates to predict short-term evolutionary change.

Boberg, E. and J. Agren 2009. Despite their apparent integration, spur length but not perianth size affects reproductive success in the moth-pollinated orchid *Platanthera bifolia*. *Functional Ecology.* 23**,** 1022-1028. .

A paper which describes an experimental approach to investigate the importance of different parts of flowers in contributing to their reproductive success.

How strong is natural selection?

There are clearly many examples of directional selection affecting many different traits in a wide variety of circumstances. One question, which remains unresolved, has been 'how strong is selection?'. Darwin (1859) thought it must generally be rather weak, and this is an assumption that has underlain much evolutionary theory. Reviews of all of the studies of selection that have taken place at first suggested that directional selection might be quite strong (Endler 1986), then that it was generally weak (Kingsolver et al 2001, Hoekstra et al 2001), then that it certainly could be strong, but we may not really know, because of biases in its estimation (Hereford et al, 2004). Hersch and Phillips (2004) take up this point and make clear that empirical studies of selection often have limited sample size to detect selection, especially when traits are correlated. The way in which the strength of directional selection fluctuates through time has been reviewed by Siepielski et al (2009) although their conclusion of regular large fluctuations in selection has also been questioned on statistical grounds (Morrissey & Hadfield, 2012)

Endler, J. A. 1986. Natural Selection in the Wild. 336. Princeton, NJ: Princeton University Press.

The first review and synthesis of studies and concepts relating to natural selection in natural populations. It contains detailed consideration of the philosophy and methods for the study of natural selection. A seminal work.

Kingsolver, J. G. et al. 2001. The strength of phenotypic selection in natural populations. *American Naturalist.* 157**,** 245-261. .

The first of a pair of papers (see also Hoekstra et al 2001, below) which reviewed the strength of natural selection occurring in natural populations. This paper deals with the different modes of selection. The authors suggested that directional selection in natural populations is often weak.

Hoekstra, H. E. et al. 2001. Strength and tempo of directional selection in the wild. *Proceedings of the National Academy of Sciences of the United States of America.* 98**,** 9157-9160. .

The second paper of the pair (see Kingsolver et al 2001, above), which dealt explicitly with the strength of directional selection in wild populations.

Hereford, J. et al. 2004. Comparing strengths of directional selection: How strong is strong? *Evolution.* 58**,** 2133-2143. .

This paper questions Kingsolver et al's conclusion, on the basis that the comparison of selection estimates depends on the way in which they are standardised, and suggests that directional selection often appears to be very strong. They point out that this appearance may arise from biased estimation and discuss how such bias may come about.

Hersch, E. I. and P. C. Phillips 2004. Power and potential bias in field studies of natural selection. *Evolution.* 58**,** 479-485. .

The authors examine statistical problems and sources of bias in the estimation of the strength of selection, and make recommendations for future studies.

Siepielski, A. M. et al. 2009. It's about time: the temporal dynamics of phenotypic selection in the wild. *Ecology Letters.* 12**,** 1261-1276. .

A synthetic analysis of temporal variation in the strength of selection which concludes that changes in the strength, direction and form of selection in natural populations are common.

Morrissey, M. B. and J. D. Hadfield 2012. Directional selection in temporally replicated studies is remarkably consistent. *Evolution.* 66**,** 435-442. .
The authors question the conclusions of Siepielski et al (2009) on the basis of statistical details and show that selection appears to change little in strength when the uncertainty of estimates is taken into consideration.

Consequences

Change in phenotypic variance and the response to selection

Directional selection has consequences beyond the immediate change in trait means that occurs by definition. Another immediate change is that the variability ('variance') of traits under selection is decreased (Brodie et al 1995, Walsh & Lynch). This leads to the paradox of variation which is considered in more detail below. Most consideration of the consequences of directional selection has focussed on its role in producing evolution, the so called 'response to selection', which is also the desired result of artificial selection. Roff 1997, in his chapter 4, provides a good outline of the basics. More detail can be found in Walsh & Lynch. The 'breeder's equation' has commonly been used in the past for predicting the response to selection (a good example is found in Grant & Grant 1995), but its use has been criticised (Morrissey et al 2010), in favour of the Robertson-Price equation (Morrissey et al 2012, Walsh & Lynch).

Brodie, E. D. et al. 1995. Visualizing and quantifying natural selection. *Trends In Ecology & Evolution.* 10**,** 313-318. .
An explicit description of the different ways ('modes') in which natural selection can shape trait distributions.

Walsh, B. and M. Lynch Evolution and Selection of Quantitative Traits: I. Foundations. Sinauer. http://nitro.biosci.arizona.edu/zbook/NewVolume_2/newvol2.html#2A
This monumental, encyclopaedic volume, which is not yet published, but available online, contains an astonishing wealth of material on the theoretical and empirical study of selection and evolution. Chapters 12 to 15 provide a thorough consideration of predicting the response to selection.

Roff, D. A. 1997. Evolutionary Quantitative Genetics. 493. New York: Chapman & Hall.
A graduate level textbook dealing with the principles of quantitative genetics from an evolutionary perspective.

Grant, P. R. and B. R. Grant 1995. Predicting microevolutionary responses to directional selection on heritable variation. *Evolution.* 49**,** 241-251. .
Provides an example of estimating the strength of selection on correlated morphological characters in Galapagos finches, and the use of such estimates to predict short-term evolutionary change.

Morrissey, M. B. et al. 2010. The danger of applying the breeder's equation in observational studies of natural populations. *Journal Of Evolutionary Biology.* 23**,** 2277-2288. . Outlines the problems of using the breeders equation to predict the evolutionery response to selection in studies of natural (cf. artificial) selection

Morrissey, M. B. et al. 2012. The prediction of adaptive evolution: empirical application of the secondary theorem of selection and comparison to the breeder's equation. *Evolution.* 66**,** 2399-2410. .
Uses an empirical example to demonstrate the use of the Price-Robertson equation in predicting the response to directional natural selection in a wild population of sheep.

The paradox of variation

Because directional selection 'uses up' variation, its continuing action should result in very limited amounts of both genetic and phenotypic variation. The demonstration of abundant variation at the genetic level (e.g. Hubby & Lewontin, 1966) was met with surprise, while phenotypic variation surrounds us (see section on phenotypic variation above). Hence there is a paradox: variation is abundant despite widespread evidence of selection. Simple theory predicts at least that traits that are closely related to fitness should show less variation. Initial analyses seemed to suggest that this was true (Mousseau & Roff, 1987), but this was later questioned (Houle, 1992). There are in fact a wide range of reasons why variation can be maintained, despite the continuing action of directional selection. Barton & Keightley (2002) and Kruuk et al (2008) give further consideration to these issues

Hubby, J. L. and R. C. Lewontin 1966. A molecular approach to the study of genic heterozygosity in natural populations. 1. The number of alleles at different loci in Drosophila pseudoobscura. *Genetics.* 54**,** 577-594. .
The original demonstration of genetic variation in natural populations using gel electrophoresis, a foundation of the science of molecular genetics.

Mousseau, T. A. and D. A. Roff 1987. Natural selection and the heritability of fitness components. *Heredity.* 59**,** 181-197. .
An early synthesis of the extent of heritable variation in different kinds of traits in wild populations.

Houle, D. 1992. Comparing evolvability and variability of quantitative traits. *Genetics.* 130**,** 195-204. .
A further review of quantitative genetic variation in wild populations. Houle showed that although the heritability of traits closely related to fitness was low, yet they often have high additive genetic variance.

Barton, N. H. and P. D. Keightley 2002. Understanding quantitative genetic variation. *Nature Reviews Genetics.* 3**,** 11-21. .
A review of approaches and ideas relevant to understanding the genetic basis of phenotypic variation, from an evolutionary perspective.

Kruuk, L. E. B. et al. 2008. New Answers for Old Questions: The Evolutionary Quantitative Genetics of Wild Animal Populations. *Annual Review of Ecology Evolution and Systematics.* 39**,** 525-548. .
A review of the use of quantitative genetic techniques in natural populations to answer evolutionary questions e.g. about the maintenance of variability.

Rates of microevolution

Directional selection often results in evolution (e.g. see Hendry & Kinnison 1999) although this can take a long time to accumulate into substantial differences (Uyeda et al 2011). Directional selection can also result in evolutionary divergence between populations (e.g. Rieseberg et al 2002, Clegg et al 2002), which may contribute to speciation (Schluter 2000), although divergence does not necessarily proceed the whole way to speciation (Hendry 2009, Nosil 2009). Sometimes directional selection does not even result in evolution within a population, and there can be many reasons for this (Merila et al, 2001). This is considered further below.

Hendry, A. P. and M. T. Kinnison 1999. Perspective: The pace of modern life: Measuring rates of contemporary microevolution. *Evolution.* 53**,** 1637-1653. .
A review of methods for estimating of rates of microevolution in contemporary natural populations with inference about the rates themselves.

Uyeda, J. C. et al. 2011. The million-year wait for macroevolutionary bursts. *Proceedings Of The National Academy Of Sciences Of The United States Of America.* 108**,** 15908-15913. .
An analysis of rates of evolution of body size, showing that substantial evolutionary changes only accrue rather slowly.

Rieseberg, L. H. et al. 2002. Directional selection is the primary cause of phenotypic diversification. *Proceedings Of The National Academy Of Sciences Of The United States Of America.* 99**,** 12242-12245. .
The authors analyse data from many studies of quantitative trait loci and infer that divergence between populations is generally consistent with directional selection

Clegg, S. M. et al. 2002. Microevolution in island forms: The roles of drift and directional selection in morphological divergence of a passerine bird. *Evolution.* 56**,** 2090-2099. .
Patterns of morphological evolution in multiple island populations of a passerine bird are used to infer directional selection's involvement in divergence.

Schluter, D. 2000. The Ecology of Adaptive Radiation. *Oxford Series in Ecology and Evolution.* Oxford: OUP.
An excellent, accessible and highly influential book reviewing the involvement of ecology in adaptive radiation. Chapter 5 reviews the contribution of divergent selection to the accumulation of phenotypic differences between populations and closely related species.

Nosil, P. et al. 2009. Ecological explanations for (incomplete) speciation. *Trends In Ecology & Evolution.* 24**,** 145-156. .
A review that explores explanations for why divergence may not result in speciation.

Hendry, A. P. 2009. Ecological speciation! Or the lack thereof? *Canadian Journal Of Fisheries And Aquatic Sciences.* 66**,** 1383-1398. .
An interesting and provocative paper which suggests that the evidence for divergent selection resulting in speciation is not as strong as it seems.

Merila, J. et al. 2001. Explaining stasis: microevolutionary studies in natural populations. *Genetica.* 112**,** 199-222. .
Documents numerous examples where directional selection in the wild has failed to result in evolution, outlines possible explanations and describes methods for testing these.

What directional selection is not
Evolution may fail to occur because an association between trait and fitness that appears like directional selection is not, in fact, really directional selection. Robertson (1968) makes the point that traits and fitness are just different measures of an organism's phenotype, and that an association can arise between the two for developmental reasons. In such situations (which are likely to be common when continuous phenotypic characters are of interest), the trait is not causing the variation in fitness, and there may be no selection taking place. De Jong (1994) takes up this point and elaborates on it philosophically and theoretically. A similar situation arises when environmental variation results in a correlation between trait and fitness, a point first made clear by Fisher (1930) and developed by Price et al (1988) to explain the specific case of a failure to evolve of breeding times in bird despite apparent directional selection which really arises because of variation in the condition of birds that nest at different times in the season. Rausher (1992) has made a similar

point for the situation when spatial variation gives rise to a trait – fitness correlation. A useful example of how environmental variation can give rise to the appearance of selection is given by Kruuk et al (2002).

Robertson, A. 1968. The spectrum of genetic variation. *In:* LEWONTIN, R. C. (ed.) *Population Biology and Evolution.* 5-16. New York: Syracuse University Press.
A very important, but overlooked, paper on the interpretation of what constitutes natural selection.

De Jong, G. 1994. The fitness of fitness concepts and the description of natural selection. *Quarterly Review of Biology.* 69**,** 3-29. .
A very thorough exploration of the concepts and definitions of fitness, and the consequences of these for the study of natural selection.

Price, T. et al. 1988. Directional selection and the evolution of breeding date in birds. *Science.* 240**,** 798-799. .
A theoretical model developed to explain lack of evolution of breeding date in birds, but with much wider application.

Rausher, M. D. 1992. The measurement of selection on quantitative traits - biases due to environmental covariances between traits and fitness. *Evolution.* 46**,** 616-626. .
Considers how environmentally induced correlations between phenotypic traits and fitness arise, giving the appearance of selection. Especially emphasises the role played by spatial variation in the environment.

Kruuk, L. E. B. et al. 2002. Antler size in red deer: Heritability and selection but no evolution. *Evolution.* 56**,** 1683-1695. .
An example, from a long-term study of red deer, in which a trait and fitness are correlated, suggesting directional selection, but in which the correlation comes about because of environmental effects on both trait and fitness.

Constraints on selection

<u>Selection but no evolution</u>

Even in the situation where what appears to be directional selection really is directional selection, evolution may not occur because of constraints on the process of selection. There are several different kinds of constraints. Merila et al (2001) Genetica is a useful introduction to these, while Kingsolver and Diamond 2011 provide an analytical review of the relative importance of some of them. More detailed consideration or examples of different kinds of constraints are given by: (1) Stearns (1989) for trade-offs. (2) Schluter and Smith (1986) for countervailing selection. (3) Gibbs and Grant (1987) and Milner et al (1999) for fluctuating selection. (4) Merila et al (2001) Nature for environmental deterioration.

Merila, J. et al. 2001. Explaining stasis: microevolutionary studies in natural populations. *Genetica.* 112**,** 199-222. .
Documents numerous examples where directional selection in the wild has failed to result in evolution, outlines possible explanations and describes methods for testing these.

Kingsolver, J. G. and S. E. Diamond 2011. Phenotypic Selection in Natural Populations: What Limits Directional Selection? *American Naturalist.* 177**,** 346-357. .
An analysis of selection from many studies that attempts to identify the factors that limit directional selection.

Stearns, S. C. 1989. Trade-Offs in Life-History Evolution. *Functional Ecology.* 3**,** 259-268. .
A clearly written review of the concepts and central relevance of trade-offs to the evolution of life-histories.

Schluter, D. and J. N. M. Smith 1986. Natural selection on beak and body size in the song sparrow. *Evolution.* 40**,** 221-231. .
A clear example of countervailing selection where larger values of a trait are favoured at one stage of the life cycle, and smaller values at another stage.

Gibbs, H. L. and P. R. Grant 1987. Oscillating selection on Darwin's finches. *Nature.* 327**,** 511-513. .
Documents substantial swings in the direction of selection on beak and body size in Galapagos finches.

Milner, J. M. et al. 1999. Repeated selection of morphometric traits in the Soay sheep on St Kilda. *Journal of Animal Ecology.* 68**,** 472-488. .
Documents large changes in the strength of directional selection in a population of wild sheep.

Merila, J. et al. 2001. Cryptic evolution in a wild bird population. *Nature.* 412**,** 76-79. .
The authors show that the evolution caused by selection may only just keep pace with changes of opposite effect caused by environmental deterioration.

<u>Conditions favouring evolution</u>
In contrast to the effort that has been invested in investigating the failure of directional selection to result in evolution, we know less about the conditions that favour evolution occurring. Reznick and Ghalambor (2001) suggest that a combination of directional selection and the opportunity for population growth are favourable to the occurrence of local adaptation, and Barrett and Schluter (2008) point out that adaptation occurs more rapidly from standing genetic variation than from new mutations, but these reviews beg the question of what conditions favour the occurrence of directional selection, about which we know almost nothing, although strong directional selection is likely to occur when organisms encounter novel environments (Reznick and Ghalambor, 2001). The importance of this in driving the explosive divergence seen in adaptive radiations is considered by Simpson (1944) and Schluter (2000).

Reznick, D. N. and C. K. Ghalambor 2001. The population ecology of contemporary adaptations: what empirical studies reveal about the conditions that promote adaptive evolution. *Genetica.* 112**,** 183-198. .
A review that explores the conditions promoting rapid adaptive evolution.

Barrett, R. D. H. and D. Schluter 2008. Adaptation from standing genetic variation. *Trends In Ecology & Evolution.* 23**,** 38-44. .
Most theory assumes that adaptation occurs through the fixation of new mutations. In this paper the authors consider the different patterns that can be expected when adaptation occurs from standing genetic variation.

Simpson, G. G. 1944. Tempo and Mode in Evolution. 237. New York: Hafner.
A important contribution to the modern synthesis. As a palaeontologist, Simpson was predominantly concerned with setting the link between selection, genetics and macroevolution on a firm footing. He was the first to apply the concept of adaptive landscapes to phenotypic characters. He saw directional selection (which he called ‘linear selection’) as instrumental in the gradual accrual of change in lineages.

Schluter, D. 2000. The Ecology of Adaptive Radiation. *Oxford Series in Ecology and Evolution.* Oxford: OUP.

An excellent, accessible and highly influential book reviewing the involvement of ecology in adaptive radiation. Chapter 4 describes the modern view of Simpson's ideas about adaptive radiation, including the relevance of environmental change in fuelling selection and adaptation.

Causes of selection

A better understanding of the conditions that favour directional selection might come from more in-depth study of the causes of selection. Ultimately directional selection occurs because of conditions in the environment that result in trait variation and fitness being associated with each other. The particular aspects of the environment that result in selection are called 'agents of selection' or 'selective agents', and much can be revealed about the workings of selection by the manipulation of environment. Clarke (1975) was the first to make this point. The importance of selective agents was touched on by Endler (1986), and examined in more detail by Wade & Kalisz (1990). MacColl (2011) has reviewed recent progress in this area, and made suggestions for how further work in this area could be rewarding.

Clarke, B. 1975. Contribution of ecological genetics to evolutionary theory - detecting direct effects of natural selection on particular polymorphic loci. *Genetics.* 79**,** 101-113. .
Clarke was mainly concerned with showing how selection on particular loci could be demonstrated unambiguously, but is worth reading for several points it makes about ways to improve understanding of the process of natural selection.

Endler, J. A. 1986. Natural Selection in the Wild. 336. Princeton, NJ: Princeton University Press.
The first review and synthesis of studies and concepts relating to natural selection in natural populations. It contains detailed consideration of the philosophy and methods for the study of natural selection. A seminal work.

Wade, M. J. and S. Kalisz 1990. The causes of natural selection. *Evolution.* 44**,** 1947-1955. .
An important and accessible paper which advocates the use of environmental manipulations better to understand how covariance between traits and fitness arise and why natural selection occurs.

MacColl, A. D. C. 2011. The ecological causes of evolution. *Trends In Ecology & Evolution.* 26**,** 514-522. .
A review and ideas paper, documenting progress in our understanding selective agents and suggesting ways in which further study of them could shed light on may problems in evolutionary ecology.

Natural versus artificial directional selection

Much of the foregoing material deals with different aspects of natural directional selection, but directional selection can also be artificially imposed, both for practical reasons, to improve domesticated plants and animals for human purposes, and academic ones, to further our understanding of the response to selection and the genetic architecture of phenotypic traits. The former topic is considered below, under 'Applications'. The remainder of this section deals with the latter. Textbooks on evolution usually contain sections on the use of artificial selection experiments in evolutionary biology, see for example Barton et al (2007) and Futuyma (2009). Bell (2008) contains a chapter that provides a useful and much more detailed consideration of artificial selection. An older review, containing references to many of the classic studies of artificial selection is Hill and Caballero (1992). The bristles of Drosophila fruitflies have often been the character of choice in artificial selection experiments. Mackay & Lyman (2005) is a thorough review of these. Artificial selection experiments have generally been used by evolutionary geneticists to explore the genetic architecture of continuous phenotypic traits, but they can also be useful in evolutionary biology for those seeking to understand trade-offs (see Kraaijeveld & Godfray, 1997) and more widely to evolutionary ecologists (Conner 2003).

Barton, N. H. et al. 2007. Evolution. 833. New York: Cold Spring Harbor Laboratory Press.
Well illustrated undergraduate text book with good basic introduction to directional selection. Lack of referencing makes it difficult to follow up on examples in detail. Very useful glossary.

Futuyma, D. J. 2009. Evolution. 633. Sunderland, MA: Sinauer Associates.
The latest edition of the standard undergraduate textbook for evolution. Contains introductory material on directional selection.

Bell, G. 2008. Selection: the Mechanism of Evolution. 2nd ed. Oxford: Oxford University Press.
A very useful advanced textbook providing thorough and detailed consideration of the operation of selection in the evolution of adaptation. Examples are biased to microbial systems. Concentrates on the evolutionary consequences, rather than the ecological context, of selection, although it includes interesting material on the latter.

Hill, W. G. and A. Caballero 1992. Artificial selection experiments. *Annual Review of Ecology and Systematics.* 23**,** 287-310. .
A thorough review of what artificial selection experiments have revealed about evolutionary genetics.

Mackay, T. F. C. and R. F. Lyman 2005. Drosophila bristles and the nature of quantitative genetic variation. *Philosophical Transactions of the Royal Society B-Biological Sciences.* 360**,** 1513-1527. .
Reviews studies that have carried out directional selection on Drosophila bristles.

Kraaijeveld, A. R. and H. C. J. Godfray 1997. Trade-off between parasitoid resistance and larval competitive ability in Drosophila melanogaster. *Nature.* 389**,** 278-280. .
Uses artificial selection on resistance to demonstrate the cost of resistance that arises from a trade-off with larval perfomance in Drosophila.

Conner, J. K. 2003. Artificial selection: A powerful tool for ecologists. *Ecology.* 84**,** 1650-1660. .
A consideration of the usefulness of artificial selection, normally applied to problems in evolutionary genetics, for addressing questions in evolutionary ecology

Applications

Crop and livestock improvement

Directional selection has been long practised by humans in the pursuit of improved yield of crops and better traits of animals. Darwin (1890) was the first to document the importance of selection in the domestication of plants and animals. A good recent overview of the patterns that occur in domestication is by Diamond (2002). Ross-Ibarra et al (2007) and Purugganan & Fuller (2009) are more detailed recent reviews of the domestication of plants by humans. Driscoll et al (2009) provide a similar review for domestic cats and dogs.

Much of the artificial selection carried out by humans during domestication has gone undocumented, but there are now long-running experiments that have used directional selection to improve crops, most notably maize (corn). The ‘Illinois Long Term Selection Experiment’ has been running for more than a century. What it has revealed about the genetics of adaptation was reviewed by Laurie et al (2004), but such experiments also provide a powerful resource for modern genomic studies to reveal the workings of directional selection (see

Moose et al. 2004). Rubin et al (2012) is one of several studies that use genomic data to provide evidence of directional selection during domestication of animals.

Darwin, C. 1868. The Variation of Animals and Plants unde Domestication. London: John Murray.
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<u>Medicine</u>

Although directional selection does not have direct application to modern medicine, yet an understanding of it is very relevant to the interpretation of important problems such as the emergence of drug resistance and the evolution of virulence among many deadly diseases. The usefulness of evolutionary thinking to medicine in general was first reviewed by Williams and Ness (1991). Substantial new information, focussing on infectious disease, was collated by Ewald (1994). An accesible popular article is Nesse and Williams (1998).

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