

- 1  
2  
3 [28] Witter, R.L. (1997), “Mareks disease: a worldwide problem.” *Avian Diseases*, 41(1), 149–  
4 163.  
5  
6  
7  
8 [29] Witter, R.L. (2001), “Marek’s disease vaccines - past, present and future. in: Current progress  
9 on marek’s disease research, proceedings of the 6th international symposium on marek’s  
10 disease.” *American Association of Avian Pathologist, Pennsylvania*, 1–9.  
11  
12  
13 [30] Witter, R.L., G.H. Burgoyne, and B.R. Burmester (1968), “Survival of marek’s disease agent  
14 in litter and droppings.” *Avian diseases*, 522–530.  
15  
16  
17 [31] Witter, R.L., J.I. Moulthrop Jr, G.H. Burgoyne, and H.C. Connell (1970), “Studies on the  
18 epidemiology of marek’s disease herpesvirus in broiler flocks.” *Avian diseases*, 255–267.  
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## 27 **5 Appendix: ESS**

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30 Recall that the evolutionary stable virulence level will maximize:

$$31 \frac{\beta(v)}{v - \frac{\ln(k\beta(v))}{T}}$$

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34 By taking the derivative of the above with respect to  $v$ , we can find an expression for  $\frac{d\beta(v^*)}{dv}$ , the  
35 slope of the transmission rate as a function of the evolutionary stable virulence level  $v^*$ .  
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$$38 \frac{d\beta(v^*)}{dv} = \frac{\beta(v^*)}{v^* - \frac{1}{T} \ln(k\beta(v^*)) + \frac{1}{T}}$$

### 39 **5.1 $dv^*/dT$**

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42 First we rewrite (10) as a function of  $v$  and  $T$  and we let this function be denoted  $R(v, T)$ .  
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$$45 \frac{d\beta(v^*)}{dv} = \frac{\beta(v)}{v - \frac{\ln(k\beta(v))}{T}}$$

Let  $R_v(v, T) = F(v^*, T)$

$$F(v^*, T) = \frac{\frac{d\beta(v^*)}{dv}(v^* - \frac{1}{T} \ln(k\beta(v^*))) - \beta(v^*)(1 - \frac{1}{T\beta(v^*)} \frac{d\beta(v^*)}{dv})}{(v^* - \frac{1}{T} \ln(k\beta(v^*)))^2}$$

If we differentiate  $F(v^*, T)$  with respect to  $T$  and then substitute in  $\frac{d\beta(v^*)}{dv}$  we get:

$$F_T(v^*, T) = -\frac{\beta(v^*)T(\ln(k\beta(v^*)) - 1)}{(-v^*T + \ln(k\beta(v^*)))^2(-v^*T + \ln(k\beta(v^*)) - 1)} < 0$$

If we differentiate  $F(v^*, T)$  with respect to  $v$  and then substitute in  $\frac{d\beta(v^*)}{dv}$  we get:

$$F_{v^*}(v^*, T) = -T \frac{A + B + C}{D} < 0$$

provided  $\frac{d^2\beta}{dv^{*2}} < 0$ .

where:

$$A = -\frac{d^2\beta(v^*)}{dv^{*2}}T^3v^{*3} + 3T^2v^{*2}\frac{d^2\beta(v^*)}{dv^{*2}}\ln(k\beta(v^*)) - 3T^2v^{*2}\frac{d^2\beta(v^*)}{dv^{*2}} + \frac{d^2\beta(v^*)}{dv^{*2}}(\ln(k\beta(v^*)))^3 > 0$$

$$B = 6Tv^*\frac{d^2\beta(v^*)}{dv^{*2}}(\ln(k\beta(v^*))) + \beta(v^*)T^2 > 0$$

$$C = -3\frac{d^2\beta(v^*)}{dv^{*2}}(\ln(k\beta(v^*)))^2 - 3\frac{d^2\beta(v^*)}{dv^{*2}}v^*T + 3\frac{d^2\beta(v^*)}{dv^{*2}}\ln(k\beta(v^*)) - \frac{d^2\beta(v^*)}{dv^{*2}} > 0$$

and

$$D = (-v^*T + \ln(k\beta(v^*)))^2(-v^*T + \ln(k\beta(v^*)) - 1)^2 > 0$$

Finally if we implicitly differentiate  $F(v^*, T) = 0$  with respect to  $T$  and treat optimal virulence,  $v^*$ , as a function of cohort duration,  $T$ , we get:

$$F_{v^*}(v^*, T) \frac{dv^*}{dT} + F_T(v^*, T) = 0$$

From which we have,

$$\frac{dv^*}{dT} = -\frac{F_T(v^*, T)}{F_{v^*}(v^*, T)} < 0$$

## 5.2 $dv^*/dk$

Next we rewrite (10) as a function of  $v$  and  $k$  and we let this function be denoted  $S(v, k)$ . We let  $G(v^*, k) = S_v(v^*, k)$  and treat the optimal virulence level,  $v^*$ , as a function of  $k$ .

$$G(v^*, k) = S_v(v^*, k) = R_v(v^*, T) = \frac{\frac{d\beta(v^*)}{dv}(v^* - \frac{1}{T} \ln(k\beta(v^*))) - \beta(v^*)(1 - \frac{1}{T\beta(v^*)} \frac{d\beta(v^*)}{dv})}{(v^* - \frac{1}{T} \ln(k\beta(v^*)))^2}$$

and by differentiating  $G(v^*, k)$  with respect to  $k$  and substituting in  $\frac{d\beta(v^*)}{dv}$  we get:

$$G_k(v^*, k) = \frac{\beta(v^*)T^2(k+1)}{k(-v^*kT + k \ln(k\beta(v^*)) - 1)(-v^*T + \ln(k\beta(v^*)))^2} < 0$$

Finally if we implicitly differentiate  $G(v^*, T) = 0$  with respect to  $k$  and treat optimal virulence,  $v^*$ , as a function of cohort duration,  $k$ , we get:

$$G_{v^*}(v^*, T) \frac{dv^*}{dk} + G_k(v^*, T) = 0$$

From which we have,

$$\frac{dv^*}{dk} = -\frac{G_k(v^*, k)}{G_{v^*}(v^*, k)} < 0$$