Derivation of the “ecological” necessary and sufficient conditions for the existence of optimisation/pessimisation principles

We start with some trivial theorems (1 and 2) and corollaries (3 and 4):

**Theorem 1:** If (assumption I) there exist functions \( \psi \) of \( X \), and \( \alpha \) of \( \psi \) and \( E \), to the real numbers, with \( \alpha \) increasing in \( \psi \), such that

\[
\text{sign } \alpha(\psi(X),E) = \text{sign } \rho(X,E), \tag{1}
\]

then evolution maximises \( \psi(X) \) (or equivalently \( \alpha(\psi(X),E) \) for any fixed \( E \)).

**Theorem 2** (Verelendungsprincip): If (assumption II) there exist functions \( \phi \) of \( E \), and \( \beta \) of \( X \) and \( \phi \), to the real numbers, with \( \beta \) increasing in \( \phi \), such that

\[
\text{sign } \beta(X,\phi(E)) = \text{sign } \rho(X,E), \tag{2}
\]

then evolution minimises \( \phi(E_{\text{attr}}(X)) \).
Corollary 3: If (assumption III) we can write $r(X,E)$ in the form

$$r(X,E) = \alpha(\psi(X),E), \quad (3)$$

with $\alpha$ increasing in $\psi$, then evolution maximises $r(X,E_V)$ (and, more generally, $r(X,E_0)$ for any fixed $E_0$).

Corollary 4: If (assumption IV) we can write $R_0(X,E)$ in the form

$$R_0(X,E) = \exp[\alpha(\psi(X),E)], \quad (4)$$

with $\alpha$ increasing in $\psi$, then evolution maximises $R_0(X,E_V)$ (and, more generally, $R_0(X,E_0)$ for any fixed $E_0$).
Questions:

i. What is the precise relations between theorems 1 and 2?

ii. Can theorems 1 and 2 be made into "if and only if" statements, by introducing some reasonable additional requirements such as the assumption that the extremisation principle should hold independent of the particular choice we may still make for a constraint on X?

ii. Can a similar result be obtained for the corollaries?
**Theorem 5** (answer to question i): The assumptions I and II are equivalent to: (assumption V) There exist functions $\phi$ of E, and $\psi$ of X to the real numbers, such that

\[
\text{sign } [\psi(X)+\phi(E)] = \text{sign } \rho(X,E). \quad (5)
\]

**Proof:**

for assumption I: Define the function $\phi$ of E to the real numbers by $\alpha(-\phi(E),E) = 0$. Then

\[
\text{sign } [\psi(X)+\phi(E)] = \text{sign } \alpha(\psi(X),E) = \text{sign } \rho(X,E). \quad (6)
\]

Therefore assumption I implies assumption V. The converse implication is obvious.

for assumption II: Let $\psi(X) := -\phi(E_{\text{attr}}(X))$. As $\beta(X,\phi(E_{\text{attr}}(X))) = 0$

\[
\text{sign } [\phi(E)+\psi(X)] = \text{sign } [\phi(E)-\phi(E_{\text{attr}}(X))] = \text{sign } \beta(X,\phi(E)) = \text{sign } \rho(X,E). \quad (7)
\]

Therefore the assumption II implies assumption V. The converse implication is obvious.

Apparently we may without loss of essential information replace $\alpha(\psi,E)$ by $\psi+\phi(E)$ respectively $\beta(X,\phi)$ by $\psi(X)+\phi$, with $\phi$ respectively $\psi$ defined above.
Remark:

The reasoning underlying theorem 5 does not extend to corollaries 3 and 4:

From \( r(X,E) = \alpha(\psi(X),E) \) we cannot even conclude that there exist functions \( \phi^\# \) of \( E \) and \( \psi^\# \) of \( X \) such that \( r(X,E) = \psi^\#(X)+\phi^\#(E) \).

Neither can we conclude from \( R_0(X,E) = \exp[\alpha(\psi(X),E)] \) that there exist functions \( \phi^\# \) of \( E \) and \( \psi^\# \) of \( X \) such that \( R_0(X,E) = \exp[\psi^\#(X)+\phi^\#(E)] \).
The next theorem is again trivial. However, it forms a natural introduction to the somewhat unexpected, though on second thought equally trivial, theorem 7.

Theorem 6 (first part of the answer to question ii):

1. If we require that we can determine the ESS under any possible constraint by maximising a function $\psi$ of $X$ then this function is uniquely determined up to an increasing transformation.

2. If we require that that we can determine the ESS under any possible constraint by minimising a function $\phi$ of $E \in E_{\text{attr}}(X)$ then this function is uniquely determined up to an increasing transformation.
Theorem 7 (second part of the answer to question ii):

1. If there exists a function $\psi$ of $X$ to the real numbers such that we can determine the ESS value of $X$ by maximising $\psi$, independent of any choice that we may still make for a constraint on $X$, then there exists a function $\phi$ of $E$ such that

$$\text{sign } [\psi(X)+\phi(E)] = \text{sign } \rho(X,E).$$  

(5)

2. If there exists a function $\phi$ of $E$ to the real numbers such that we can determine the ESS value of $X$ by minimising $\phi(E_{\text{attr}}(X))$, independent of any choice that we may still make for a constraint on $X$, then there exists a function $\psi$ of $X$ such that (5) applies.

3. The functions $\phi$ respectively $\psi$ are uniquely determined by their counterparts.

Proof: In case 1 we define $\phi$ by $\phi(E_{\text{attr}}(X)) := -\psi(X)$. In case 2 we define $\psi(X) := -\phi(E_{\text{attr}}(X))$. (5) is derived by considering all possible constraints of the type $X \in \{X_1, X_2\}$. Maximising $\psi(X)$ or minimising $\phi(E_{\text{attr}}(X))$ will only predict the right ESS for this constraint if

$$\text{sign } [\psi(X_i)+\phi(E_{\text{attr}}(X_j))] = \text{sign } \rho(X_i,E_{\text{attr}}(X_j))$$

for all values of $i$ and $j$. Uniqueness of $\phi$ respectively $\psi$ follows from the fact that we should have

$$\text{sign } [\psi(X)+\phi(E_{\text{attr}}(X))] = 0.$$

Corollary 8: Any optimisation principle $\psi$ automatically carries a matched pessimisation principle $\phi$ in its wake, and vice versa.
**Corollary 9** (*last part of the answer to question ii)*:

We may replace the opening "if"s of theorems 1 and 2 by "iff"s:

**Proof:**
Converse of theorem 1: If there exists an optimisation principle then there exists by definition a function $\psi$ with the appropriate properties. The function $\alpha$ may then be defined as $\alpha(\psi,E) := \psi + \phi(E)$, with $\phi$ given by theorem 7.

Converse of theorem 2: If there exists a pessimisation principle then there exists by definition a function $\phi$ with the appropriate properties. The function $\beta$ may then be defined as $\beta(X,\phi) := \psi(X) + \phi(E)$, with $\psi$ given by theorem 7.
Corollary 10 (first part of the answer to question iii):

1. If we can determine the ESS value of $X$ by maximising $r(X,E_0)$ for some special value $E_0$ of $E$, independent of any choice that we may still make for a constraint on $X$, then there exists a function $\phi$ of $E$ such that

$$\text{sign} \ [r(X,E_0)+\phi(E)] = \text{sign} \ r(X,E). \quad (8)$$

2. If we can determine the ESS value of $X$ by maximising $R_0(X,E_0)$ for some special value $E_0$ of $E$, independent of any choice that we may still make for a constraint on $X$, then there exists a function $\phi$ of $E$ such that

$$\text{sign} \ [\ln[R_0(X,E_0)]+\phi(E)] = \text{sign} \ \ln[R_0(X,E)]. \quad (9)$$
**Theorem 11** (last part of the answer to question iii):

1. If the maximisation principle from corollary 10.1 holds good for all possible choices of $E_0$, then it is possible to write

   $$ r(X,E) = \alpha(\psi(X),E), $$

   (10)

   with $\alpha$ increasing in its first argument and $\psi(X) = r(X,E_0)$ for some, arbitrary but fixed, $E_0$.

2. If the maximisation principle from corollary 9.2 holds good for all possible choices of $E_0$, then it is possible to write

   $$ R_0(X,E) = \exp[\beta(\psi(X),E)], $$

   (11)

   with $\beta$ increasing in its first argument and $\psi(X) = \ln[R_0(X,E_0)]$ for some, arbitrary but fixed, $E_0$.

**Proof:** The maximisation of, say, $\gamma(X,E)$, $E$ fixed, can only lead to the same value of the maximum as the maximisation of $\gamma(X,E_0)$ for all possible constraints if $\gamma(X,E_0)$ and $\gamma(X,E)$, considered as functions of $X$, are related by an increasing function: $\gamma(X,E) = f(\gamma(X,E_0),E,\gamma)$, where the last argument is put in to indicate that the choice of $f$ is necessarily dependent on the specific function $\gamma$ under consideration. For any given $E$ and $\gamma$ the function $f$ is necessarily unique.

In cases 1 and 2 we define $\alpha(\psi,E) := f(\psi,E,r)$ respectively $\beta(\psi,E) := \ln[f(\psi,E,R_0)]$. 