

Phenotypic selection in natural populations: what have we learned in 40 years?

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Abstract

In 1983, Russell Lande and Stevan Arnold published “*The measurement of selection on correlated characters*,” which became a highly influential citation classic in evolutionary biology. This paper stimulated a cottage industry of field studies of natural and sexual selection in nature and resulted in several large-scale meta-analyses, statistical developments, and method papers. The statistical tools they suggested contributed to a breakdown of the traditional dichotomy between ecological and evolutionary time scales and stimulated later developments such as “eco-evolutionary dynamics.” However, regression-based selection analyses also became criticized from philosophical, methodological, and statistical viewpoints and stimulated some still ongoing debates about causality in evolutionary biology. Here I return to this landmark paper by Lande and Arnold, analyze the controversies and debates it gave rise to and discuss the past, present, and future of selection analyses in natural populations. A remaining legacy of Lande & Arnold, 1983 is that studies of selection and inheritance can fruitfully be decoupled and be studied separately, since selection acts on phenotypes regardless of their genetic basis, and hence selection and evolutionary responses to selection are distinct processes.

Keywords: agents of selection, environmental covariance, fitness, multivariate selection, phenotypic traits, quantitative genetics

Natural selection is not evolution (Fisher, 1930).

Natural selection acts on phenotypes, regardless of their genetic basis, and produces immediate phenotypic effects within a generation that can be measured without recourse to principles of heredity or evolution. In contrast, evolutionary response to selection, the genetic change that occurs from one generation to the next, does depend on genetic variation. (Lande & Arnold, 1983).

In 1983, Russell Lande and Stevan Arnold published “*The measurement of selection on correlated characters*” in *Evolution*, which became one of the most cited papers in this journal (Lande & Arnold, 1983). The first author was the young evolutionary biologist Lande, who had made a name by himself from his work beginning with a key paper in 1976 (Lande, 1976). Lande took statistical tools from the plant and animal breeding literature and merged them with the paleontologist George Gaylord Simpson’s version of the adaptive landscape for phenotypic characters, thereby giving birth to a new discipline: evolutionary quantitative genetics (Arnold et al., 2001; Lande, 1976, 1977, 1979, 1980a, 1980b; Svensson & Calsbeek, 2012). The second author was Arnold, a herpetologist and field biologist interested in animal behavior (Arnold, 1983). In their paper, Lande and Arnold introduced regression analysis as a novel tool to estimate selection simultaneously on multiple phenotypic characters in the field, provided that individual fitness data could be connected to individual trait variation.

Central to the new approach proposed by Lande and Arnold was that selection and inheritance were empirically separable and distinct processes. Thus, estimating selection

on a character does not require any information about the genetic basis of the trait. Indeed selection can operate on traits without any heritable basis at all, although then there will of course be no evolutionary change. This insight was not entirely new; the first sentence in the mathematical population geneticist Fisher’s classical book “*The Genetical Theory of Natural Selection*” (Fisher, 1930) states something similar (see quotation above): selection is a within-generation process whereby some phenotypes are more successful than others, whereas evolution by natural selection is the transmission of such selection to the next generation, which requires that phenotypes are at least partly heritable (Lewontin, 1970). This key point made by Lande’s former doctoral advisor Richard Lewontin was re-emphasized by Lande and Arnold, but was not entirely new. This message had been made explicit already in 1948 in a pioneering paper in one of the first issues of the new journal *Evolution* by Michael Lerner and Everett Dempster. They made an explicit analogy between plant and animal breeding and evolution, and they suggested that insights from the former literature could be used to study selection in natural populations (Lerner & Dempster, 1948). However, Lerner and Dempster’s paper seemed to have been largely forgotten in 1983 (and was interestingly not cited by Lande and Arnold), so Lande and Arnold re-introduced their idea to introduce and methods from the breeding literature to the evolutionary biology community. The Lande and Arnold paper also proposed solutions for how to estimate selection on several characters simultaneously, when characters were correlated with each other, as well as suggestions of how to estimate nonlinear selection.

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Here, I discuss the scientific legacy of the paper by Lande and Arnold, the discussions it gave rise to, and the criticisms their approach encountered. I also briefly suggest some profitable future directions of phenotypic selection studies in natural populations in light of the many methodological and statistical advancements that have been made in the four decades since 1983. The title of the present paper has been inspired by similar titles of *Perspectives in Evolution* on reproductive isolation and speciation (Gavrilets, 2003; Rice & Hostert, 1993). My rationale is that it often takes several decades to evaluate the impact of papers in a slow-moving and largely conceptual field like evolutionary biology.

The new approach proposed by Lande and Arnold

The importance of Lande and Arnold's paper for studies of selection on multiple characters simultaneously (multivariate selection) cannot be overstated. Before their paper, field biologists had typically estimated selection in a univariate fashion and on a trait-by-trait basis (Boag & Grant, 1981; Endler, 1986). Estimating the strength of selection on a single character is relatively straightforward and can be done using the linear selection differential (Falconer, 1989; Figure 1A). When selection operates on a single trait, the evolutionary response to selection (R) is simply the selection differential (S) times the heritability (h^2) following the classical breeder's equation in quantitative genetics:

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

When selection operates on a single trait, the evolutionary response to selection (R) is therefore perfectly aligned with the direction of selection (S) and the population will move directly to the closest adaptive peak, the rate of evolution only being limited by the additive genetic variance which is part of h^2 (h^2 is the additive genetic variance V_a divided by the phenotypic variance V_p , i.e., V_a/V_p ; Figure 1A).

However, when traits are correlated with each other, the population will not necessarily follow a straightest path towards the closest adaptive peak, although it might eventually end up there (Figure 1B). Instead, when traits are correlated, the rate of adaptive evolution towards the optimum will be delayed and the population will follow a curved trajectory through phenotype space (Schluter, 1996; Figure 1B). In the case of such multivariate selection on two or more traits, the individual fitness surface (W) can be estimated as (from equation 3 in [Phillips & Arnold, 1989], modified from Equation 16 in [Lande & Arnold, 1983]):

$$W = \alpha + \sum_{i=1}^n \beta_i z_i + \sum \frac{1}{2} \gamma_{ii} z_i^2 + \sum_{i < d} \sum_d \gamma_{ij} z_i z_j + \epsilon \quad (2)$$

Here, W is relative fitness (absolute fitness divided by mean absolute fitness), α is a constant (an intercept in a multiple regression), β_i is the directional selection gradient for trait z_i , γ_{ii} is the quadratic selection gradient (indicating concave or convex selection) for trait z_i , γ_{ij} is the quadratic selection gradient for trait interactions between z_i and z_j (indicating correlational selection) and ϵ is an error term. These selection gradients can be obtained from the partial regression

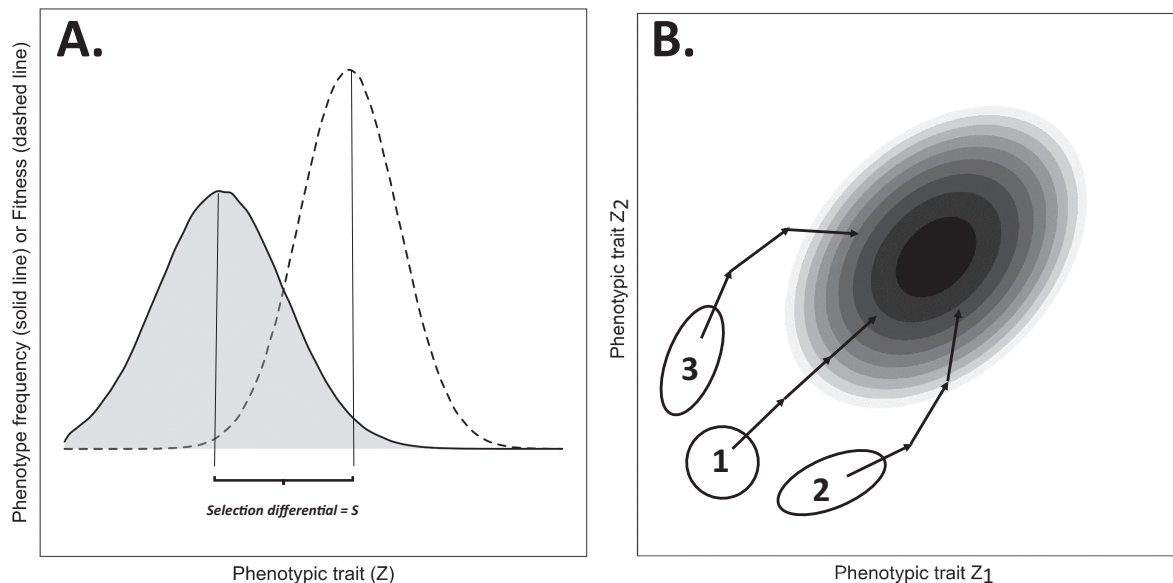


Figure 1. Illustration of the difference between univariate selection and multivariate selection and the effects of correlations between traits on the latter. (A) Univariate selection on a single trait towards a fitness optimum. Here, the selection differential (S) is simply the distance between the population trait mean and the location of the fitness optimum, which can both be estimated. The selection differential can either be expressed as the absolute distance in units of the scale on which the trait is measured (e.g., grams in the case of body mass) or be standardized with either the standard deviation (Lande & Arnold, 1983) or the phenotypic mean (Hereford et al., 2004). (B) Multivariate selection towards a joint fitness optimum (showed in gray shading) determined by two phenotypic traits (Z_1 and Z_2). Three different populations with different initial locations and multivariate phenotypes are shown (Populations 1–3) and these populations also differ in their trait correlations. In population 1, there is no correlation between Z_1 and Z_2 , which is shown as spherical ellipse depicting the population variation. In this case, the population evolves as if selection operates independently on the two traits and it climbs straight up towards the fitness peak. In contrast, in populations 2 and 3, Z_1 and Z_2 are correlated with each other, meaning that both direct selection on each trait and indirect selection operates. When trait covariation is not aligned with the direction of maximum fitness, the consequences of this is that the populations will follow curved trajectories through phenotype space, and evolution towards the optimum will be delayed, compared to the univariate case (Lande & Arnold, 1983; Schluter, 1996).

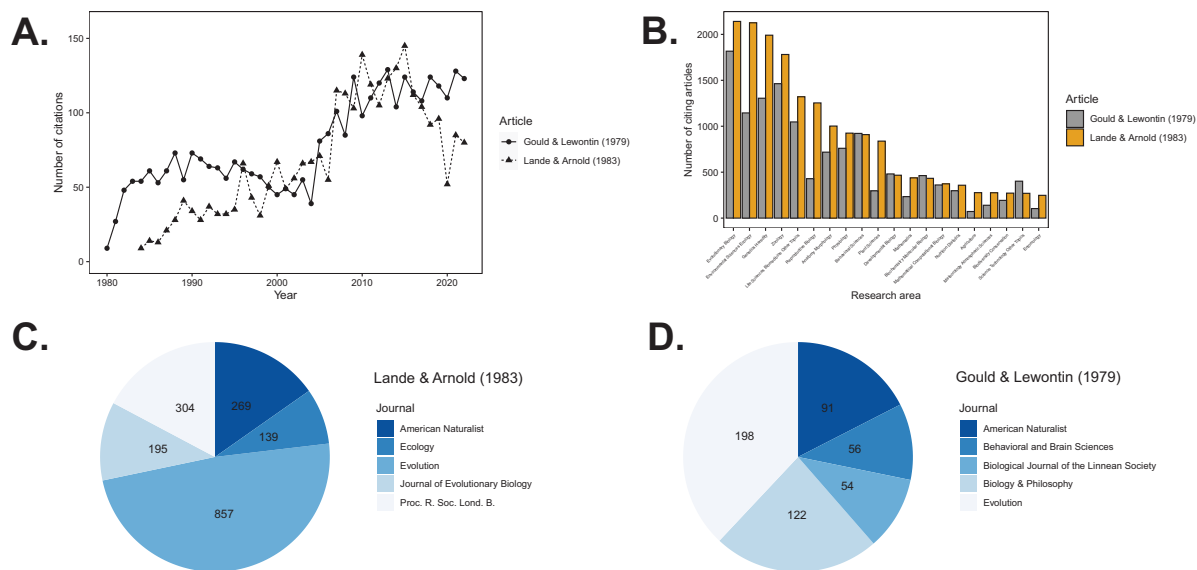


Figure 2. Accumulated citation statistics over different years (1979–2022) and influences on various fields (ecology, evolutionary biology, philosophy of science etc.) for Lande and Arnold (1983) and Gould and Lewontin (1979). Data obtained from a Web of Science (WoS) search in November 2022. (A) Annual number of new citations for both these papers. Note that although Lande and Arnold (1983) was published four years later than Gould and Lewontin (1979) it did soon catch up, and for most of the last four decades they have been cited equally many times. (B) Number of citations to Lande and Arnold (1983) from different research areas (as defined by WoS). Note that a single paper can be classified in to multiple areas so the numbers in each category are overlapping. Shown are citations to the same research areas for Gould and Lewontin (1979) for comparison. Lande and Arnold have been cited more than Gould and Lewontin (1979) in evolution, environmental science/ecology, zoology, and in applied research areas like plant sciences and agriculture, in spite of being published four years later. (C–D) Top five scientific journals among the papers that cited Lande and Arnold (1983) vs. Gould and Lewontin (1979). Note that citations to Lande and Arnold (1983) are dominated by five leading journals in ecology and evolution (*American Naturalist*, *Ecology*, *Evolution*, *Journal of Evolutionary Biology* and *Proc. R. Soc. Lond. B.*), whereas Gould and Lewontin (1979) has also influenced other fields, as revealed by *Biology and Philosophy* representing almost a quarter of the citations from the top five journals in which this paper was cited ($N = 122$; 23%).

coefficients in a standard parametric multiple regression (Lande & Arnold, 1983). Note that to obtain the quadratic selection coefficients (i.e., stabilizing and disruptive selection), the partial regression coefficient in front of the term γ_{ij} should be multiplied by two (Stinchcombe et al., 2008).

Historical context: the influence of the Spandrels paper by Gould and Lewontin

An adaptationist programme has dominated evolutionary thought in England and the United States during the past 40 years. It is based on faith in the power of natural selection as an optimizing agent. It proceeds by breaking an organism into unitary ‘traits’ and proposing an adaptive story for each considered separately. (Gould & Lewontin, 1979).

Critiques of the “adaptationist program” (Gould & Lewontin, 1979; Lewontin, 1978) stress that adaptation and selection are often invoked without strong supporting evidence. We suggest quantitative measurements of selection as the best alternative to the fabrication of adaptive scenarios...The essential fact is that selection and adaptation can be measured. (Lande & Arnold, 1983).

In motivating their study, Lande and Arnold referred to Stephen Jay Gould’s and Richard Lewontin’s famous paper “*The Spandrels of San Marco and the Panglossian Paradigm: A Critique of the Adaptationist Programme*” that was published only four years earlier (Gould & Lewontin, 1979). They refer to this paper on the first page in their introduction.

The Spandrels-paper is a highly cited paper in evolutionary biology; more cited than Lande and Arnold (1983), although it has also had four more years to accumulate citations (Figure 2A). Obviously, Lande and Arnold motivated their new approach to estimate selection with an aim increasing the scientific rigor in evolutionary biology. It was precisely this lack of rigor that Gould and Lewontin had criticized when they argued that many biologists just presented adaptive “Just So”-stories without strong evidence (Gould & Lewontin, 1979). Lande and Arnold clearly thought that this new method where selection could be estimated and quantified, rather than just vaguely inferred, they would increase rigor and empirical standards, thereby responding to the criticism by Gould and Lewontin. Thus, Lande and Arnold saw selection analyses as a constructive solution to the problem of documenting adaptation and selection.

General impact

Lande and Arnold’s paper had a huge impact, judged by the number of citations following its publication in 1983, particularly in ecology and field studies of selection (Figure 2A). Compared to the Spandrels paper published four years earlier, its main impact has been in empirical studies in ecology, evolution, plant sciences, and agriculture. In contrast, Gould and Lewontin’s paper has had less influence on empirical research in ecology and population biology but has instead influenced other areas of evolutionary biology, developmental biology, and philosophy of biology (Figure 2B–D). Their paper gave rise to a flurry of selection studies in natural populations. This increasingly popular research approach was

even jokingly called “*The Chicago School of Evolutionary Biology*” (Grafen, 1988), alluding to the neoliberal economic school led by Milton Friedman that thrived simultaneously at the same university.

Empirical applications: why were Lande and Arnold so successful?

...natural selection is daily and hourly scrutinising, throughout the world, every variation, even the slightest; rejecting that which is bad, preserving and adding up all that is good; silently and insensibly working, whenever and wherever opportunity offers, at the improvement of each organic being in relation to its organic and inorganic conditions of life. We see nothing of these slow changes in progress, until the hand of time has marked the long lapse of ages. (Darwin, 1859).

The success and popularity of the new approach suggested by Lande and Arnold was probably not only because they provided the formal theory behind selection analyses but also because they demonstrated empirical and statistical solutions of how to quantify selection in natural populations. They provided two worked-through empirical examples illustrating their new method. First, they used an old dataset on the mortality of House Sparrows (*Passer domesticus*) that were found dead after a winter storm and that were collected by Hermon Bumpus and which was compared with live individuals (Bumpus, 1899). They complemented this with a new and similar dataset collected by Arnold along the shores of Lake Michigan on the mortality of pentatomid bugs (*Euschistus variolarius*), also following a storm. Both these datasets were so-called cross-sectional fitness data, as opposed to longitudinal data, where individuals are followed throughout their lives. Selection on different phenotypes is thus estimated by comparing survivors and nonsurvivors or comparing mated and nonmated individuals (in the case of sexual selection). Such cross-sectional selection analyses have been carried out many times afterwards (Campbell-Staton et al., 2017; Svensson & Friberg, 2007; Young et al., 2004) and they are often the only practical alternative available to estimate selection. In contrast, longitudinal data using life-time reproductive success (LRS) are only possible to obtain for a limited number of species, usually long-lived vertebrates where researchers can mark individuals and follow them over their entire lives (Grafen, 1988).

Using the cross-sectional fitness data on mortality, Lande and Arnold estimated the variance-standardized directional selection gradients (β :as) on size-related morphological traits to vary between -0.27 and -0.52 for size in the House Sparrows (i.e., selection for smaller birds) and between -0.74 (wing length) and 0.58 (thorax) in the bugs (Lande & Arnold, 1983). These surprising findings indicated unexpectedly strong selection. These estimates indicated that relative fitness would change between 27% and 74% for a change in standard deviation of these traits experiencing selection.

It is important to underscore how unexpected these results were in this era when the neutral theory in population genetics was well-established (Kimura, 1983) and when many were increasingly skeptical of the pervasiveness of natural selection. Neutral theory was preceded by and partly stimulated by a paradox discussed by the population geneticist

J. B. S. Haldane's about the demographic “costs of selection” (Haldane, 1937, 1957). Other findings of strong selection at about the same time as Lande and Arnold's paper was published (Boag & Grant, 1981) raised the question how populations could persist in the long run in the face of such strong selection. As Lande and Arnold noted themselves, the persistence of a population in the long run requires that the total selective mortality should not exceed the reproductive rate, otherwise the population would go extinct (Lande & Arnold, 1983). They suggested that a solution to this dilemma is that most of the directional selection within a generation may be concentrated in a few relatively short periods of mortality (Lande & Arnold, 1983), whereas during other periods or in other generations selection might be weak or even nonexistent, allowing the population to recover demographically.

Research in the decades after Lande and Arnold have also revealed strong directional selection and sometimes rapid evolutionary change after brief intense selective episodes, such as winter storms (Campbell-Staton et al., 2017), in response to anthropogenic disturbances such as traffic (Brown & Brown, 1998; Price et al., 2000), hunting or fishing pressure (Allendorf & Hard, 2009; Campbell-Staton et al., 2021; Sanderson et al., 2022), or when organisms invade novel environments, such as cities (Santangelo et al., 2022). Natural or sexual selection is often strong, driving rapid evolutionary change in response to new predators, or when organism invade novel selective environments (Endler, 1980; Hendry & Kinnison, 1999; Reznick et al., 1997; Svensson, 2019; Svensson & Gosden, 2007).

The later emerging field of “eco-evolutionary dynamics” can also partly be traced back to the influence of Lande and Arnold and a growing awareness that evolutionary and ecological time scales are often similar and therefore that ecological and evolutionary processes interact and feedback on each other (Hendry, 2016; Schoener, 2011; Svensson, 2019). This is a marked change from 1983 when ecology and evolution were still largely separate fields. Back in 1983, it was often assumed that ecological processes were fast, relatively to evolutionary processes, and that therefore ecologists could largely ignore evolutionary processes in their day-to-day research. A central message from Lande and Arnold was that studies of selection, inheritance, and evolutionary response to selection are conceptually different and can be separated which made it possible for ecologists who only had access to data on fitness components and phenotypic trait data of individuals to contribute to the evolutionary literature by estimating selection using the common currency provided by evolutionary quantitative genetics (Barton & Turelli, 1989; Hansen & Pélabon, 2021; Lynch & Walsh, 1998; Walsh & Lynch, 2018). Lande and Arnold might have contributed to breaking up the borders between the still separated fields ecology and evolutionary biology. It is worth underscoring that both Laurent Slobodkin, author of *Growth And Regulation of Animal Populations* (Slobodkin, 1961) and Eric Pianka, author of *Evolutionary Ecology* (Pianka, 1988) were two out of several authors of influential ecology text books who emphasized the distinction between ecological and evolutionary time scales. This dichotomy only started breaking down several decades after Lande and Arnold (1983), catalyzed by an influential paper by Thomas Schoener and the growing field of eco-evolutionary dynamics (Schoener, 2011; Svensson, 2019).

Before Lande and Arnold, there were very few formal selection studies in natural populations and no studies estimating multivariate selection, simply because biologists did not have any statistical tools to carry out such studies. The major architects of the Modern Synthesis (primarily Mayr and Dobzhansky) argued for the pervasive role of natural selection as a major evolutionary process but interestingly none of them estimated selection themselves, presumably because they considered selection to be too weak for such an effort to be worthwhile (Antonovics, 1987; Endler & McLellan, 1988). Thus, it took almost four decades after the Modern Synthesis and after 1983 before biologists regularly started to estimate selection in natural populations. Presumably, many biologists—even those confident about the power of natural selection and its ability to evolutionarily transform populations—still implicitly adhered to Darwin's view that natural selection was a too slow process so that it could only be inferred, but not observed directly (Darwin, 1859).

How representative were these strong selection gradients documented by Lande and Arnold? In the first major meta-analysis of published selection gradients in nature, Kingsolver and colleagues found that the average variance-standardized selection gradient across thousands of studies was 0.16 (Kingsolver et al., 2001b). Thus, relative fitness is expected to change by 16% for each standard deviation in a trait, indicating considerable evolutionary potential of natural populations, under the assumptions that traits are at least partly heritable, which they almost always are (Lynch & Walsh, 1998; Mousseau & Roff, 1987; Walsh & Blows, 2009). Issues have been raised, however, about the utility of the variance-standardized selection gradient and it has been proposed that the mean-standardized selection gradient is more appropriate (Hansen & Pélabon, 2021; Hereford et al., 2004). A related methodological issue is at what spatial scale fitness should be relativized and traits should be standardized when one is interested in comparing selection among groups or populations (De Lisle & Svensson, 2017).

Another methodological issue is sampling error of the selection gradients. A rough estimate of the extent of sampling error can be obtained from temporal replicated selection studies (Morrissey & Hadfield, 2012). Analyses of a small subset of temporally replicated studies suggest that the mean variance-standardized selection gradient could be as low as 0.05 when sampling error is taken into account (Morrissey & Hadfield, 2012). However, in population genetic terms, this is still strong selection and would indicate high evolutionary potential of most populations, especially in combination with the existence of large amounts of additive genetic variances of most phenotypic traits as well as fitness itself (Bonnet et al., 2022; Mousseau & Roff, 1987). Finally, the issue about fluctuating selection that was raised by Lande and Arnold as an explanation of their findings has gained some subsequent empirical support (Calsbeek et al., 2012; Gibbs & Grant, 1987; Gosden & Svensson, 2008; Grant & Grant, 2002; Siepielski et al., 2009). However, it is still unclear how much of such observed fluctuations in selection that are due to sampling error *vs.* real fluctuations (Morrissey & Hadfield, 2012).

Criticisms and issues about causality

The question, “what is the causal relationship between fitness and the characters?” cannot be answered conclusively

by an observational approach, simply because the paths of causation, particularly for life-history traits and fitness itself, are so numerous. (Mitchell-Olds & Shaw, 1987).

The multivariate analysis of selection is insufficient for identifying the causal agents of selection. We discuss how the observational approach of multivariate selection analysis can be complemented by experimental manipulations of the phenotypic distribution and the environment to identify not only how selection is operating on the phenotypic distribution but also why it operates in the observed manner... The biotic and abiotic environment is the context that gives rise to the relationship between phenotype and fitness (selection). The analysis of the causes of selection is in essence a problem in ecology. (Wade & Kalisz, 1990).

In the decade following 1983, influential papers by Thomas Mitchell-Olds, Ruth Shaw, Michael Wade, and Susan Kalisz stand out in criticizing the regression approach to study selection (Mitchell-Olds & Shaw, 1987; Wade & Kalisz, 1990). These and other criticisms (Kingsolver & Schemske, 1991) did not only discuss technical and statistical issues but also raised the deeper question about causal inference. In particular, how can we know that a trait-fitness covariance relationship reflects a causal influence of the trait? It is important to note that the question about causality cannot be solved by statistical methods alone but would require additional biological and ecological data and ideally complemented with functional analysis, experiments, and natural history information (Figures 3–5).

Mitchell-Olds and Shaw (1987) emphasized that an observed selection gradient—even if statistically significant—would not in itself prove that the trait is target of selection, especially if the trait is correlated with other characters that are not included in the statistical analyses. They suggested that any documented selection gradient should be considered as a provisional hypothesis, in need of experimental verification. Experimental manipulations of suspected targets of selection—such as the sexually selected tail length in male widowbirds (Andersson, 1982) or egg size in lizards (Sinervo et al., 1992)—would complement any inferred selection on unmanipulated phenotypic variation (Figure 3). Alternatively, when traits could not be easily experimentally manipulated such as beak sizes in birds or body size, functional analyses (Opedal, 2021), and careful natural history observations are needed before any safe conclusions could be made (Mitchell-Olds & Shaw, 1987). Of particular concern are environmental covariances, such as when individuals vary in condition that independently affects both traits and fitness (Rausher, 2000). Such environmental covariances can lead to a false impression of directional selection on a trait (Price et al., 1988). One solution is to incorporate condition as a covariate in the selection analyses, in effect an additional trait (Rausher, 2000; Stinchcombe et al., 2002), although this is not always feasible. One can also try to verify causal relationships between traits using a combination path analysis, causal modeling, and/or structural equation modeling (Edelaar et al., 2022; Kingsolver & Schemske, 1991; Otsuka, 2019; Shipley, 2002). It is important to emphasize that the multiple regression approach proposed by Lande and Arnold is only a subset of all possible causal relationships between a set of traits and fitness (Figure 4). The underlying assumption in the multiple regression approach is that traits act on the same level in the biological

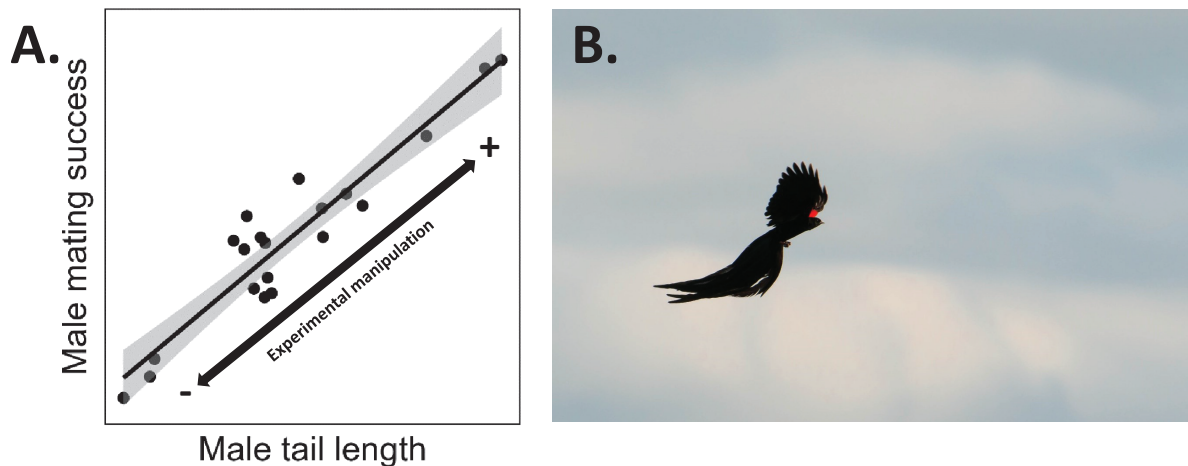


Figure 3. Illustrations of the problems of inferring causality when estimating selection using regression analysis on unmanipulated phenotypic variation. (A) Suppose we observed a positive relationship between male mating success and male tail length in a bird population. Such a positive correlation could indicate sexual selection for longer tails in this species, but ideally one would like to confirm any such putative selection by experimentally manipulating the trait (tail length) as the relationship could be caused by purely environmental covariance. For instance, males in high condition could be able to both grow long tails and achieve high mating success and the observed correlation could then reflect a noncausal spurious relationship (Mitchell-Olds & Shaw, 1987; Price et al., 1988; Rausher, 2000). (B) In the long-tailed widowbird (*Euplectes progne*) in Africa, such an experiment was actually carried out by Malte Andersson (1982), who experimentally manipulated tail length by cutting and gluing and showed that longer tails did indeed increase male mating success. Photograph from KwaZulu Natal (South Africa) by Erik Svensson.

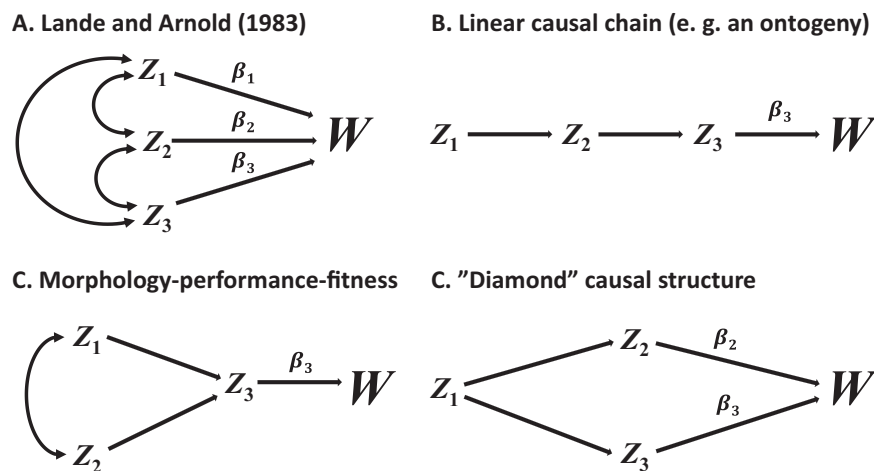


Figure 4. Hypothetical relationships between three phenotypic traits (z_1 – z_3) and fitness (W). (A) Lande and Arnold's multiple regression approach: These three traits can act at the same level of the biological hierarchy, where they all influence fitness direct (single-headed arrows from z_i to W). Such a causal structure makes it possible to estimate directional selection gradients when all three traits are included in a multiple regression analysis, and three separate directional selection gradients can then be estimated (β_i). In addition to direct selection on these three traits, traits can also indirectly influence fitness through noncausal covariances between the traits (double-headed arrows). (B–D) Alternative trait configurations that are not captured in the classical regression framework suggested by Lande and Arnold. These causal scenarios would require explicitly different models which are here visualized as different path models. (B) The three phenotypic traits can be linearly arranged, such as when the same trait is measured at different time points during ontogeny. Traits measured earlier in the ontogeny affect traits measured later in the ontogeny, but only the final trait affects fitness directly. (C) The "morphology-performance-fitness"-paradigm proposed by Arnold (1983). Here, two of the traits (e.g., two morphological traits; z_1 and z_2) affects some aspects of organismal performance or behavior, such as feeding rate (z_3) that is the direct target of selection and which causally influences fitness. Although only z_3 is under direct selection, the two underlying morphological traits are also causally affecting fitness, albeit indirectly through z_3 . (D) A "diamond" causal structure, where only two traits (z_1 and z_2) experience direct selection, but the third trait (z_3) is indirectly also influencing fitness through its effect on these two traits (e.g., some trait that operates earlier in ontogeny and with legacies up to the adult stage when selection operates on z_1 and z_2).

hierarchy (Figure 4A, cf. Figure 4B–D). Thus, the multiple regression approach is one specific causal model in a greater universe of alternative causal scenarios that can be captured by different path models (Figure 4).

Verifying the causality of trait-fitness covariance relationships is not sufficient, however, for a full understanding of selection. There is also the additional causal layer: the ecology of selection (MacColl, 2011; Wade & Kalisz, 1990). We thus

also need to know *why* the trait-fitness covariance relationship looks like it does, i.e. what is the *cause* of selection? This is an ecological question: what agents or environmental factors cause this fitness-trait covariance? Natural selection and sexual selection are processes that arise due to *interactions* between individual phenotypes and their local selective environments (Hull, 1980; MacColl, 2011; Wade & Kalisz, 1990). A full understanding of selection therefore requires not only

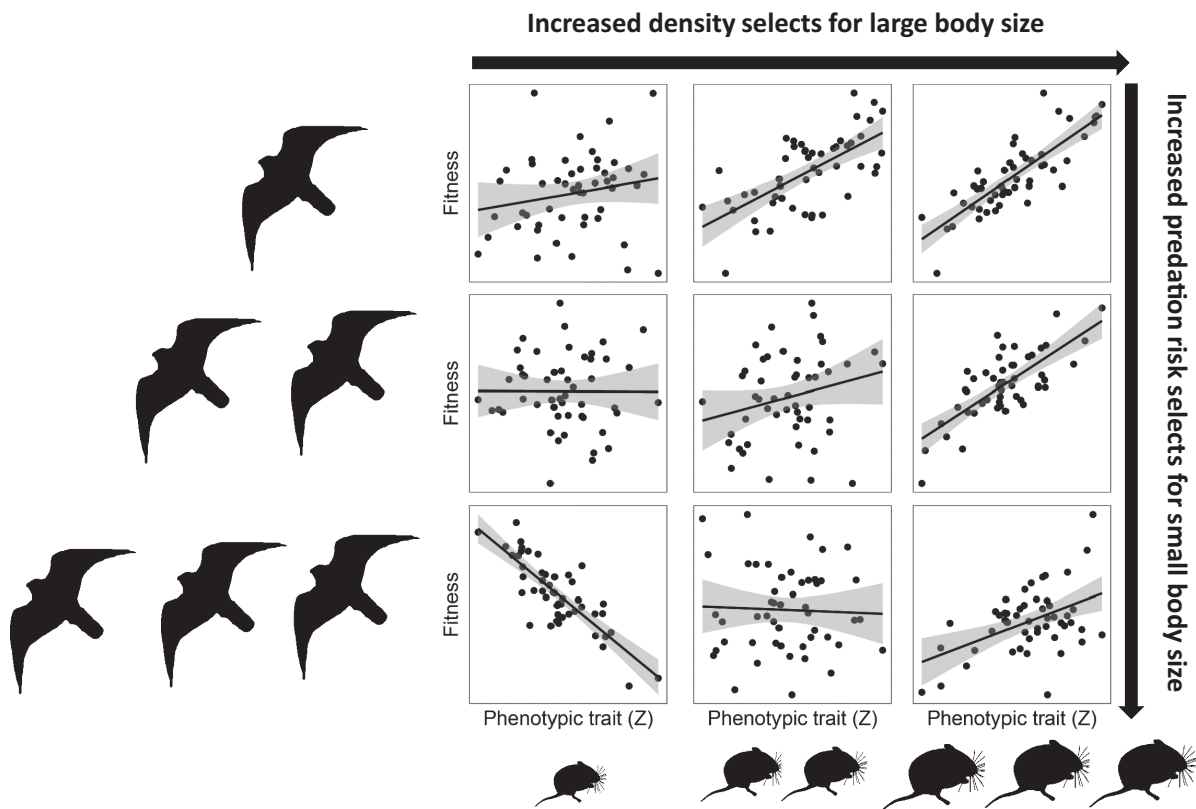


Figure 5. Conceptual illustration of the multiple levels of causality of selection, including the environmental drivers and ecological causes of selection. These multiple levels of causality encompass both the causality of trait-fitness covariances and how local selective agents causally shape trait-fitness covariances. A hypothetical example is shown where the selective environment varies along two dimensions: predation risk (vertical axis; shown as increasing number of birds of prey, in this case kestrels, *Falco tinnunculus*) and conspecific density (horizontal axis; shown as increasing number of voles, genus *Microtus*). The selective environment is typically multidimensional (White & Butlin, 2021), but for simplicity, I here illustrate only two environmental factors and agents of selection. It is assumed that higher predation risk favors smaller individuals, which is shown as weaker selection or even negative selection on body size with increasing predation pressure (from top to bottom). In contrast, higher conspecific density favors larger body size due to increased intraspecific competition, which is shown as steeper and more positive slopes of the fitness functions as one moves from the left to the right (and larger voles). Different combinations of predation and conspecific density can causally interact and shape local selective environments, resulting in different trait-fitness covariances in different populations. In this particular example, the selective environment is thus two-dimensional, but in nature selection is most likely multidimensional. The selective environment can also be described for both con- and heterospecific phenotype frequencies and the various social interactions that can arise from such interactions, sometimes in combination with path analytical tools (cf. Figure 4; see De Lisle et al., 2022; McGlothlin & Fisher, 2022; Wolf et al., 2001). This example illustrates the importance of measuring not only phenotypic traits and fitnesses, but also to quantify and (when possible) experimentally manipulate the local selective environments to gain a full understanding of selection. Silhouettes of the kestrels reproduced with permission from Rebecca Groom under the Creative Commons CC-BY 3.0 license (<https://creativecommons.org/licenses/by-sa/3.0/>) and voles obtained from Phylopic (<http://phylopic.org/>). Example inspired by Wade and Kalisz (1990).

knowledge about trait and fitnesses or even the causality of trait-fitness covariances, but also information about how ecological agents and causes of selection—such as competitors, mates, parasites, pollinators or parasites, or abiotic factors such as temperature and precipitation—give rise to trait-fitness covariances (MacColl, 2011; Opedal, 2021; Siepielski et al., 2017; Svensson & Sinervo, 2000; Wade & Kalisz, 1990).

Experimentally manipulating or measuring different selective environments across multiple populations provides a many logistical hurdles (Figure 5) as the selective environment is typically multidimensional (White & Butlin, 2021). It is considerably more challenging than simply manipulating individual phenotypes within a local population (Figure 3). The ecological causes of selection can be elucidated by using spatial or temporal—replication across multiple populations in space or time (MacColl, 2011). This can sometimes be achieved, but requires large sample sizes, often in the order of thousands of individual phenotypes (Gosden & Svensson, 2008; Svensson & Sinervo, 2004). In some

systems, experimental studies could be designed that manipulate *both* individual phenotypes *and* their local selective environments simultaneously, that is “double-level” manipulations (Sinervo & Basolo, 1996; Svensson & Sinervo, 2000). Experimental manipulations of selective agents such as removing plant herbivores (Mauricio & Rausher, 1997), plant pollinators (Sletvold et al., 2016), or changing the density or frequency of intra- or inter-specific competitors or predators (Calsbeek & Cox, 2010; Schluter, 1994, 2003; Svensson & Sinervo, 2000) can sometimes be carried out. In many cases, however, experimental manipulations of selective agents are practically impossible. In these cases, identifying the environmental drivers and causes of selection from temporally or spatially replicated selection studies adds to a deeper understanding of the ecology of selection (MacColl, 2011; Siepielski et al., 2017). It is also worth noting that an important source of bias in selection studies could be density, just as has been noted in behavioral ecology (Stamps, 2011): biologists measuring selection are likely to focus on

high-density populations simply for practical and logistical reasons and the need for large sample sizes.

In summary, Lande and Arnold stimulated some still ongoing discussions about causality in evolutionary biology and in philosophy of biology. These discussions include question at what level selection operates and whether there are “cross-over effects” between different levels (Heisler & Damuth, 1987; Okasha, 2006), whether natural selection is a force or only a statistical outcome of lower-level events and the fates of individual organisms (Endler, 1986; Otsuka, 2016; Sober, 1984; Walsh, 2015; Walsh et al., 2002) and whether genes (“replicators”) or phenotypes (“vehicles” or “interactors”) are the true targets of selection (Ågren, 2021; Dawkins, 1976; Hull, 1980; Lewontin, 1970). Many evolutionary biologists now view phenotypes as the true targets of selection, regardless of their heritable basis, in the spirit of Lande and Arnold (1983).

Alan Grafen's critique: adaptation vs. selection in progress

In making their claims for their methods, Arnold, Wade and Lande do not always distinguish clearly between the analysis of adaptation and the detection of selection in progress. It is clear, however, that the design of their methods is to detect selection in progress...I believe that most evolutionists and behaviorists would say they were primarily interested in adaptation, as opposed to selection in progress, once the distinction is brought to their attention. Their primary concern is why male red deer have such big antlers, not whether there are genes now changing in frequency that affect antler size...The methods of analysis of LRS data proposed by Wade & Arnold (1984), Lande & Arnold (1983), and Arnold and Wade (1984a,b) seem primarily designed to study selection in progress—that is to say, gene frequencies changing now rather than adaptation. (Grafen, 1988).

Did Lande and Arnold succeed in convincing Gould, Lewontin and other contemporary critics of naïve adaptationism? Not really, according to British theoretical biologist Alan Grafen (Grafen, 1988).

Grafen criticized the regression approach suggested by Lande and Arnold for failing to address what he claimed that most biologists really are interested in: adaptation and the current utility of traits (Grafen, 1988). He argued that their approach was more designed to detect selection in progress than to identify adaptations. Grafen criticized such a purely correlative approach, relying on unmanipulated variation in phenotypic traits and fitness, and he argued that biologists interested in adaptation should rather carry out manipulative experiments to clarify the adaptive significance of traits (if any). Grafen's criticism in a nutshell was thus that Lande and Arnold had conflated selection in progress (an evolutionary process) with adaptation (an optimum phenotypic state of a population) (Grafen, 1988). Following the logic of G. C. Williams (1966), he argued that fitness is a property of design, not a property of an individual, and that using too all-encompassing fitness measures such as Lifetime Reproductive Success (LRS) would not answer the question about the adaptive significance of traits that have their most important function during restricted parts of the life cycle, such as among juveniles or during mating (Grafen, 1988).

Grafen used a hypothetical example of the wing spots on the hindwing of the butterfly *Maniola jurtina* to illustrate his reasoning. He argued that the really interesting question was the adaptive significance of these hindspots, rather than if they were currently under selection, and he suggested that biologists would gain more insights by experimentally increasing or decreasing the number of spots instead of measuring natural variation in spot number or spot size, using Lande and Arnold's approach (Grafen, 1988). That is, evolutionary biologists should focus on current utility of traits, rather than on selection in progress.

Although Grafen's distinction between adaptation and current utility vs. selection in progress is important, it is not always that clearcut. Current utility of a trait implies that the current population trait mean (presumably located at some intermediate optimum) maximizes fitness, compared to alternative variants. This is just another way of saying that the trait is currently experiencing stabilizing selection, thus it is a claim about selection in progress! Moreover, Lande and Arnold's regression approach was not only designed to detect directional selection, but could also reveal stabilizing and disruptive selection (Lande & Arnold, 1983), so it is strange that Grafen did not embrace this complementary approach to experimental manipulations.

Behavioral ecologists in the British research tradition that Grafen represents tend to focus only on evolutionary endpoints and equilibria, asking questions like: “Is this trait adaptive?” but also tend to ignore the equally interesting question “How did the trait end up here?”. This obsession with evolutionary endpoints and the adaptive significance of traits is quite evident in the research tradition Grafen belongs to, where phenotypic models based on optimization theory and game theory are valued more highly than dynamic quantitative and population genetic models aimed to detect selection in progress. Many evolutionary biologists—the present author included—are more interested in selection in progress than if a trait is an adaptation (or not). Thus, Grafen's value-laden statement that evolutionary biologists are more interested in whether a trait is an adaptation than they are interested in selection in progress may well reflect his own cultural and scientific bias than the majority of the evolutionary biologists, but that is ultimately an empirical question for historians and sociologists of science to investigate. The historian Tim Lewens has characterized the British research tradition in behavioral ecology and phenotypic modeling as “Neo-Paleyan Biology” (Lewens, 2019), referring to the natural theologian William Paley who in the pre-Darwinian times saw adaptive design everywhere in nature, which he interpreted as a sign of God's designing ability. Paley made famous the analogy with a watchmaker, and Richard Dawkins openly expressed his admiration of Paley in his book “*The Blind Watchmaker*” (Dawkins, 1986). The provocative title demonstrates how Dawkins was largely in agreement with Paley that adaptive design is the important question in evolutionary biology. Neo-Paleyan biology today, according to Lewens and Arvid Ågren, is primarily alive in Britain, and with Dawkins, Grafen, and Andy Gardner as its main representatives (Ågren, 2021; Lewens, 2019). Neo-Paleyan biology can be characterized as a research program focused on the adaptive design and current utility of traits but with little interest in evolutionary history or selection in progress (Reeve & Sherman, 1993). However, the distinction between adaptation and selection in progress largely disappears if we realize that claims about

adaptation and current utility are also implicit claims about selection in progress, namely stabilizing selection around a current local optimum (Hansen, 1997).

Conclusion

Lande and Arnold's paper had a long-lasting impact on evolutionary biology, particularly in field ecological studies (Figure 2). It stimulated several discussions about the nature and limitations of statistical tools vs. experiments and general issues about causal inference (Figures 1–5) and it uncovered both the power but also the limitations of selection and adaptation. The main influence of their paper was providing a useful empirical tool that resulted in hundreds of field studies documenting and quantifying natural selection (Figure 2). This stimulated several influential meta-analyses that have enriched our understanding about the strength and variability of phenotypic selection in natural populations (Kingsolver & Diamond, 2011; Kingsolver et al., 2001b; Siepielski et al., 2009, 2011, 2013, 2017). Given this large body of empirical work, what remains to be done and what is the future of selection studies in natural populations? Five remaining challenges come to my mind.

First, measuring and analyzing individual phenotypes is time-consuming and a major bottleneck. New automated data collecting techniques and high-throughput phenotyping (“phenomics”) combining digital data with tools from machine learning and Artificial Intelligence, including Computer Vision can hopefully overcome some of the bottlenecks of limiting sample sizes in selection studies (Lürig et al., 2021). However, formidable challenges remain to quantify fitness or fitness components in the field.

Second, our knowledge about multivariate selection—including various forms of nonlinear selection—still lags behind our knowledge about directional selection. In particular, how common is stabilizing vs. disruptive selection? How common and strong is correlational selection, i.e., selection for trait combinations, compared to selection on traits in isolation and what are the genomic, developmental, and evolutionary consequences of such selection (Sinervo & Svensson, 2002; Svensson et al., 2021)? There is still no major meta-analysis of correlational selection, largely because this form of selection is seldom quantified in field studies, in spite of statistical tools being available (Blows, 2007; Blows et al., 2003, 2004; Phillips & Arnold, 1989; Svensson et al., 2021).

Third, what are the demographic and life-history consequences of phenotypic selection on individuals for population growth rate, extinction risk (Martins et al., 2018), or evolutionary rescue (Bell, 2017)? This is an area that is largely unexplored empirically, although the theoretical framework has been available for decades (Lande, 1982).

Fourth, how can we better integrate ecological selection studies in the field with research on phenotypic plasticity and development? A theoretical and analytical framework is available to quantify selection on function-valued traits (Stinchcombe & Kirkpatrick, 2012), such as reaction norm slopes and intercepts, but empirical studies are still few, largely because of the need of large sample sizes (Chevin et al., 2010; Kingsolver et al., 2001a; Lande, 2009; Svensson et al., 2020).

Finally, how can we connect short-term ecological studies of selection on fitness components to the macroevolutionary time scales that are the focus of phylogenetic comparative

studies (Uyeda et al., 2011)? In particular, how are phylogenetic signatures of multiple optima that are often interpreted as stabilizing selection (Beaulieu et al., 2012; Hansen, 1997) related to the estimates of stabilizing selection in microevolutionary studies? Solving these challenges will require close collaborations between experimental and comparative evolutionary biologists, empiricists, and theoreticians with complementary expertise.

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Data availability

The only data in this paper are from the citation analyses in Figure 2. These citation data are available on Dryad Digital Repository (<https://datadryad.org/stash>): <https://datadryad.org/stash/dataset/doi:10.5061/dryad.cjsxksnb6>.

Author contribution

E.I.S. came up with the idea to write this paper, carried out all the analyses, made all the figures and wrote the manuscript.

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