Fitness Sets

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Video Notes

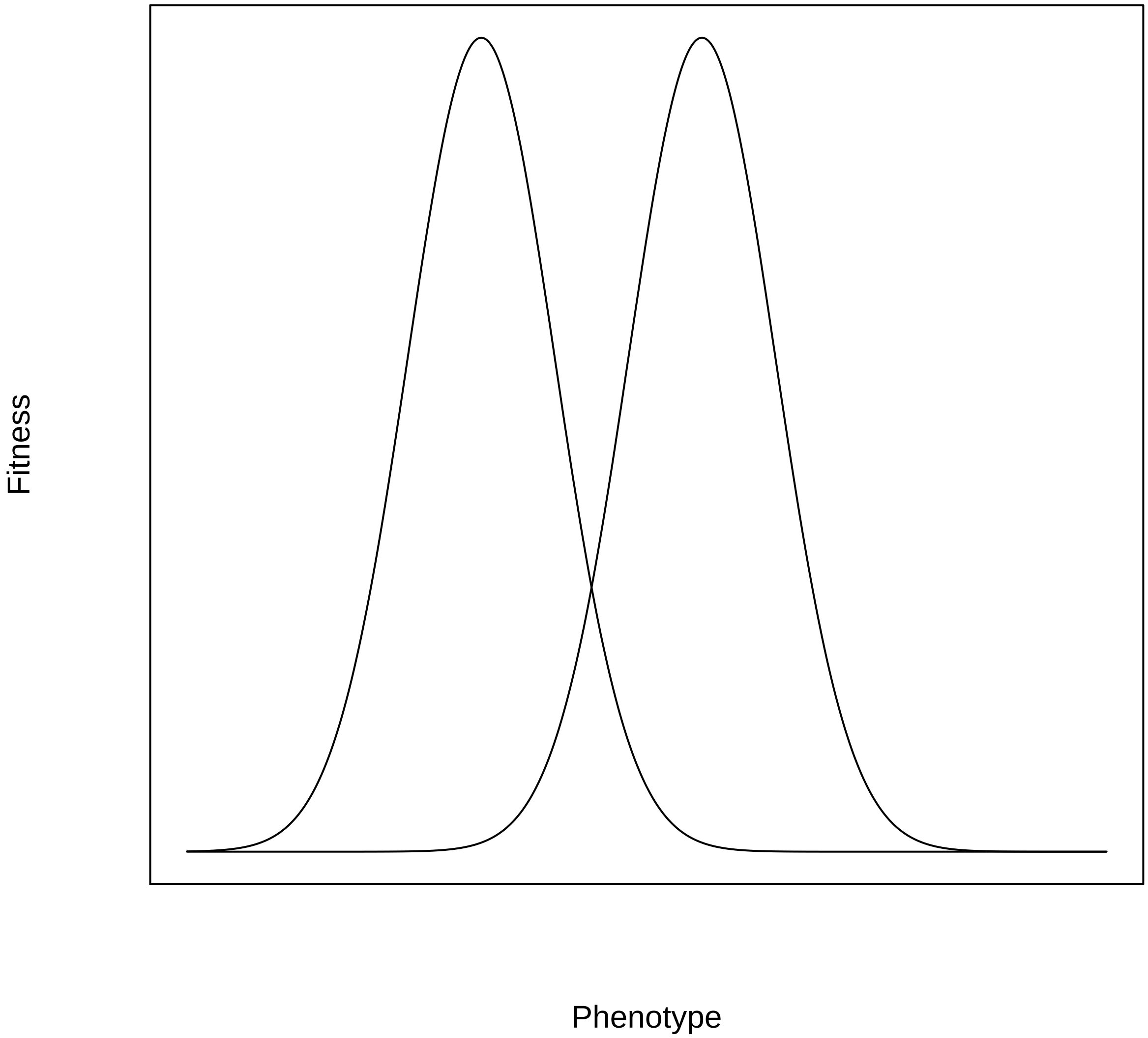
Video hopefully coming soon. These notes are quite half-baked, so stay tuned for updates.

Fitness Sets

Levins (1962) introduced a the idea of *fitness sets* as a way to think about evolution in variable environments. This approach was more fully fleshed out in his subsequent monograph (Levins, 1968). The fundamental idea is to represent the fitness of organisms in the different conditions that make up their variable environments and then find the strategy that maximizes fitness across these environments. The optimum can be a generalized compromise across the different environments or it can be the production of polymorphic specialized phenotypes that better match specific environmental conditions.

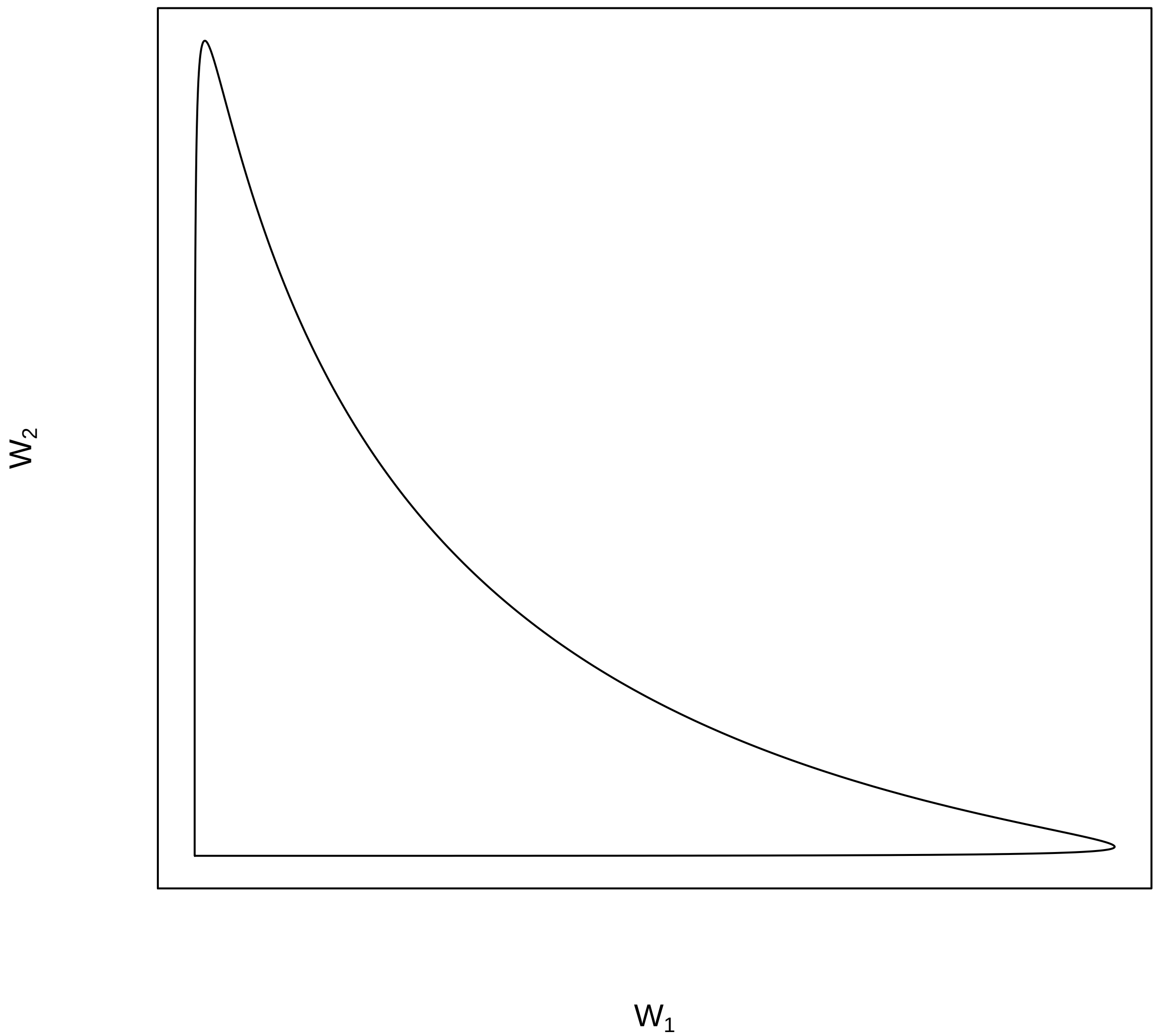
Consider first a population with two phenotypes where the peak fitness in the two environments are quite separated from each other such that the fitness functions do not overlap tremendously. We can assume Gaussian distributions of fitnesses with respect to the environment for simplicity. The basic idea behind using these bell-shaped functions is that there is an optimum for the environment and that fitness falls off as you move away from this optimum value of the phenotype. A Gaussian distribution just makes quite specific assumptions about how fitness falls off as the phenotype differs from the optimum: it does so symmetrically around the maximum and it declines exponentially in the squared difference from the optimum. The actual form of the fitness function will depend on the particulars of the environment and the phenotypes in question.

```
x <- seq(0,25,length=1000)
mu1 <- 8
sd1 <- 2
mu2 <- 14
sd2 <- 2

plot(x,dnorm(x,mu1,sd1), type="l", axes = FALSE,
     xlab="Phenotype", ylab="Fitness")
lines(x,dnorm(x,mu2,sd2))
box()
```



In this figure, we plotted the fitness functions against the environment. We can cut out the middleman, as it were, and simply plot the fitness functions against each other in a manner analogous to phase-plane analysis of, e.g., the Lotka-Volterra predator-prey model. Environment becomes implicit in the plots. What we have done is represent all possible phenotypes in our 2-dimensional fitness space.

```
f1 <- dnorm(x,mu1,sd1)
f2 <- dnorm(x,mu2,sd2)

plot(f1,f2, type="l", axes=FALSE,
     xlab=expression(W[1]), ylab=expression(W[2]))
box()
```



This is a *fitness set*. What we see is a quite concave fitness set for these phenotypes, which arises because of the broad separation of the optima of the individual fitness functions. The concavity in the northeast corner of this plot arises because there is a trough in the fitness where the two fitness functions overlap only in their tails. A quick note on convexity is probably warranted here. A space is said to be convex if, for any two points contained within the space, the entirety of the line segment that connects these points is also contained within the space. It's easy to see that a line segment connecting points in horns of this fitness set would not be entirely contained within the set.

We can generate a convex fitness set by creating fitness functions with greater overlap. This suggests the geometrical interpretation of convexity, namely, that it implies the ability of a compromise phenotype.

```
mu3 <- 10
sd3 <- 2
mu4 <- 12
sd4 <- 3
# fitness functions
plot(x,dnorm(x,mu3,sd3), type="l", axes = FALSE,
```

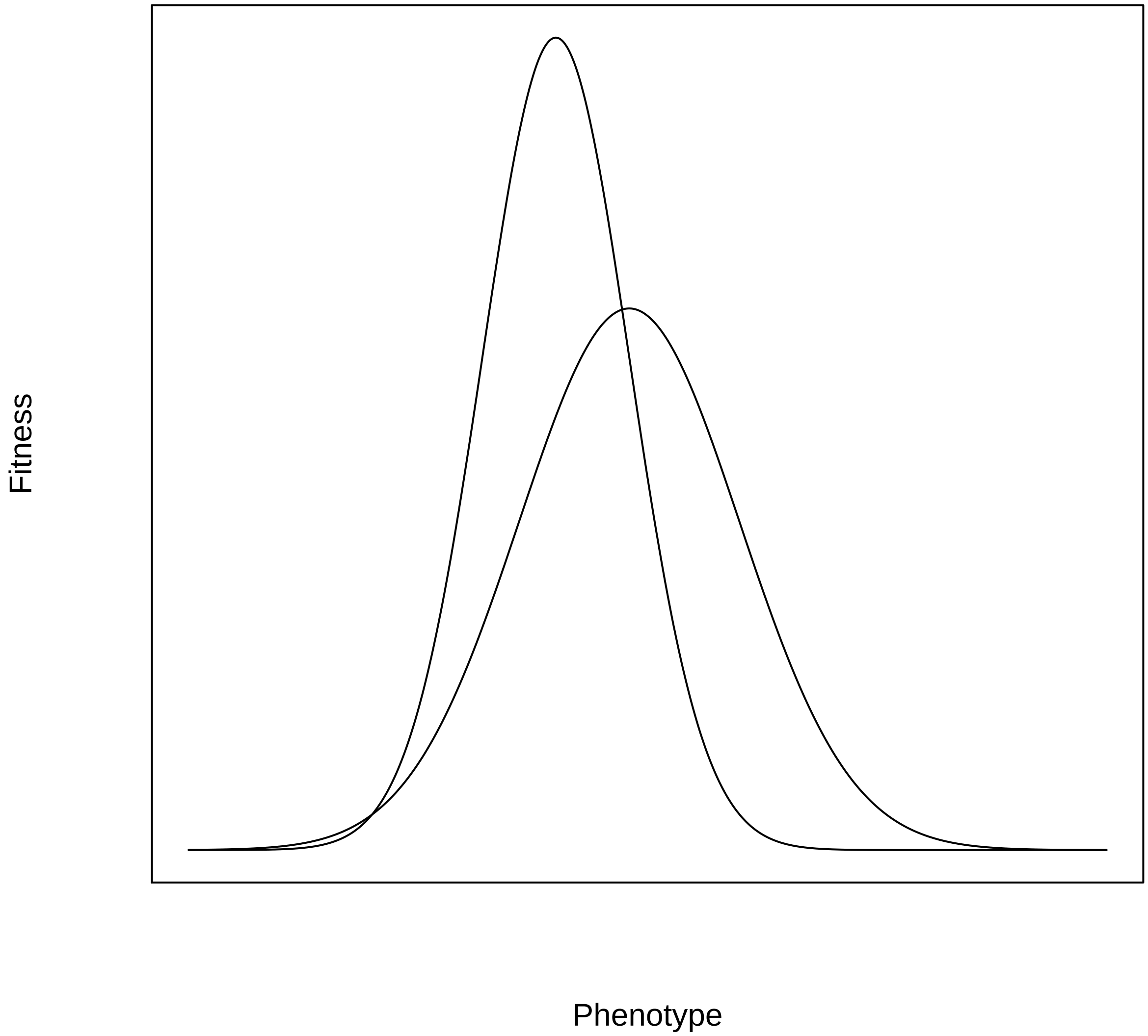


Figure 1: Convex fitness set.

```
     xlab="Phenotype", ylab="Fitness")
lines(x,dnorm(x,mu4,sd4))
box()
```

```
# fitness set
plot(dnorm(x,mu3,sd3),dnorm(x,mu4,sd4),
     type="l", axes = FALSE,
     xlim=c(0,0.3), ylim=c(0,0.25),
     xlab=expression(W[1]), ylab=expression(W[2]))
box()
```

Of course, we can use functions other than a normal distribution. A gamma distribution will give us more skew in the right tail. Fitness declines asymmetrically from its peak.

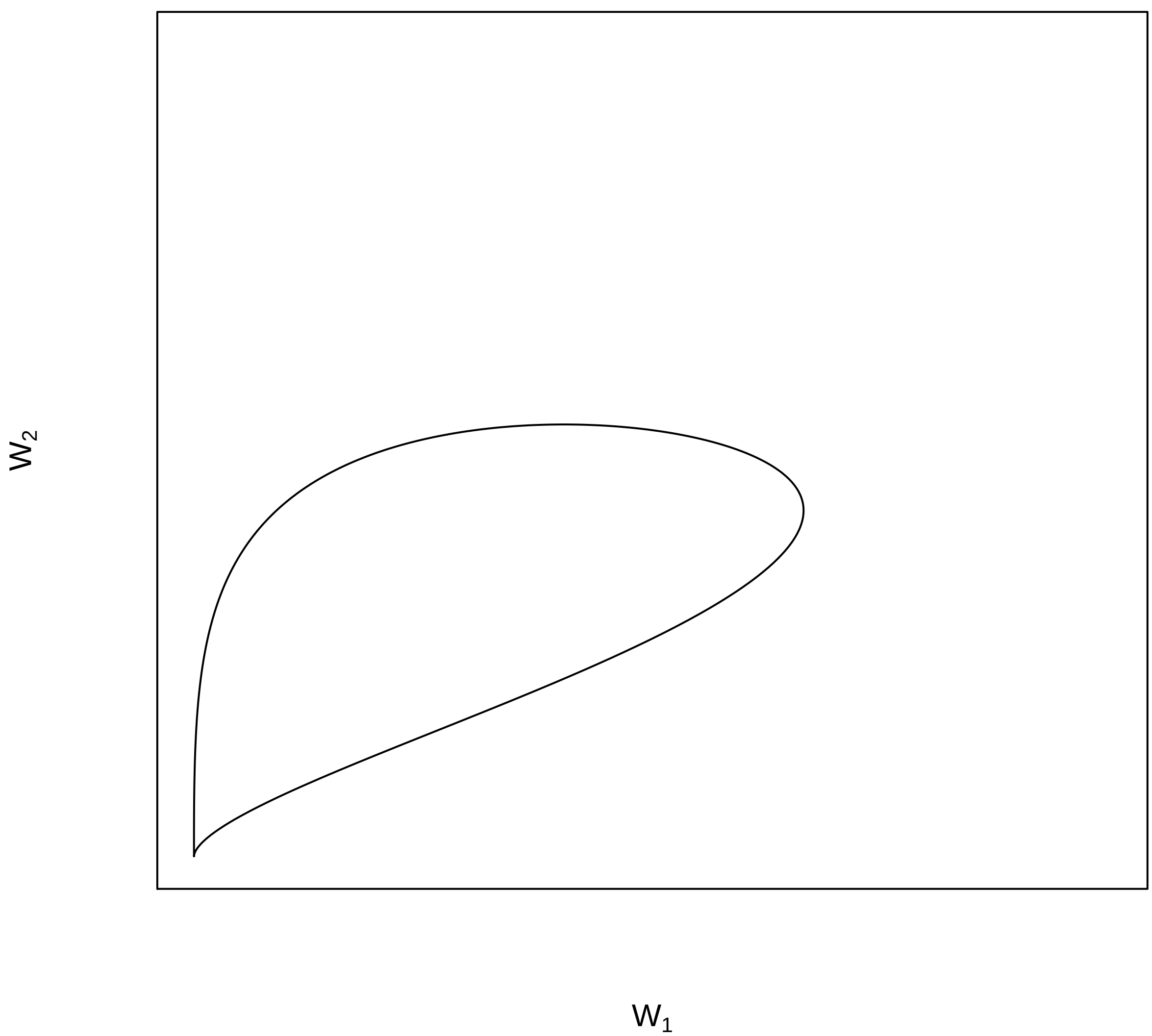
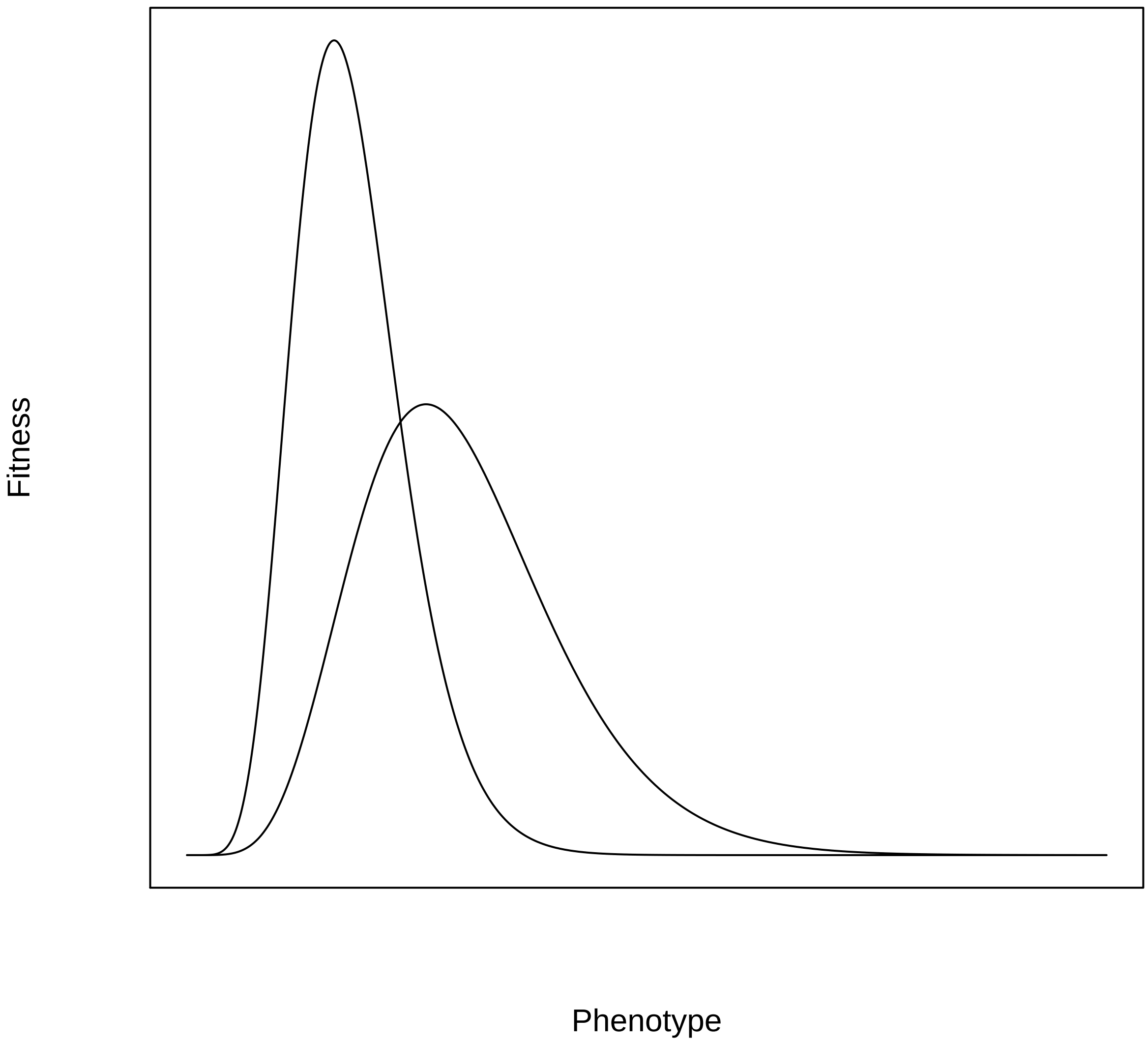


Figure 2: Convex fitness set.

```
## skewed gamma distributions
k1 <- 9
s1 <- 0.5
k2 <- 7.5
s2 <- 1

plot(x,dgamma(x,shape=k1,scale=s1), type="l", axes = FALSE,
     xlab="Phenotype", ylab="Fitness")
lines(x,dgamma(x,shape=k2,scale=s2))
box()
```



Add adaptive functions for a coarse-grained environment. For a coarse-grained environment, the adaptive function will have a hyperbolic form. Here again, the issue of convexity arises. An adaptive function that takes the hyperbolic form as in figure 3, is also said to be convex. Just as a convex fitness set implies an an optimum phenotype that is a compromise, convexity in the adaptive function suggests that average values have higher fitness than extremes. As the adaptive-function isoclines move from the center to the extremes, the increase in fitness in one dimension must be greater than the reduction of fitness in the other dimension. This is also related to diminishing marginal rate of substitution. Note, for example, as the isocline moves away from its convex center upward in the direction of W_2, it takes increasing fitness in the W_2 dimension to make up for lost fitness in the W_1 direction.

```r
## for the isoclines
G <- seq(0,0.5,length=100)
alpha <- 0.5
beta <- 0.5
# simple function to calculate hyperbolic isolclines following Cobb-Douglas form
kf <- function(G,W,alpha,beta) (W/G^alpha)^(1/beta)

## fitness set
plot(dgamma(x,shape=k1,scale=s1),dgamma(x,shape=k2,scale=s2), lwd=3,
     type="l", axes = FALSE, las=1,
     xlim=c(0,0.4), ylim=c(0,0.25),
     xlab=expression(W[1]), ylab=expression(W[2]))
box()
## convex adaptive functions
lines(G,kf(G=G,W=0.05,alpha=0.75,beta=1), lty=2)
lines(G,kf(G=G,W=0.05,alpha=0.85,beta=1), lty=2)
lines(G,kf(G=G,W=0.05,alpha=0.63,beta=1), lty=2)
```

Why is a coarse-grain adaptive function convex? Suppose that the mortality probability in some time interval Δt is $m(t)$. Then the cumulative survival probability to age $t + \Delta t$ is

$$P(t + \Delta t) = P(t)[1 - m(t)]\Delta t,$$

where $P(t)$ is the probability of surviving to t.

Starting from birth, the probability of surviving to age t is

$$P(t) = \prod_{s=1}^{t-1}(1 - m(t)\Delta t)$$

Suppose there are two environments (e.g., good and bad) that occur with probabilities q and $1 - q$. In a coarse-grained environment, the organism can expect to spend a substantial amount of her time in each of these. If q is the probability of the good environment, then the adaptive function will take on a functional form such as $W_g^q W_b^{1-q}$ (where we have equated survival with "fitness" to keep the notation consistent). When we solve this form for one of the fitnesses, it will be hyperbolic. This form favors compromise phenotypes since organisms are going to have to get by in both environments.

In a fine-grained environment, the higher powers of Δt will become negligible. The time that the organism spends in environments to which it is poorly adapted is smaller since it is spending less time in each patch. This then becomes more of a continuous-time model so that survival to age t is given by

$$P(t) = P_0 e^{-\int m(t)dt}.$$

Obviously, survival is maximized when this integral is smallest, and Levins (1968) notes that this occurs "when the linear average of the fitnesses $pW_1 + (1 - p)W_2$ is greatest." I'm still working out why that is. . .

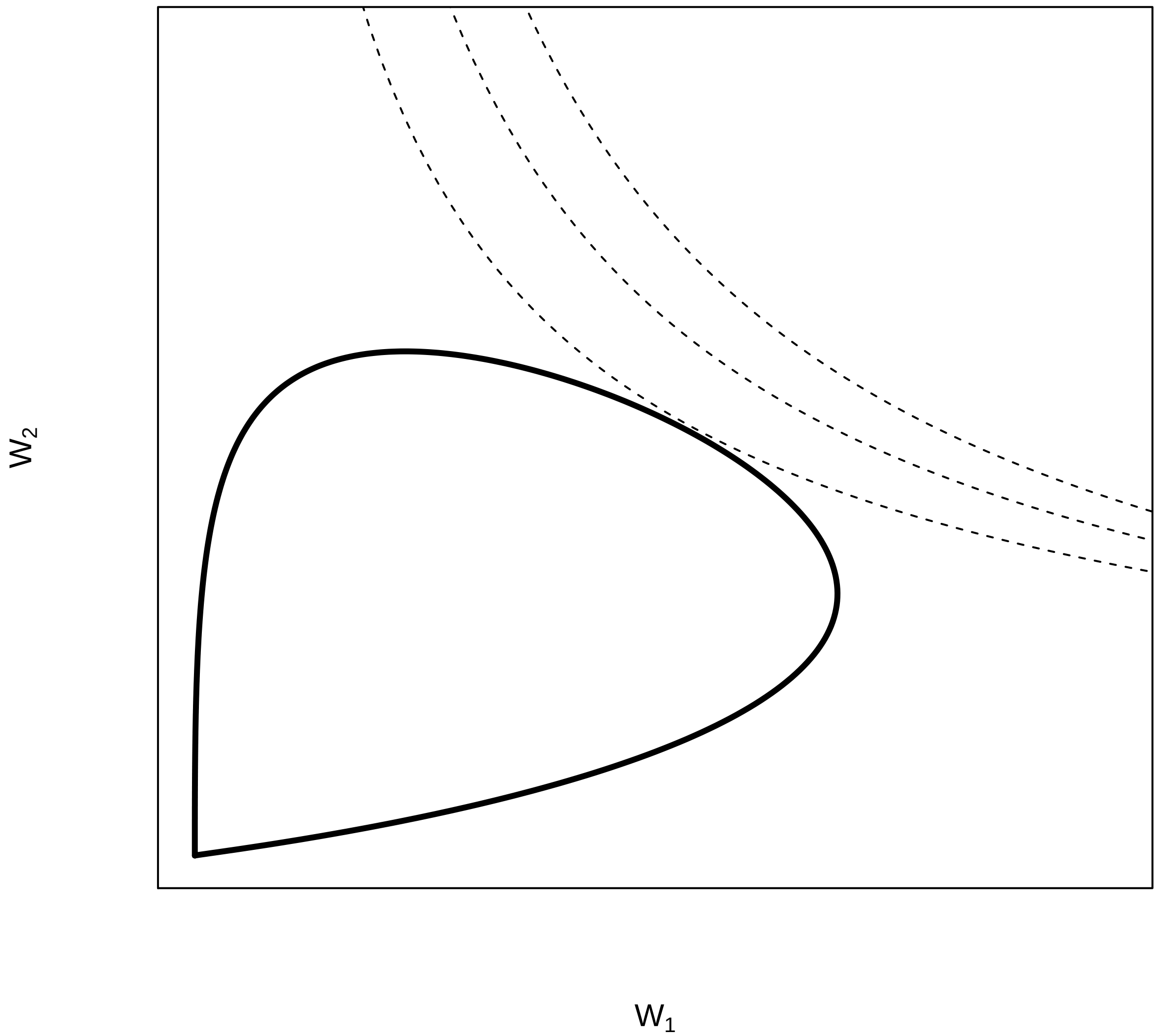


Figure 3: Convex fitness set with convex adaptive function.

References

Levins, R. (1962). Theory of Fitness in a Heterogeneous Environment. I. The Fitness Set and Adaptive Function. *The American Naturalist 96*(891), 361–373.

Levins, R. (1968). *Evolution in changing environments*. Princeton: Princeton University Press.