SOME THOUGHTS ON \( R_0 \) AND \( r \).

Generally, a population grows as (Krebs, p.140):

\[
N_t = N_0 e^{rt}
\]

(1)

where:
- \( e \) is a constant (approx. 2.71828, the base of natural logarithms)
- \( N \) is population density
- \( t \) is time (0 at the start, and \( t \) some time-period “\( t \)” later)
- \( r \) is the intrinsic rate of population increase under prevailing conditions

If you wish to know how quickly a population grows per generation, use \( G \) (generation time) as a substitute in equation (1) for the more general \( t \):

\[
N_G = N_0 e^{rG}
\]

(2)

(remember that generation time is given as “\( T \)” instead of “\( G \)” in Krebs’ notation)

Take the natural log of equation (2), rearrange it, and you get:

\[
\ln \left( \frac{N_G}{N_0} \right) = rG
\]

(3)

The value in the brackets in equation (3) is essentially the multiplier by which population size has changed in one generation, or the relative change in number of breeders per generation. We also call this term the population net reproductive rate, and symbolize it as \( R_0 \). If the bracketed term in equation (3) is replaced with \( R_0 \), you get the following:

\[
r \approx \frac{\ln R_0}{G}
\]

(4)

[This value can also be derived from life-table data; see downloadable Demography document.]

Equation (4) gives the approximate value only for \( r \), since it assumes non-overlapping generations.

The theoretically ideal value for \( r \) – a population’s theoretic intrinsic maximum capacity for growth, or \( r_{\text{max}} \) – can never be realized. An exponentially growing population may approach the theoretical \( r_{\text{max}} \) early in its growth, but never be actually “at” it.

A population will exhibit a realized situation-specific value of \( r \), called \( r_a \) or \( r_{\text{obs}} \) (“actual”, or “observed”, \( r \)), which varies from a little less than \( r_{\text{max}} \), through positive values (when population density increases), and zero (stable population size), to negative values (when population density declines). See Box 11.1, page 162, in Krebs for a different explanation of this point.
The units of $r$ are individuals/individual/time, and it’s an \textit{instantaneous} rate, saying how the population is changing “right now”. Another interpretation of this is to re-cast the formula for exponential growth in density:

\[
\frac{dN}{dt} = rN
\]  

(5)

by a simple rearrangement, the $N$ on the right becoming $1/N$ on the left, so it looks like this:

\[
r = \frac{dN}{dt} \cdot \frac{1}{N}
\]  

(6)

Equation (6) says, literally: “The intrinsic rate $r$ is in the units of the change of density per unit time, multiplied by one over the density”, or “$r$ is in the units $N$, over $N$, over $t$”. Such a measure of $r$ is an \textit{instantaneous} rate, since $dt$ is a limit as $t$ approaches zero.

If you want a \textit{finite} rate (a prediction of what will happen a finite period into the future), use the calculation of $\lambda$ (lambda):

\[
\lambda = e^r
\]  

(7)

Krebs offers an example of this at the end of Box 10.2, p.145, but it is \textit{not} examinable material.

\textbf{TO SUM UP:}

$R_0$ is a \textit{population-level characteristic} describing how quickly the size of the population is changing per generation.

$r$ is a \textit{per capita (per individual) characteristic} describing the capacity of an individual to make its population grow.

$r_{\text{max}}$ is the \textit{theoretical maximum value} of $r$ exhibited by individuals of a given population; $r_a$ is the \textit{range of actual values} of $r$ exhibited by members of a population under differing \textit{circumstances} (especially, of \textit{density}).

An exactly self-replacing population (one not being replenished by immigration), because it \textit{stays the same size over generations}, will show a characteristic value of $1.0$ for $R_0$. Density a generation from now will be the same as density now, \textit{i.e.} the quotient of (later/now) sizes will be $1.0$ (though most individuals alive a generation from now will be individuals not yet alive now, they will be born over the next generation-period and will replace individuals dying over the same period). A growing population will multiply at a rate greater than $1.0$, and a declining population will multiply at a fractional rate less than $1.0$.

An exactly self-replacing population will also show a characteristic value for $r_a$; this will be $0$ (zero), indicating that on average each individual breeder present in the population will add \textit{no (i.e. zero) extra} individuals to the population in its lifetime, or at least none in addition to replacing itself (and its mate). This is another way of saying that the capacity each breeder has to add individuals is zero... so no extras remain in the population, and its total size in the next period of time will be the same as the present size. Just enough individuals survive to maintain the same size population (though, of course, the identity of living individuals will change over time as some die and are replaced by new ones). In a growing population, the average breeder will leave behind \textit{some} extra offspring in addition to replacement, and thus the $r_a$ will be a positive value; in a declining population, the average breeder will not even replace herself and her mate before dying, and this shortfall will appear as a negative value of $r_a$ (insufficient reproduction to replace population-members).