Influence of caste polyethism on longevity of workers in social insect colonies
Appendix

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This is a *Mathematica* 4.0 notebook.

1 Simplified model

It is assumed that there are two sets of tasks, A and B, which are associated with aging-independent mortality rates **mA** and **mB** respectively. In the simplified model aging does not affect the mortality of workers until a certain age is reached, when resources become exhausted. At that time all workers die. A worker cannot spend more than the maximum resource **k** available for the whole life. The rates of resource expenditure during tasks A and B are **cA** and **cB** respectively. In the model the expected longevity of workers in colonies with and without caste polyethism is compared. If there is no polyethism, the workers perform tasks A and B in turn. If caste polyethism is present the workers from caste A perform only A-type tasks during the whole life and the workers from caste B perform only B-type tasks during the whole life. It is assumed that a fixed proportion of time **f** is devoted in the colony to A-type tasks, $\mathbf{f} = \frac{\mathbf{tA}}{\mathbf{tA} + \mathbf{tB}}$, where **tA** and **tB** are the time spent in the colony on tasks A and B respectively. To simplify further computations it is better to write it another way:

$$\mathbf{tB} = \frac{\mathbf{tA}\,(1 - \mathbf{f})}{\mathbf{f}};$$

In colonies with caste polyethism the proportion of workers from caste A is given by

$$\mathbf{fw} = \frac{\frac{tA}{wA}}{\frac{tA}{wA} + \frac{tB}{wB}}$$

```
fw = Simplify[%]
```

$$\frac{\frac{tA}{wA}}{\frac{tA}{wA} + \frac{(1-f)\,tA}{f\,wB}}$$

$$\frac{f\,wB}{wA - f\,wA + f\,wB}$$

1.1 General case

Error messages are switched off.

```
Off[General::spell1]
Off[General::inum]
```

The expected longevity of workers in colonies without polyethism (for details see Tofilski 2002) is given by

$$\mathbf{p0} = \int_0^{\frac{k}{cA\,f + cB\,(1-f)}} \mathbf{Exp}[-(mA\,f + mB\,(1 - f))\,t]\,dt$$

```
p0 = Simplify[%]
```

$$\frac{1}{f\,mA + mB - f\,mB} - \frac{e^{-\frac{k\,(f\,mA + mB - f\,mB)}{cB\,(1-f) + cA\,f}}}{f\,mA + mB - f\,mB}$$

$$-\frac{-1+e^{\frac{k\,(f\,(mA-mB)+mB)}{cB\,(-1+f)-cA\,f}}}{f\,(mA-mB)+mB}$$

The expected longevity of workers from caste A is given by

```
wA = Integrate[Exp[-mA t], {t, 0, k/cA}]
wA = Simplify[%]
```

$$\frac{1}{mA}-\frac{e^{-\frac{k\,mA}{cA}}}{mA}$$

$$\frac{1-e^{-\frac{k\,mA}{cA}}}{mA}$$

The expected longevity of workers from caste B is given by

```
wB = Integrate[Exp[-mB t], {t, 0, k/cB}]
wB = Simplify[%]
```

$$\frac{1}{mB}-\frac{e^{-\frac{k\,mB}{cB}}}{mB}$$

$$\frac{1-e^{-\frac{k\,mB}{cB}}}{mB}$$

The proportion of workers from caste A is given by

```
fw = wB f / (wA (1 - f) + wB f)
```

$$\frac{\left(1-e^{-\frac{k\,mB}{cB}}\right)f}{\left(\frac{\left(1-e^{-\frac{k\,mA}{cA}}\right)(1-f)}{mA}+\frac{\left(1-e^{-\frac{k\,mB}{cB}}\right)f}{mB}\right)mB}$$

The expected longevity of workers in colonies with caste polyethism is given by

```
pw = wA fw + wB (1 - fw)
pw = Simplify[%]
```

$$\frac{\left(1-e^{-\frac{k\,mA}{cA}}\right)\left(1-e^{-\frac{k\,mB}{cB}}\right)f}{mA\left(\frac{\left(1-e^{-\frac{k\,mA}{cA}}\right)(1-f)}{mA}+\frac{\left(1-e^{-\frac{k\,mB}{cB}}\right)f}{mB}\right)mB}+\frac{\left(1-e^{-\frac{k\,mB}{cB}}\right)\left(1-\frac{\left(1-e^{-\frac{k\,mB}{cB}}\right)f}{\left(\frac{\left(1-e^{-\frac{k\,mA}{cA}}\right)(1-f)}{mA}+\frac{\left(1-e^{-\frac{k\,mB}{cB}}\right)f}{mB}\right)mB}\right)}{mB}$$

$$-\frac{\left(-1+e^{\frac{k\,mA}{cA}}\right)\left(-1+e^{\frac{k\,mB}{cB}}\right)}{e^{\frac{k\,mA}{cA}}\,f\,mA-e^{\frac{k\,mB}{cB}}\,(-1+f)\,mB+e^{\frac{k\,mA}{cA}+\frac{k\,mB}{cB}}\,(-f\,mA-mB+f\,mB)}$$

Mathematica is unable to calculate analytically under what **mB** the expected longevity of workers in colonies with and without caste polyethism is the same.

```
Solve[pw == p0, mB]
```

```
Solve::tdep : The equations appear to involve the variables to be solved for in an essentially non-algebraic way.
```

$$\text{Solve}\left[-\frac{\left(-1+e^{\frac{k\,mA}{cA}}\right)\left(-1+e^{\frac{k\,mB}{cB}}\right)}{e^{\frac{k\,mA}{cA}}\,f\,mA-e^{\frac{k\,mB}{cB}}\,(-1+f)\,mB+e^{\frac{k\,mA}{cA}+\frac{k\,mB}{cB}}\,(-f\,mA-mB+f\,mB)}==-\frac{-1+e^{\frac{k\,(f\,(mA-mB)+mB)}{cB\,(-1+f)-cA\,f}}}{f\,(mA-mB)+mB},\ mB\right]$$

1.2 Solution

It was noticed that the expected longevity of workers in colonies with and without caste polyethism is the same when

$$mB=\frac{cB\,mA}{cA};$$

The expected longevity of workers in colonies without polyethism is given by

$$p0s=\int_0^{\frac{k}{cA\,f+cB\,(1-f)}}\text{Exp}[-(mA\,f+mB\,(1-f))\,t]\,dt$$

$$p0s=\text{Simplify}[\%]$$

$$\frac{cA}{(cB+cA\,f-cB\,f)\,mA}-\frac{cA\,e^{-\frac{(cB+cA\,f-cB\,f)\,k\,mA}{cA\,(cB\,(1-f)+cA\,f)}}}{(cB+cA\,f-cB\,f)\,mA}$$

$$\frac{cA-cA\,e^{-\frac{k\,mA}{cA}}}{cB\,mA+cA\,f\,mA-cB\,f\,mA}$$

The expected longevity of workers from caste A is given by

$$wAs=\int_0^{\frac{k}{cA}}\text{Exp}[-mA\,t]\,dt$$

$$wAs=\text{Simplify}[\%]$$

$$\frac{1}{mA}-\frac{e^{-\frac{k\,mA}{cA}}}{mA}$$

$$\frac{1-e^{-\frac{k\,mA}{cA}}}{mA}$$

The expected longevity of workers from caste B is given by

$$wBs=\int_0^{\frac{k}{cB}}\text{Exp}[-mB\,t]\,dt$$

$$wBs=\text{Simplify}[\%]$$

$$\frac{cA}{cB\,mA}-\frac{cA\,e^{-\frac{k\,mA}{cA}}}{cB\,mA}$$

$$\frac{cA-cA\,e^{-\frac{k\,mA}{cA}}}{cB\,mA}$$

The proportion of workers from caste A is given by

```
fws = wBs f / (wAs (1 - f) + wBs f)
fws = Simplify[%]
```

$$\frac{\left(cA - cA\, e^{-\frac{k\, mA}{cA}}\right) f}{cB\left(\frac{\left(1 - e^{-\frac{k\, mA}{cA}}\right)(1-f)}{mA} + \frac{\left(cA - cA\, e^{-\frac{k\, mA}{cA}}\right) f}{cB\, mA}\right) mA}$$

$$\frac{cA\, f}{cB + cA\, f - cB\, f}$$

The expected longevity of workers in colonies with caste polyethism is given by

```
pws = wAs fws + wBs (1 - fws)
pws = Simplify[%]
```

$$\frac{cA\left(1 - e^{-\frac{k\, mA}{cA}}\right) f}{(cB + cA\, f - cB\, f)\, mA} + \frac{\left(cA - cA\, e^{-\frac{k\, mA}{cA}}\right)\left(1 - \frac{cA\, f}{cB + cA\, f - cB\, f}\right)}{cB\, mA}$$

$$\frac{cA - cA\, e^{-\frac{k\, mA}{cA}}}{cB\, mA + cA\, f\, mA - cB\, f\, mA}$$

It can be demonstrated that the expected longevity of workers in colonies with and without caste polyethism is the same when $mB = \frac{cB\, mA}{cA}$.

```
pws == p0s
```

```
True
```

1.3 Numerical solution

The way in which the problem was solved does not imply that there is only one solution. Therefore the equations are solved numerically here.

Numerical values are assigned to the parameters.

```
cA = 2;
cB = 4;
k = 200;
f = 0.5;
mA = 0.01;
mB = .
```

It is calculated numericaly under what `mB` the expected longevity of workers in colonies with and without caste polyethism is the same.

```
FindRoot[pw == p0, {mB, 0.001}, AccuracyGoal → 15, MaxIterations → 50]
```

```
{mB → 0.02}
```

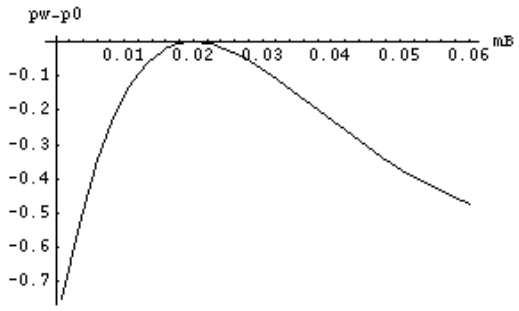
It is confirmed that the value calculated above equals

```
cB mA / cA
```

```
0.02
```

The difference in expected longevity of workers between colonies with and without caste polyethism is plotted.

```
Plot[pw - p0, {mB, 0.001, 0.06}, AxesLabel → {"mB", "pw-p0"}];
```



1.3 Absence of aging

The previous definition of the parameters has to be removed to allow analytical computation.

```
cA = .
cB = .
k = .
f = .
mA = .
mB = .
```

If there is no aging (`cA` = `cB` = 0) the maximum life span is infinity.

The expected longevity of workers in colonies without polyethism is given by

```
p00 = ∫_0^∞ Exp[-(mA f + mB (1 - f)) t] dt
p00 = Simplify[% /. {Re[f mA + mB - f mB] > 0 → True}]
```

$$\text{If}\left[\text{Re}[f\,mA + mB - f\,mB] > 0,\ \frac{1}{f\,mA + mB - f\,mB},\ \int_0^{\infty} e^{(-f\,mA-(1-f)\,mB)\,t}\,dt\right]$$

$$\frac{1}{f\,mA + mB - f\,mB}$$

The expected longevity of workers from caste A is given by

```
wA0 = ∫_0^∞ Exp[-mA t] dt
wA0 = % /. {Re[mA] > 0 → True}
```

$$\text{If}\left[\text{Re}[mA] > 0,\ \frac{1}{mA},\ \int_0^{\infty} e^{-mA\,t}\,dt\right]$$

$$\frac{1}{mA}$$

The expected longevity of workers from caste B is given by

```
wB0 = ∫_0^∞ Exp[-mB t] dt
wB0 = % /. {Re[mB] > 0 → True}
```

$$\text{If}\left[\text{Re}[mB] > 0,\ \frac{1}{mB},\ \int_0^{\infty} e^{-mB\,t}\,dt\right]$$

$$\frac{1}{mB}$$

The proportion of workers from caste A is given by

```
fw0 = wB0 f / (wA0 (1 - f) + wB0 f)
fw0 = Simplify[%]
```

$$\frac{f}{\left(\frac{1-f}{mA} + \frac{f}{mB}\right) mB}$$

$$\frac{f\,mA}{f\,mA + mB - f\,mB}$$

The expected longevity of workers in colonies with caste polyethism is given by

```
pw0 = wA0 fw0 + wB0 (1 - fw0)
pw0 = Simplify[%]
```

$$\frac{f}{f\,mA + mB - f\,mB} + \frac{1 - \frac{f\,mA}{f\,mA+mB-f\,mB}}{mB}$$

$$\frac{1}{f\,mA + mB - f\,mB}$$

It can be demonstrated that the expected longevity of workers in colonies with caste polyethism is the same as in colonies without polyethism when there is no aging (`cA = cB = 0`).

```
pw0 == p00
```

```
True
```

2 More general model

It is assumed that mortality rate `r` increases exponentially with age `t`: $r = m + \alpha t^{\beta}$, where `m` is aging-independent mortality. Aging-related mortality is described by two parameters: `α` controlling the magnitude of this mortality, and `β` controlling the shape of the curve depicting changes of aging-related mortality with age. Aging-related mortality `α` associated with tasks A and B is `αA` and `αB` respectively. Tasks A and B are associated with the same `β` .

The expected longevity of workers in colonies without polyethism (for details see Tofilski 2002) is given by

$$p0x = \int_0^{\infty} Exp\left[-(mA\,f + mB\,(1-f))\,t - \frac{1}{\beta+1}\,\alpha B\left((1-f)\,t + \sqrt[\beta+1]{\frac{\alpha A}{\alpha B}}\,f\,t\right)^{\beta+1}\right] dt;$$

The expected longevity of workers from caste A is given by

$$wAx = \int_0^{\infty} Exp\left[-mA\,t - \frac{\alpha A\,t^{\beta+1}}{\beta+1}\right] dt;$$

The expected longevity of workers from caste B is given by

$$wBx = \int_0^{\infty} Exp\left[-mB\,t - \frac{\alpha B\,t^{\beta+1}}{\beta+1}\right] dt;$$

The proportion of workers from caste A is given by

```
fwx = wBx f / (wAx (1 - f) + wBx f);
fwx = Simplify[%];
```

The expected longevity of workers in colonies with caste polyethism is given by

```
pwx = wAx fwx + wBx (1 - fwx);
pwx = Simplify[%];
```

Numerical values are assigned to the parameters.

```
αA = 1.*^-7;
αB = 1.*^-7;
β = 3;
f = 0.5;
mA = 0.01;
mB = .
```

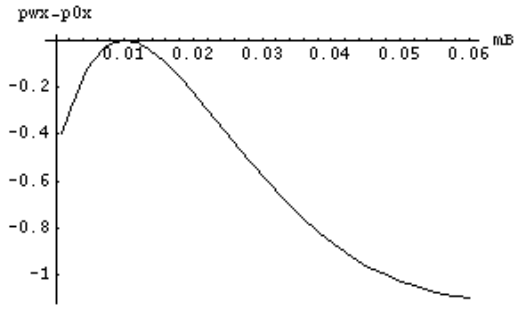
It can be demonstrated that the expected longevity of workers in colonies with and without caste polyethism is the same when aging-related mortalities are the same (`αA = αB`) and aging-independent mortalities are the same (`mA = mB`).

```
FindRoot[pwx == p0x, {mB, {0.001, 0.1}}, AccuracyGoal → 15, MaxIterations → 50]
```

```
{mB → 0.01}
```

The difference in expected longevity of workers between colonies with and without caste polyethism is plotted.

```
Plot[pwx-p0x,{mB, 0.001, 0.06},AxesLabel->{"mB","pwx-p0x"}];
```



Reference

Tofilski A (2002) Influence of age polyethism on longevity of workers in social insects. Behav Ecol Sociobiol 51:234-237.