Supplementary Figure S1

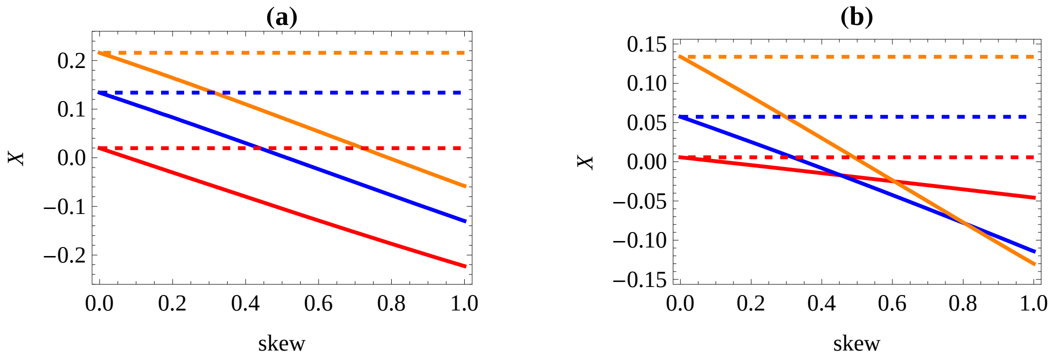

Figure S1. Equilibrium mean phenotype and mode of adaptive landscape. Solid lines display the equilibrium mean phenotype, obtained by solving eq. (2) in the main text, as a function of the skew of the phenotype distribution. The skewed Gaussian fitness surface (eq. (5) in the main text) is assumed. Therefore, the mode of the individual fitness surface is at 0. Dashed lines show the mode of the adaptive landscape. In Figure (a) the variance is fixed at $S = 0.25$, and the skew ψ of the individual fitness surface is varied as follows: $\psi = 0.5$ (red), $\psi = 1.5$ (blue), and $\psi = 10$ (orange). In Figure (b), $\psi = 1.5$ is fixed and the variance is varied: $S = 0.01$ (red), $S = 0.1$ (blue), $S = 0.25$ (orange). If $X > 0$, the mean is on the flatter shoulder of the individual fitness surface; if $X < 0$, it is on the steeper shoulder. The latter occurs only for sufficiently strong skew.

Supplementary Methods

Throughout, x indicates the trait value of an individual, X , S, and C_3 its mean, variance, and third cumulant (equal to the third central moment) in the population.

A complete account of the theory with all derivations is contained in the supplementary *Mathematica* notebook (Supplementary Data 1)..

Mode of adaptive landscape for asymmetric fitness surfaces

We investigate the influence of the shape of the individual fitness surface near its optimum on the displacement of the mode of the adaptive landscape from the optimum of the individual fitness surface. On each side of the optimum (assumed to be at 0 with value 1), we approximate the individual fitness surface $w(x)$ by a cubic polynomial as in eq. (3) in the main text. Because we require that w(0) = 1 is the maximum, we must have $a_1 \le 0$ and $b_1 \ge 0$. If $a_1 = b_1 = 0$ (so that $w(x)$ is differentiable at x=0), we require $a_2 < 0$ and $b_2 < 0$.

To calculate mean fitness (or the adaptive landscape), defined by $\bar{w}(X) = \int w(x)\, p(x)\, dx$, we assume a Gaussian trait distribution $p(x)$ with mean X and variance S. Then straightforward calculations yield the following expression for the mean fitness:

$$\bar{w}(X) = \frac{e^{-\frac{X^2}{2S}}\sqrt{S}\,\left(a_1 + a_2 X + a_3\left(2S + X^2\right)\right)}{\sqrt{2\pi}} + \frac{1}{2}\left(1 + a_1 X + 3 a_3 S X + a_3 X^3 + a_2\left(S + X^2\right)\right)\left(1 + \text{Erf}\left[\frac{X}{\sqrt{2}\sqrt{S}}\right]\right) - \frac{e^{-\frac{X^2}{2S}}\sqrt{S}\,\left(b_1 + 2 b_3 S + b_2 X + b_3 X^2\right)}{\sqrt{2\pi}} + \frac{1}{2}\left(1 + b_1 X + 3 b_3 S X + b_3 X^3 + b_2\left(S + X^2\right)\right)\text{Erfc}\left[\frac{X}{\sqrt{2}\sqrt{S}}\right]. \quad \text{(S1)}$$

To derive the condition for the mode of $\bar{w}(X)$ being positive, we first calculate the derivative of $\bar{w}(X)$. It is given by

$$\partial_X \bar{w}(X) = \frac{1}{2\sqrt{\pi}} e^{-\frac{X^2}{2S}}\left(\sqrt{2}\sqrt{S}\left(2a_2 - 2b_2 + 3\left(a_3 - b_3\right)X\right) + e^{\frac{X^2}{2S}}\sqrt{\pi}\left(\left(a_1 + 2a_2 X + 3a_3\left(S + X^2\right)\right)\left(1 + \text{Erf}\left[\frac{X}{\sqrt{2}\sqrt{S}}\right]\right) + \left(b_1 + 2b_2 X + 3b_3\left(S + X^2\right)\right)\text{Erfc}\left[\frac{X}{\sqrt{2}\sqrt{S}}\right]\right)\right). \quad \text{(S2)}$$

The mode of the adaptive landscape (mean fitness) is positive if $\partial_X \bar{w}(0) < 0$. Because

$$\partial_X \overline{w}\,(0) = \frac{2\sqrt{2}\,(a_2 - b_2)\,\sqrt{S} + \sqrt{\pi}\,(a_1 + b_1 + 3\,(a_3 + b_3)\,S)}{2\sqrt{\pi}}, \tag{S3}$$

it follows that the position of the optimum of the adaptive landscape is at a positive value if eq. (4) in the main text holds.

For the fitness surface of the predator-prey example (eq. (7) in the main text), which has mode at 1/2 if we set $a_{\max} = \gamma/2$ (as in Figure 4), we obtain $a_1 = -r_s$, $a_2 = a_3 = 0$, $b_1 = -r_s + \gamma P$, $b_2 = \gamma P\left(-r_s + \frac{1}{2}\gamma P\right)$, $b_3 = \frac{1}{2}\gamma^2 P^2\left(-r_s + \frac{1}{3}\gamma \mathrm{P}\right)$, where $r_s = c\, r\big/\left(1 + \left(1 - \frac{c}{2} - \frac{N}{K}\right) r\right)$.

It follows that the mode of the adaptive landscape is > 1/2, i.e., shifted to the right, if

$$r_s < \frac{\gamma P\left(2 - 2\sqrt{\frac{2}{\pi}}\,\sqrt{S}\,\gamma P + S\,\gamma^2 P^2\right)}{4 - 4\sqrt{\frac{2}{\pi}}\,\sqrt{S}\,\gamma P + 3\,S\,\gamma^2 P^2}. \tag{S4}$$

It is easy to show that this is satisfied whenever $r_{\mathrm{simp}} < \gamma / 4$, which is the condition ensuring that the right shoulder of the individual fitness surface is flatter.

The skewed Gaussian landscape

We assume the individual fitness surface $w(x)$, as given in eq. (5) in the main text.To calculate mean fitness (or the adaptive landscape), we again assume a Gaussian trait distribution $p(x)$ with mean X and variance S. Then integration yields the following expression for mean fitness:

$$\overline{w}\,(X,\,S) = e^{\frac{\psi^2}{2}}\sqrt{1+\psi^2}\left(\frac{e^{-\frac{1+S\,(-1+\psi^2)^2+\psi\left(\psi+X^2\,\psi+2\,X\sqrt{1+\psi^2}\right)}{2\,S\,\psi^2}}\,\psi\sqrt{S}}{\sqrt{2\pi}\,\left(1+S+\psi^2\right)} + \left(e^{-\frac{\left(X+\psi\sqrt{1+\psi^2}\right)^2}{2\,(1+S+\psi^2)}}\left(\left(1+S+\psi^2-S\,\psi^2\right)+X\,\psi\sqrt{1+\psi^2}\right)\left(1+\mathrm{Erf}\left[\frac{1+S+\psi^2-S\,\psi^2+X\,\psi\sqrt{1+\psi^2}}{\sqrt{2}\,\psi\sqrt{S\,\left(1+S+\psi^2\right)}}\right]\right)\right)\Big/\left(2\,\left(1+S+\psi^2\right)^{3/2}\right)\right), \tag{S5}$$

which is used to generate Figure 2B.

The linear and quadratic selection gradients are defined by

$$L_1 = \partial_X \ln \overline{w}\,(X,\,S) = \frac{\partial_X \overline{w}\,(X,\,S)}{\overline{w}\,(X,\,S)}, \tag{S6}$$

$$L_2 = \partial_S \ln \overline{w}\,(X,\,S) = \frac{\partial_S \overline{w}\,(X,\,S)}{\overline{w}\,(X,\,S)}. \tag{S7}$$

For the derivatives $\partial_X \overline{w}\,(X,\,S)$ and $\partial_S \overline{w}\,(X,\,S)$ we obtain:

$$\partial_X \overline{w}\,(X,\,S) = e^{\frac{\psi^2}{2}}\sqrt{1+\psi^2}\left(\frac{e^{-\frac{1+(1+X^2)\,\psi^2+S\,(-1+\psi^2)^2+2\,X\,\psi\sqrt{1+\psi^2}}{2\,S\,\psi^2}}\left(-X\,\psi-\sqrt{1+\psi^2}\right)}{\sqrt{2\pi}\,\sqrt{S}\,\left(1+S+\psi^2\right)} + \right.$$

$$\begin{aligned}
&\left(e^{-\frac{1+\left(1+X^2\right)\psi^2+S\left(-1+\psi^2\right)^2+2X\psi\sqrt{1+\psi^2}}{2S\psi^2}}\sqrt{\frac{1+\psi^2}{S}}\left(1+S+\psi^2-S\psi^2+X\psi\sqrt{1+\psi^2}\right)\right)\Big/\left(\sqrt{2\pi}\left(1+S+\psi^2\right)^2\right)+\\
&\left(e^{-\frac{\left(X+\psi\sqrt{1+\psi^2}\right)^2}{2\left(1+S+\psi^2\right)}}\psi\sqrt{1+\psi^2}\left(1+\mathrm{Erf}\left[\frac{1+S+\psi^2-S\psi^2+X\psi\sqrt{1+\psi^2}}{\sqrt{2}\,\psi\sqrt{S\left(1+S+\psi^2\right)}}\right]\right)\right)\Big/\left(2\left(1+S+\psi^2\right)^{3/2}\right)-\\
&\frac{1}{2\left(1+S+\psi^2\right)^{5/2}}e^{-\frac{\left(X+\psi\sqrt{1+\psi^2}\right)^2}{2\left(1+S+\psi^2\right)}}\left(X+\psi\sqrt{1+\psi^2}\right)\left(1+S+\psi^2-S\psi^2+X\psi\sqrt{1+\psi^2}\right)\\
&\left.\left(1+\mathrm{Erf}\left[\frac{1+S+\psi^2-S\psi^2+X\psi\sqrt{1+\psi^2}}{\sqrt{2}\,\psi\sqrt{S\left(1+S+\psi^2\right)}}\right]\right)\right),
\end{aligned}\tag{S8}$$

$$\begin{aligned}
\partial_S\,\overline{w}\,(X,\,S)=e^{\frac{\psi^2}{2}}\sqrt{1+\psi^2}\Bigg(&-\frac{e^{-\frac{1+S\left(-1+\psi^2\right)^2+\psi\left(\psi+X^2\psi+2X\sqrt{1+\psi^2}\right)}{2S\psi^2}}\sqrt{S}\,\psi}{\sqrt{2\pi}\left(1+S+\psi^2\right)^2}+\frac{e^{-\frac{1+S\left(-1+\psi^2\right)^2+\psi\left(\psi+X^2\psi+2X\sqrt{1+\psi^2}\right)}{2S\psi^2}}\psi}{2\sqrt{2\pi}\sqrt{S}\left(1+S+\psi^2\right)}+\\
&\left(e^{-\frac{1+\left(1+X^2\right)\psi^2+S\left(-1+\psi^2\right)^2+2X\psi\sqrt{1+\psi^2}}{2S\psi^2}}\left(1+\left(1+X^2\right)\psi^2+2X\psi\sqrt{1+\psi^2}\right)\right)\Big/\left(2\sqrt{2\pi}\,S^{3/2}\psi\left(1+S+\psi^2\right)\right)+\\
&\left(e^{-\frac{1+\left(1+X^2\right)\psi^2+S\left(-1+\psi^2\right)^2+2X\psi\sqrt{1+\psi^2}}{2S\psi^2}}\left(-1-\psi^2+S\left(-1+\psi^2\right)-X\psi\sqrt{1+\psi^2}\right)\right.\\
&\left.\left(\left(1+\psi^2\right)\left(1+\psi^2+X\psi\sqrt{1+\psi^2}\right)+S\left(1+2\psi^2+\psi^4+2X\psi\sqrt{1+\psi^2}\right)\right)\right)\Big/\left(2\sqrt{2\pi}\,S^{3/2}\psi\left(1+S+\psi^2\right)^3\right)-\\
&\frac{e^{-\frac{\left(X+\psi\sqrt{1+\psi^2}\right)^2}{2\left(1+S+\psi^2\right)}}\left(-1+\psi^2\right)\left(1+\mathrm{Erf}\left[\frac{1+S+\psi^2-S\psi^2+X\psi\sqrt{1+\psi^2}}{\sqrt{2}\,\psi\sqrt{S\left(1+S+\psi^2\right)}}\right]\right)}{2\left(1+S+\psi^2\right)^{3/2}}-\frac{1}{4\left(1+S+\psi^2\right)^{5/2}}\,3\,e^{-\frac{\left(X+\psi\sqrt{1+\psi^2}\right)^2}{2\left(1+S+\psi^2\right)}}\\
&\left(1+S+\psi^2-S\psi^2+X\psi\sqrt{1+\psi^2}\right)\left(1+\mathrm{Erf}\left[\frac{1+S+\psi^2-S\psi^2+X\psi\sqrt{1+\psi^2}}{\sqrt{2}\,\psi\sqrt{S\left(1+S+\psi^2\right)}}\right]\right)+\\
&\frac{1}{4\left(1+S+\psi^2\right)^{7/2}}e^{-\frac{\left(X+\psi\sqrt{1+\psi^2}\right)^2}{2\left(1+S+\psi^2\right)}}\left(X+\psi\sqrt{1+\psi^2}\right)^2\left(1+S+\psi^2-S\psi^2+X\psi\sqrt{1+\psi^2}\right)\Bigg(1+\\
&\mathrm{Erf}\left[\frac{1+S+\psi^2-S\psi^2+X\psi\sqrt{1+\psi^2}}{\sqrt{2}\,\psi\sqrt{S\left(1+S+\psi^2\right)}}\right]\Bigg)\Bigg).
\end{aligned}\tag{S9}$$

The mode of mean fitness is obtained by solving $\partial_X \overline{w}(X, S) = 0$ for X. This is a complicated transcendental equation. It is solved numerically to obtain Figure 2C. However, by series expansion the following simple approximation can be derived:

$$X_{\text{modeapp}} = \frac{1}{2\psi\sqrt{1+\psi^2}}\left(\sqrt{\left(1+S+\psi^2\right)\left(S\left(1-\psi^2\right)^2+\left(1+\psi^2\right)^3\right)} - S\left(1-\psi^2\right) - \left(1+\psi^2\right)^2\right). \qquad (\text{S10})$$

This is an excellent approximation to the true mode if S is not too large, i.e., if approximately $S < 0.1$ (results not shown).

To calculate the equilibrium mean phenotype, we apply the theory described in Bürger (2000, Chap.5; in particular p. 194). According to this theory, equilibrium distributions are (approximate) solutions of $S L_1 + C_3 L_2 + M = 0$, i.e., of eq. (2) in the main text. The mutation term M is needed here because the mutation model used in our simulations changes the mean.We have equal forward and backward mutation between the + and the - allele at each locus. The total mutation rate per locus is u and there are n loci. Hence, $p' = p(1-u/2) + (1-p)u/2$ or, equivalently, $\Delta p = p' - p = (1-2p)u/2$. Because the loci contribute additively to the trait, the mean trait value is $X = \delta\sum_{i=1}^{n}(p_i - 1/2)$, where the allelic effects are $+\delta$ and $-\delta$. A simple calculation yields that the change of the mean caused by mutation is $M = \Delta X = -u X$. We define skew = $C_3/S^{3/2}$ and rewrite $S L_1 + C_3 L_2 + M = 0$ in the form $L_1 + \text{skew}\sqrt{S}\, L_2 - u X/S = 0$. For given ψ, u, S, and skew, this can be solved numerically to obtain the equilibrium mean phenotype X. To generate the theoretical predictions in Figure 3, the values of S and skew were taken from the simulations with the corresponding parameters ψ and u.

Skewed phenotype distribution effects on selection gradients

We show that for smooth (individual) fitness functions, to leading order, the linear and quadratic selection gradients L_1 and L_2, as defined in (S6) and (S7), are independent of the skew of the phenotype distribution provided the variance of the phenotype distribution is small.

To this end, we assume that the mean X of the phenotype distribution $p(x)$ is close to 0 and its variance S is sufficiently small, such that individual fitness $w(x)$ can be approximated by $w(x) = 1 + a_2 x^2 + a_3 x^3$. This will be a good approximation if selection is weak.

We assume $a_2 < 0$ (stabilizing selection) and Abs(a_3) is small enough such that $w(x)$ has its maximum at $x = 0$.
Then mean fitness is

$$\overline{w}(X, S) = \int w(x)\, p(x)\, dx = 1 + a_2 (S + X) + a_3\left(C_3 + 3 X S + X^3\right). \qquad (\text{S11})$$

Therefore,

$$\partial_X \overline{w}(X, S) = a_2 + 3 a_3\left(S + X^2\right), \qquad (\text{S12})$$

which is independent of C_3. As a consequence, the mode of mean fitness, obtained by solving $\partial_X \overline{w}(X, S) = 0$ for X, is independent of C_3. Similarly,

$$\partial_S \overline{w}(X, S) = a_2 + 3 a_3 X, \qquad (\text{S13})$$

which is also independent of C_3.

The landscape of the predator-prey example

We assume the individual fitness surface given in eq. (7) of the main text.We set $a_{\max} = \gamma/2$, so that the maximum is at $x = 1/2$.

It is straightforward to show that the skew of this fitness surface is positive if and only if $\gamma P > a\, r_s$, where $r_s = c\, r\Big/\left(1 + \left(1 - \frac{c}{2} - \frac{N}{K}\right) r\right)$ and $a \approx 6.8285$. In addition, it decreases faster from its maximum for $x<1/2$ than for $x>1/2$ if and only if $\gamma P > 2$.

Assuming that the trait distribution $p(x)$ is Gaussian with mean X and variance S, integration yields, up to the multiplicative constant, the following expression for mean fitness:

$$\overline{w}(X, S) = r_s \frac{\sqrt{S}}{\sqrt{2\pi}}\, e^{-\frac{\left(\frac{1}{2}+\frac{1}{r_s}-X\right)^2}{2S}} - \frac{1}{2}\left(\left(1 + r_s\left(\frac{1}{2} - X\right)\right)\left(\text{Erf}\left[\frac{\frac{1}{2} - X}{\sqrt{2}\sqrt{S}}\right] - \text{Erf}\left[\frac{\frac{1}{2}+\frac{1}{r_s} - X}{\sqrt{2}\sqrt{S}}\right]\right) - e^{\frac{1}{2}\gamma P\,(-1+2X+S\gamma P)}\left(1 + r_s\left(\frac{1}{2} - X - S\gamma P\right)\right)\left(1 - \text{Erf}\left[\frac{-\frac{1}{2} + X + S\gamma P}{\sqrt{2}\sqrt{S}}\right]\right)\right). \qquad (\text{S14})$$

The linear and quadratic selection gradients L_1 and L_2, defined in (S6) and (S7) are obtained from the following expressions:

$$\partial_X \overline{w}\,(X,\,S) = \frac{1}{4}\left(2\,r_s\left(-1+e^{-\frac{(1-2X)^2}{8S}}\sqrt{\frac{2}{\pi}}\,\sqrt{S}\,\gamma P+\text{Erf}\left[\frac{\frac{1}{2}-X}{\sqrt{2}\,\sqrt{S}}\right]+\text{Erfc}\left[\frac{\frac{1}{2}+\frac{1}{r_s}-X}{\sqrt{2}\,\sqrt{S}}\right]\right)-e^{\frac{1}{2}\gamma P\,(-1+2X+S\gamma P)}\right.$$
$$\left.(-2\gamma P+r_s\,(2+\gamma P\,(-1+2X+2S\gamma P)))\,\text{Erfc}\left[\frac{-\frac{1}{2}+X+S\gamma P}{\sqrt{2}\,\sqrt{S}}\right]\right), \qquad (S15)$$

$$\partial_S \overline{w}\,(X,\,S) = \frac{1}{8}\left(\frac{2\,e^{-\frac{(2+r_s-2r_sX)^2}{8r_s^2S}}\sqrt{\frac{2}{\pi}}\,r_s}{\sqrt{S}}+\frac{2\,e^{-\frac{(1-2X)^2}{8S}}\sqrt{\frac{2}{\pi}}\,\gamma P\,(-1+r_s S\gamma P)}{\sqrt{S}}-\right.$$
$$e^{\frac{1}{2}\gamma P\,(-1+2X+S\gamma P)}\,\gamma P\,(-2\gamma P+r_s\,(4+\gamma P\,(-1+2X+2S\gamma P)))+e^{\frac{1}{2}\gamma P\,(-1+2X+S\gamma P)}\,\gamma P$$
$$\left.(-2\gamma P+r_s\,(4+\gamma P\,(-1+2X+2S\gamma P)))\,\text{Erf}\left[\frac{-\frac{1}{2}+X+S\gamma P}{\sqrt{2}\,\sqrt{S}}\right]\right). \qquad (S16)$$

The equilibrium mean phenotype is then obtained in the same way as for the skewed Gaussian fitness surface. The only difference here is that the mutation term is of the form $M=\Delta X=-u\,(X\text{-}1/2)$. The reason for this difference is that, here, the optimum of the individual fitness surface is at 1/2, and not at 0.