

APPENDIX A: DYNAMIC PROGRAMMING EQUATIONS

Here we specify the dynamic programming equations that apply in each situation. For convenience, we use the same classification of circumstance and choice used in Table 2 of the main text. In each scenario, (a) to (g), females are presented with a series of options, $1 \dots n$. The payoffs for these options are denoted $H_1 \dots H_n$. Note that H_i in any given scenario is unique to that scenario. Changes in time are expressed as $t+1$, etc. If the increment results in a time that exceeds $t = 364$, then time is reset to $t' = t - 364$ in the following year. Similarly, increments of time that result in a foetus exceeding the gestation term (without being born) are assumed to result in resorption of the foetus.

Dynamic programming equations are based on the notation that $V(x,a,y,f,t)$ is the residual reproductive value of a female characterized by the state variables x , a , y and f at time t .

(a) *Neither pregnant nor tending* ($a = 0$)

Forage and implant:

$$H_1 = p \cdot V[x + e(t) - m_F(x), 1, 0, 0, t+1] + (1-p) \cdot V[x - m_F(x), 1, 0, 0, t+1] \quad \text{Eq. A.1}$$

Forage and don't implant:

$$H_2 = p \cdot V[x + e(t) - m_F(x), 0, 0, 0, t+1] + (1-p) \cdot V[x - m_F(x), 0, 0, 0, t+1] \quad \text{Eq. A.2}$$

Rest and implant:

$$H_3 = V[x - m_R, 1, 0, 0, t+1] \quad \text{Eq. A.3}$$

Rest and don't implant:

$$H_4 = V[x - m_R, 0, 0, 0, t+1] \quad \text{Eq. A.4}$$

So, $V(x,0,0,0,t) = S_A(x) \cdot \max(H_1, H_2, H_3, H_4)$,
where S_A is the survival of adults to the next time step.

(b) *Pregnant, not tending* ($0 < a < G$)

Note that aborting is assumed to take a full day, so metabolics of a female that chooses to abort are still those of a pregnant female.

Forage and retain:

$$H_1 = p \cdot V[x + e(t) - m_F(x), a+1, 0, 0, t+1] + (1-p) \cdot V[x - m_F(x), a+1, 0, 0, t+1] \quad \text{Eq. A.5}$$

Forage and abort:

$$H_2 = p \cdot V[x + e(t) - m_F(x), 0, 0, 0, t+1]$$

$$+ (1-p). V(x - m_F(x), 0, 0, 0, t+1] \quad \text{Eq. A.6}$$

Rest and retain:

$$H_3 = V[x - m_R, a+1, 0, 0, t+1] \quad \text{Eq. A.7}$$

Rest and abort:

$$H_4 = V[x - m_R, 0, 0, 0, t+1] \quad \text{Eq. A.8}$$

$$\text{So, } V(x, a, 0, 0, t) = S_A(x). \max(H_1, H_2, H_3, H_4)$$

(c) *At term, not tending ($a = G; f = 0$)*

Both aborting and giving birth are assumed to take a full day, so metabolics of a female on the day of partum are those of a pregnant female regardless of her behavioral decisions.

Forage and abort:

$$H_1 = p. V[x + e(t) - m_F(x), 0, 0, 0, t+1] + (1-p). V(x - m_F(x), 0, 0, 0, t+1] \quad \text{Eq. A.9}$$

Rest and give birth:

$$H_2 = V[x - m_R - E_{birth}, a+1, Y_{birth}, 0, t+1] \quad \text{Eq. A.10}$$

where E_{birth} is the energy lost in birth by the female and Y_{birth} is the initial energy reserves of the pup.

Rest and abort:

$$H_3 = V[x - m_R, 0, 0, 0, t+1] \quad \text{Eq. A.11}$$

$$\text{So, } V(x, G, 0, 0, t) = S_A(x). \max(H_1, H_2, H_3)$$

(d) *Tending, not pregnant, cannot implant ($G < a < G + U_R$)*

Note here, that tending and resting also permits lactation. This implies optimization over a range of possible values of L , requiring maximizing H_2 over L (see further in Appendix B). Note, also, that death is assumed to be instantaneous at the start of a period. This permits two simplifications, including (1) that if the female dies, it is assumed that the pup immediately becomes independent, and (2) that if the pup dies, the female will be faced with the same decision as described by scenario (a), where she is neither pregnant nor tending. Equally, abandonment is assumed to be immediate, with the same consequences.

Tend and forage:

$$H_1 = S_A(x) \left\{ p.V[x + e(t) - m_F(x), a + 1, y - m_P(y), 0, t + 1] \right. \\ \left. + (1 - p).V[x - m_F(x), a + 1, y - m_P(y), 0, t + 1] \right\} \\ + [1 - S_A(x)].R(a, y, t) \quad \text{Eq. A.12}$$

Note here that we do not permit both lactation and foraging within the minimum time step. That the female continues to “Tend” in this option is indicative only of the fact that she hasn’t yet abandoned the pup.

Tend and rest, $0 \leq L \leq \min[L_{\max}, x]$:

$$H_2 = S_A(x) \{ V[x - m_R - L, a + 1, y + \alpha L - m_P(y), 0, t + 1] \} \\ + [1 - S_A(x)].R(a, y, t) \quad \text{Eq. A.13}$$

Here, α is the efficiency of energy transfer from mother to pup (by lactation). The range of L is determined by the smaller of L_{\max} , the maximum amount of energy that can be passed from mother to pup in a single day, and x , the amount of reserves available (where the two values are expressed in units relative to the maximum possible reserves that a female can carry).

Abandon:

$$H_3 = R(a, y, t) + V(x, 0, 0, 0, k, t) \quad \text{Eq. A.14}$$

$$\text{So, } V(x, a, y, 0, t) = S_P(y). \max(H_1, H_2, H_3) + [1 - S_P(y)]. V(x, 0, 0, 0, t)$$

(e) *Tending, can implant* ($a \geq G + U_R; f = 0$)

As in scenario (a), implantation is assumed to be immediate. Note that a need never exceed $U_R + 1$ because, beyond that, no behaviour is restricted by the value of a . Thus, here we use a' to indicate any value of $a > G + U_R$.

Tend, forage and implant:

$$H_1 = S_A(x) \left\{ p.V[x + e(t) - m_F(x), a', y - m_P(y), 1, t + 1] \right. \\ \left. + (1 - p).V[x - m_F(x), a', y - m_P(y), 1, t + 1] \right\} \\ + [1 - S_A(x)].R(a, y, t) \quad \text{Eq. A.15}$$

Tend, forage and don’t implant:

$$H_2 = S_A(x) \left\{ p.V[x + e(t) - m_F(x), a', y - m_P(y), 0, t + 1] \right. \\ \left. + (1 - p).V[x - m_F(x), a', y - m_P(y), 0, t + 1] \right\} \\ + [1 - S_A(x)].R(a, y, t) \quad \text{Eq. A.16}$$

Tend, rest and implant, $0 \leq L \leq \min[L_{\max}, x]$:

$$H_3 = S_A(x) \{ V[x - m_R - L, a', y + \alpha L - m_P(y), 1, t + 1] \} \\ + [1 - S_A(x)].R(a, y, t) \quad \text{Eq. A.17}$$

Tend, rest and don't implant, $0 \leq L \leq \min[L_{\max}, x]$:

$$H_4 = S_A(x) \{ V[x - m_R - L, a', y + \alpha L - m_P(y), 0, t + 1] \} \\ + [1 - S_A(x)].R(a, y, t) \quad \text{Eq. A.18}$$

Abandon:

$$H_5 = R(a, y, t) + V(x, 0, 0, 0, k, t) \quad \text{Eq. A.19}$$

So, $V(x, a, y, 0, t) = S_P(y). \max(H_1, H_2, H_3, H_4, H_5) + [1 - S_P(y)].V(x, 0, 0, 0, t)$

(f) *Tending and pregnant* ($0 < f < G$)

Tend, forage and retain:

$$H_1 = S_A(x) \left\{ p.V[x + e(t) - m_F(x), a', y - m_P(y), f + 1, t + 1] \right. \\ \left. + (1 - p).V[x - m_F(x), a', y - m_P(y), f + 1, t + 1] \right\} \\ + [1 - S_A(x)].R(a, y, t) \quad \text{Eq. A.20}$$

Tend, forage and abort:

$$H_2 = S_A(x) \left\{ p.V[x + e(t) - m_F(x), a', y - m_P(y), 0, t + 1] \right. \\ \left. + (1 - p).V[x - m_F(x), a', y - m_P(y), 0, t + 1] \right\} \\ + [1 - S_A(x)].R(a, y, t) \quad \text{Eq. A.21}$$

Tend, rest and retain, $0 \leq L \leq \min[L_{\max}, x]$:

$$H_3 = S_A(x) V[x - m_R - L, a', y + \alpha L - m_P(y), f + 1, t + 1] \\ + [1 - S_A(x)].R(a, y, t) \quad \text{Eq. A.22}$$

Tend, rest and abort, $0 \leq L \leq \min[L_{\max}, x]$:

$$H_4 = S_A(x) V[x - m_R - L, a', y + \alpha L - m_P(y), 0, t + 1] \\ + [1 - S_A(x)].R(a, y, t) \quad \text{Eq. A.23}$$

Abandon:

$$H_5 = R(a, y, t) + V(x, f, 0, 0, t) \quad \text{Eq. A.24}$$

So, $V(x, a, y, f, t) = S_P(y). \max(H_1, H_2, H_3, H_4, H_5) + [1 - S_P(y)].V(x, f, 0, 0, t)$

(g) *Tending with foetus at term ($f = G$)*

Note that (in our model) a female cannot tend two pups simultaneously, hence she must either abandon her pup when a second foetus reaches term, or must abort the foetus. The options here are effectively the same as in scenario (f) but we separate scenarios (f) and (g) in order to emphasize that difference.

Tend, forage and abort:

$$H_1 = S_A(x) \left\{ p.V[x + e(t) - m_F(x), a', y - m_P(y), 0, t + 1] \right. \\ \left. + (1 - p).V[x - m_F(x), a', y - m_P(y), 0, t + 1] \right\} \\ + [1 - S_A(x)].R(a, y, t) \quad \text{Eq. A.25}$$

Tend, rest and abort, $0 \leq L \leq \min[L_{\max}, x]$:

$$H_2 = S_A(x)V[x - m_R - L, a', y + \alpha L - m_P(y), 0, t + 1] \\ + [1 - S_A(x)].R(a, y, t) \quad \text{Eq. A.26}$$

Abandon:

$$H_3 = R(a, y, t) + V(x, f, 0, 0, t) \quad \text{Eq. A.27}$$

$$\text{So, } V(x, a, y, f, t) = S_P(y). \max(H_1, H_2, H_3) + [1 - S_P(y)].V(x, f, 0, 0, t)$$

In general, we seek the decisions that maximize reproductive value, defined (for any given state) as $V(x, a, y, f, t)$. Reproductive value is maximized at each decision epoch and maxima are assumed to be reached when the summed annual change in reproductive values of all states at $t = 0$ is less than 10^{-5} .