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1 **Estimation of environmental, genetic and parental age at conception effects on telomere length in**  
2 **a wild mammal**

3 Sil H.J. van Lieshout, Alexandra M. Sparks, Amanda Bretman, Chris Newman, Christina D. Buesching,

4 Terry Burke, David W. Macdonald & Hannah L. Dugdale

5

6 **Table S1** Metrics of the Wytham badger pruned pedigree (1987 – 2010).

| <b>Relationship</b>   | <b><i>n</i></b> | <b>Relationship</b>               | <b><i>n</i></b> |
|-----------------------|-----------------|-----------------------------------|-----------------|
| Records               | 753             | Paternal grandmothers             | 261             |
| Max. pedigree depth   | 7               | Paternal grandfathers             | 214             |
| Maternities           | 486             | Founders                          | 206             |
| Paternities           | 458             | Mean maternal sibship size        | 2.48            |
| Full sibs             | 194             | Mean paternal sibship size        | 2.59            |
| Maternal sibs         | 691             | Non-zero F                        | 29              |
| Paternal sibs         | 880             | F > 0.125                         | 11              |
| Maternal half sibs    | 497             | Mean pairwise relatedness         | 0.007           |
| Paternal half sibs    | 686             | Pairwise relatedness $\geq 0.125$ | 0.023           |
| Maternal grandmothers | 196             | Pairwise relatedness $\geq 0.25$  | 0.013           |
| Maternal grandfathers | 174             | Pairwise relatedness $\geq 0.5$   | 0.004           |

7

8 **Table S2** Additive genetic and environmental effects on relative leukocyte telomere length (RLTL) in European badgers, estimated using the ‘animal model’  
9 with *MCMCglmm* 2.25 (Hadfield 2010). Nine models are presented with random effects for additive genetic and permanent environment variance  
10 components (models 1–7,  $n=1248$ ; model 8,  $n=997$ , model 9,  $n=837$ ). Model 8 only includes offspring in the pedigree that have at least one parent assigned.  
11 Subsequently, fixed and random effects are sequentially added to determine their effect on heritability. Values represent the posterior modes and 95%  
12 credible intervals of the variance estimates ( $V_A$  = additive genetic,  $V_{PE}$  = permanent environment,  $V_{PLATE}$  = plate,  $V_{ROW}$  = Row,  $V_{CO}$  = cohort,  $V_{YEAR}$  = year,  $V_{SG}$  =  
13 social group,  $V_{MAT}$  = maternal,  $V_{PAT}$  = paternal,  $V_R$  = residual,  $V_P$  = phenotypic). Age = threshold age,  $h^2$  = heritability.

| Model | Parameters   | $V_A$  | $V_{PE}$   | $V_{PLATE}$   | $V_{ROW}$  | $V_{CO}$  | $V_{YEAR}$  | $V_{SG}$   | $V_{MAT}$  | $V_{PAT}$  | $V_R$   | $h^2$  |
|-------|--|--|--|---|--|---|---|--|--|--|---|--|
| 1     | RLTL = $V_A + V_{PE}$  | 1.514*10 <sup>-5</sup><br>(3.251*10 <sup>-9</sup> –<br>2.903*10 <sup>-3</sup> )  | 1.195*10 <sup>-5</sup><br>(1.727*10 <sup>-10</sup> –<br>2.252*10 <sup>-3</sup> ) |   |  |   |   |  |  |  | 3.278*10 <sup>-2</sup><br>(2.940*10 <sup>-2</sup> –<br>3.514*10 <sup>-2</sup> ) | 3.847*10 <sup>-4</sup><br>(9.000*10 <sup>-8</sup> –<br>8.442*10 <sup>-2</sup> )  |
| 2     | RLTL = $V_A + V_{PE} + \text{Age} + \text{Season}$   | 1.994*10 <sup>-5</sup><br>(9.028*10 <sup>-11</sup> –<br>2.574*10 <sup>-3</sup> ) | 1.551*10 <sup>-5</sup><br>(1.386*10 <sup>-11</sup> –<br>2.141*10 <sup>-3</sup> ) |   |  |   |   |  |  |  | 3.173*10 <sup>-2</sup><br>(2.888*10 <sup>-2</sup> –<br>3.475*10 <sup>-2</sup> ) | 3.408*10 <sup>-4</sup><br>(2.974*10 <sup>-9</sup> –<br>7.599*10 <sup>-2</sup> )  |
| 3     | RLTL = $V_A + V_{PE} + \text{Age} + \text{Season} + V_{PLATE} + V_{ROW}$   | 1.371*10 <sup>-5</sup><br>(8.968*10 <sup>-11</sup> –<br>2.679*10 <sup>-3</sup> ) | 8.569*10 <sup>-6</sup><br>(4.241*10 <sup>-10</sup> –<br>2.157*10 <sup>-3</sup> ) | 1.842*10 <sup>-3</sup><br>(7.412*10 <sup>-4</sup> –<br>3.728*10 <sup>-3</sup> ) | 2.281*10 <sup>-4</sup><br>(2.168*10 <sup>-7</sup> –<br>2.087*10 <sup>-3</sup> )  |   |   |  |  |  | 2.960*10 <sup>-2</sup><br>(2.682*10 <sup>-2</sup> –<br>3.248*10 <sup>-2</sup> ) | 3.589*10 <sup>-4</sup><br>(2.636*10 <sup>-9</sup> –<br>7.943*10 <sup>-2</sup> )  |
| 4     | RLTL = $V_A + V_{PE} + \text{Age} + \text{Season} + V_{PLATE} + V_{ROW} + V_{CO}$  | 1.544*10 <sup>-5</sup><br>(2.218*10 <sup>-9</sup> –<br>1.816*10 <sup>-3</sup> )  | 6.133*10 <sup>-6</sup><br>(1.152*10 <sup>-9</sup> –<br>1.739*10 <sup>-3</sup> )  | 2.014*10 <sup>-3</sup><br>(7.811*10 <sup>-4</sup> –<br>3.681*10 <sup>-3</sup> ) | 2.541*10 <sup>-4</sup><br>(3.329*10 <sup>-14</sup> –<br>2.050*10 <sup>-3</sup> ) | 1.755*10 <sup>-3</sup><br>(7.539*10 <sup>-4</sup> –<br>5.310*10 <sup>-3</sup> ) |   |  |  |  | 2.898*10 <sup>-2</sup><br>(2.617*10 <sup>-2</sup> –<br>3.124*10 <sup>-2</sup> ) | 3.445*10 <sup>-4</sup><br>(5.715*10 <sup>-8</sup> –<br>5.102*10 <sup>-2</sup> )  |
| 5     | RLTL = $V_A + V_{PE} + \text{Age} + \text{Season} + V_{PLATE} + V_{ROW} + V_{CO} + V_{YEAR}$                                       | 8.043*10 <sup>-6</sup><br>(4.165*10 <sup>-12</sup> –<br>1.571*10 <sup>-3</sup> ) | 5.448*10 <sup>-6</sup><br>(1.352*10 <sup>-9</sup> –<br>1.528*10 <sup>-3</sup> )  | 1.898*10 <sup>-3</sup><br>(1.011*10 <sup>-3</sup> –<br>4.073*10 <sup>-3</sup> ) | 3.323*10 <sup>-4</sup><br>(6.150*10 <sup>-9</sup> –<br>2.372*10 <sup>-3</sup> )  | 1.147*10 <sup>-3</sup><br>(3.697*10 <sup>-4</sup> –<br>3.632*10 <sup>-3</sup> ) | 1.196*10 <sup>-2</sup><br>(4.353*10 <sup>-3</sup> –<br>2.470*10 <sup>-2</sup> ) |  |  |  | 2.574*10 <sup>-2</sup><br>(2.339*10 <sup>-2</sup> –<br>2.807*10 <sup>-2</sup> ) | 2.284*10 <sup>-4</sup><br>(8.823*10 <sup>-11</sup> –<br>3.443*10 <sup>-2</sup> ) |
| 6     | RLTL = $V_A + V_{PE} + \text{Age} + \text{Season} + V_{PLATE} + V_{ROW} + V_{CO} + V_{YEAR} + V_{SG}$                              | 4.427*10 <sup>-6</sup><br>(4.073*10 <sup>-10</sup> –<br>1.455*10 <sup>-3</sup> ) | 8.682*10 <sup>-6</sup><br>(3.660*10 <sup>-10</sup> –<br>1.522*10 <sup>-3</sup> ) | 1.874*10 <sup>-3</sup><br>(9.780*10 <sup>-4</sup> –<br>4.132*10 <sup>-3</sup> ) | 3.104*10 <sup>-4</sup><br>(8.686*10 <sup>-9</sup> –<br>2.325*10 <sup>-3</sup> )  | 1.215*10 <sup>-3</sup><br>(4.251*10 <sup>-4</sup> –<br>3.651*10 <sup>-3</sup> ) | 1.027*10 <sup>-2</sup><br>(4.887*10 <sup>-3</sup> –<br>2.563*10 <sup>-2</sup> ) | 3.283*10 <sup>-6</sup><br>(1.556*10 <sup>-10</sup> –<br>7.129*10 <sup>-4</sup> ) |  |  | 2.554*10 <sup>-2</sup><br>(2.355*10 <sup>-2</sup> –<br>2.817*10 <sup>-2</sup> ) | 1.786*10 <sup>-4</sup><br>(1.122*10 <sup>-8</sup> –<br>3.214*10 <sup>-2</sup> )  |
| 7     | RLTL = $V_A + V_{PE} + \text{Age} + \text{Season} + V_{PLATE} + V_{ROW} + V_{CO} + V_{YEAR} + V_{SG} + V_{MAT} + V_{PAT}$          | 8.544*10 <sup>-6</sup><br>(1.012*10 <sup>-9</sup> –<br>1.185*10 <sup>-3</sup> )  | 8.635*10 <sup>-6</sup><br>(3.867*10 <sup>-10</sup> –<br>1.227*10 <sup>-3</sup> ) | 2.035*10 <sup>-3</sup><br>(9.682*10 <sup>-4</sup> –<br>4.117*10 <sup>-3</sup> ) | 5.146*10 <sup>-4</sup><br>(6.728*10 <sup>-7</sup> –<br>2.456*10 <sup>-3</sup> )  | 1.210*10 <sup>-3</sup><br>(2.855*10 <sup>-4</sup> –<br>3.360*10 <sup>-3</sup> ) | 1.161*10 <sup>-2</sup><br>(4.662*10 <sup>-3</sup> –<br>2.586*10 <sup>-2</sup> ) | 2.560*10 <sup>-6</sup><br>(3.780*10 <sup>-10</sup> –<br>6.397*10 <sup>-4</sup> ) | 1.119*10 <sup>-5</sup><br>(7.704*10 <sup>-12</sup> –<br>1.352*10 <sup>-3</sup> ) | 5.819*10 <sup>-6</sup><br>(6.900*10 <sup>-11</sup> –<br>1.107*10 <sup>-3</sup> ) | 2.525*10 <sup>-2</sup><br>(2.322*10 <sup>-2</sup> –<br>2.783*10 <sup>-2</sup> ) | 7.660*10 <sup>-5</sup><br>(2.033*10 <sup>-8</sup> –<br>2.580*10 <sup>-2</sup> )  |
| 8     | RLTL = $V_A + V_{PE} + \text{Age} + \text{Season} + V_{PLATE} + V_{ROW} + V_{CO} + V_{YEAR} + V_{SG} + V_{MAT} + V_{PAT}$          | 6.550*10 <sup>-6</sup><br>(3.662*10 <sup>-11</sup> –<br>1.033*10 <sup>-3</sup> ) | 5.740*10 <sup>-6</sup><br>(4.314*10 <sup>-10</sup> –<br>1.064*10 <sup>-3</sup> ) | 1.866*10 <sup>-3</sup><br>(7.640*10 <sup>-4</sup> –<br>3.900*10 <sup>-3</sup> ) | 5.874*10 <sup>-4</sup><br>(6.255*10 <sup>-5</sup> –<br>3.739*10 <sup>-3</sup> )  | 1.459*10 <sup>-3</sup><br>(8.142*10 <sup>-5</sup> –<br>3.594*10 <sup>-3</sup> ) | 1.083*10 <sup>-2</sup><br>(5.096*10 <sup>-3</sup> –<br>2.859*10 <sup>-2</sup> ) | 7.111*10 <sup>-6</sup><br>(1.153*10 <sup>-11</sup> –<br>1.148*10 <sup>-3</sup> ) | 6.540*10 <sup>-6</sup><br>(6.564*10 <sup>-10</sup> –<br>1.656*10 <sup>-3</sup> ) | 4.610*10 <sup>-6</sup><br>(1.073*10 <sup>-11</sup> –<br>1.361*10 <sup>-3</sup> ) | 2.648*10 <sup>-2</sup><br>(2.338*10 <sup>-2</sup> –<br>2.833*10 <sup>-2</sup> ) | 1.293*10 <sup>-4</sup><br>(6.117*10 <sup>-10</sup> –<br>2.159*10 <sup>-2</sup> ) |
| 9     | Juvenile RLTL = $V_A + V_{PE} + \text{Age} + \text{Season} + V_{PLATE} + V_{ROW} + V_{CO} + V_{YEAR} + V_{SG} + V_{MAT} + V_{PAT}$ | 1.270*10 <sup>-5</sup><br>(1.787*10 <sup>-9</sup> –<br>1.800*10 <sup>-3</sup> )  | 1.120*10 <sup>-5</sup><br>(1.308*10 <sup>-9</sup> –<br>2.119*10 <sup>-3</sup> )  | 1.566*10 <sup>-3</sup><br>(6.601*10 <sup>-4</sup> –<br>3.729*10 <sup>-3</sup> ) | 4.296*10 <sup>-5</sup><br>(9.762*10 <sup>-9</sup> –<br>1.435*10 <sup>-3</sup> )  | 1.767*10 <sup>-3</sup><br>(1.347*10 <sup>-4</sup> –<br>5.652*10 <sup>-3</sup> ) | 8.607*10 <sup>-3</sup><br>(3.172*10 <sup>-3</sup> –<br>2.303*10 <sup>-2</sup> ) | 3.139*10 <sup>-6</sup><br>(1.736*10 <sup>-9</sup> –<br>9.264*10 <sup>-4</sup> )  | 5.353*10 <sup>-6</sup><br>(3.911*10 <sup>-12</sup> –<br>1.401*10 <sup>-3</sup> ) | 5.807*10 <sup>-6</sup><br>(1.214*10 <sup>-9</sup> –<br>1.159*10 <sup>-3</sup> )  | 2.492*10 <sup>-2</sup><br>(2.278*10 <sup>-2</sup> –<br>2.886*10 <sup>-2</sup> ) | 2.490*10 <sup>-4</sup><br>(4.057*10 <sup>-8</sup> –<br>4.009*10 <sup>-2</sup> )  |

15 **Table S3** Parameter estimates from mixed model testing paternal and maternal age at conception  
 16 (PAC & MAC, respectively) effects on offspring relative leukocyte telomere length (Z-score) in  
 17 European badgers.  $\beta$  = direction and magnitude of effect, S.E. = standard error, 95% CI = 95%  
 18 confidence interval, reference terms in brackets = reference level for factors; \* = interaction.  
 19 Significant parameters (95% CI does not overlap zero) are in bold.

| Parameter (reference level)                      | $\beta$       | S.E.         | 95% CI                  |
|--|---------------|--------------|-------------------------|
| Intercept  | -0.012        | 0.129        | -0.265 to 0.240         |
| Age ( $\leq 29$ months)                          | -0.016        | 0.070        | -0.154 to 0.125         |
| <b>(&gt;29 and <math>\leq 65</math> months)</b>  | <b>0.180</b>  | <b>0.081</b> | <b>0.023 to 0.335</b>   |
| <b>(&gt;65 and <math>\leq 112</math> months)</b> | <b>-0.176</b> | <b>0.072</b> | <b>-0.319 to -0.037</b> |
| <b>(&gt; 112 months)</b>                         | <b>0.125</b>  | <b>0.055</b> | <b>0.019 to 0.235</b>   |
| Sex (Female)                                     | -0.021        | 0.094        | -0.205 to 0.159         |
| Season (Spring)                                  |               |              |                         |
| Summer   | 0.091         | 0.107        | -0.117 to 0.298         |
| Autumn   | -0.020        | 0.192        | -0.382 to 0.372         |
| Winter   | 0.012         | 0.252        | -0.464 to 0.527         |
| PAC  | 0.046         | 0.067        | -0.087 to 0.174         |
| MAC  | -0.029        | 0.061        | -0.152 to 0.085         |
| Sex (Female) * PAC                               | -0.018        | 0.092        | -0.207 to 0.170         |
| Sex (Female) * MAC                               | -0.009        | 0.097        | -0.199 to 0.182         |

20 Random effect estimates (variance): Cohort ( $1.920 \times 10^{-2}$ ), Social group ( $2.116 \times 10^{-2}$ ), Year ( $5.795 \times 10^{-2}$ ),  
 21 Plate ( $6.640 \times 10^{-2}$ ), Row ( $1.613 \times 10^{-2}$ ), Individual ID ( $3.938 \times 10^{-8}$ ), Mother ID ( $3.021 \times 10^{-10}$ ), Father ID  
 22 ( $1.440 \times 10^{-8}$ ), Residual ( $8.503 \times 10^{-1}$ ).

23 **Table S4** Parameter estimates from mixed model testing paternal and maternal age at conception  
 24 (PAC & MAC, respectively) effects on offspring relative leukocyte telomere length (Z-score) in  
 25 European badgers (without the interaction between PAC/MAC and sex).  $\beta$  = direction and magnitude  
 26 of effect, S.E. = standard error, 95% CI = 95% confidence interval, reference terms in brackets =  
 27 reference level for factors. Significant parameters (95% CI does not overlap zero) are in bold.

| Parameter (reference level)                      | $\beta$       | S.E.         | 95% CI                  |
|--|---------------|--------------|-------------------------|
| Intercept  | -0.011        | 0.128        | -0.264 to 0.239         |
| Age ( $\leq 29$ months)                          | -0.017        | 0.069        | -0.153 to 0.124         |
| <b>(&gt;29 and <math>\leq 65</math> months)</b>  | <b>0.180</b>  | <b>0.081</b> | <b>0.024 to 0.334</b>   |
| <b>(&gt;65 and <math>\leq 112</math> months)</b> | <b>-0.176</b> | <b>0.072</b> | <b>-0.318 to -0.038</b> |
| <b>(&gt; 112 months)</b>                         | <b>0.126</b>  | <b>0.055</b> | <b>0.020 to 0.235</b>   |
| Sex (Female)                                     | -0.020        | 0.095        | -0.208 to 0.162         |
| Season (Spring)                                  |               |              |                         |
| Summer   | 0.090         | 0.106        | -0.116 to 0.296         |
| Autumn   | -0.019        | 0.192        | -0.378 to 0.374         |
| Winter   | 0.011         | 0.252        | -0.464 to 0.527         |
| PAC  | 0.036         | 0.048        | -0.055 to 0.133         |
| MAC  | -0.033        | 0.050        | -0.134 to 0.062         |

28 Random effect estimates (variance): Cohort ( $1.866 \times 10^{-2}$ ), Social group ( $2.108 \times 10^{-2}$ ), Year ( $5.777 \times 10^{-2}$ ),  
 29 Plate ( $6.633 \times 10^{-2}$ ), Row ( $1.602 \times 10^{-2}$ ), Individual ID ( $2.666 \times 10^{-7}$ ), Mother ID ( $<1.000 \times 10^{-12}$ ), Father ID  
 30 ( $<1.000 \times 10^{-12}$ ), Residual ( $8.469 \times 10^{-1}$ ).

31 **Table S5** Parameter estimates from mixed model testing paternal and maternal age at conception  
 32 (PAC & MAC, respectively) effects on offspring relative leukocyte telomere length (Z-score) in  
 33 European badgers (only using cub measurements).  $\beta$  = direction and magnitude of effect, S.E. =  
 34 standard error, 95% CI = 95% confidence interval, reference terms in brackets = reference level for  
 35 factors; \* = interaction. Significant parameters (95% CI does not overlap zero) are in bold.

| <b>Parameter (reference level)</b> | <b><math>\beta</math></b> | <b>S.E.</b> | <b>95% CI</b>   |
|------------------------------------|---------------------------|-------------|-----------------|
| Intercept                          | 0.040                     | 0.210       | -0.372 to 0.442 |
| Age ( $\leq$ 29 months)            | 0.060                     | 0.220       | -0.377 to 0.474 |
| Sex (Female)                       | -0.108                    | 0.139       | -0.371 to 0.153 |
| Season (Spring)                    |                           |             |                 |
| Summer                             | 0.057                     | 0.291       | -0.505 to 0.635 |
| Autumn                             | -0.862                    | 0.669       | -2.131 to 0.474 |
| Winter                             | -0.429                    | 0.943       | -2.198 to 1.354 |
| PAC                                | -0.040                    | 0.092       | -0.224 to 0.145 |
| MAC                                | -0.073                    | 0.084       | -0.242 to 0.098 |
| Sex (female) * PAC                 | 0.186                     | 0.132       | -0.075 to 0.441 |
| Sex (female) * MAC                 | 0.013                     | 0.140       | -0.247 to 0.286 |

36 Random effect estimates (variance): Cohort ( $8.221 \times 10^{-2}$ ), Social group ( $<1.000 \times 10^{-12}$ ), Plate  
 37 ( $1.669 \times 10^{-1}$ ), Row ( $3.728 \times 10^{-2}$ ), Mother ID ( $<1.000 \times 10^{-12}$ ), Father ID ( $3.631 \times 10^{-3}$ ), Residual ( $6.391 \times 10^{-1}$ ).

38 **Table S6** Parameter estimates from mixed model testing paternal and maternal age at conception  
 39 (PAC & MAC, respectively) effects on offspring relative leukocyte telomere length (Z-score) in  
 40 European badgers (only using cub measurements and without the interaction between PAC/MAC and  
 41 sex).  $\beta$  = direction and magnitude of effect, S.E. = standard error, 95% CI = 95% confidence interval,  
 42 reference terms in brackets = reference level for factors; \* = interaction. Significant parameters (95%  
 43 CI does not overlap zero) are in bold.

| <b>Parameter (reference level)</b> | <b><math>\beta</math></b> | <b>S.E.</b> | <b>95% CI</b>   |
|------------------------------------|---------------------------|-------------|-----------------|
| Intercept                          | 0.032                     | 0.212       | -0.388 to 0.437 |
| Age ( $\leq$ 29 months)            | 0.054                     | 0.219       | -0.368 to 0.466 |
| Sex (Female)                       | -0.103                    | 0.138       | -0.365 to 0.157 |
| Season (Spring)                    |                           |             |                 |
| Summer                             | 0.067                     | 0.289       | -0.486 to 0.639 |
| Autumn                             | -0.860                    | 0.664       | -2.113 to 0.470 |
| Winter                             | -0.360                    | 0.933       | -2.126 to 1.380 |
| PAC                                | 0.055                     | 0.064       | -0.072 to 0.179 |
| MAC                                | -0.064                    | 0.065       | -0.196 to 0.066 |

44 Random effect estimates (variance): Cohort ( $7.980 \cdot 10^{-2}$ ), Social group ( $1.297 \cdot 10^{-3}$ ), Plate ( $1.625 \cdot 10^{-1}$ ),  
 45 Row ( $4.936 \cdot 10^{-2}$ ), Mother ID ( $<1.000 \cdot 10^{-12}$ ), Father ID ( $9.624 \cdot 10^{-4}$ ), Residual ( $6.385 \cdot 10^{-1}$ ).

46 **Table S7** Parameter estimates from mixed model testing within- and between-parent effects for  
 47 fathers (PAC) and mother (MAC) on offspring relative leukocyte telomere length (Z-score) in European  
 48 badgers.  $\beta$  = direction and magnitude of effect, S.E. = standard error, 95% CI = 95% confidence interval,  
 49  $\beta_w$  = within-individual effect,  $\beta_B$  = between-individual effect, reference terms in brackets = reference  
 50 level for factors. Significant parameters (95% CI does not overlap zero) are in bold.

| Parameter (reference level)                      | $\beta$       | S.E.         | 95% CI                  |
|--|---------------|--------------|-------------------------|
| Intercept  | -0.008        | 0.127        | -0.257 to 0.240         |
| Age ( $\leq 29$ months)                          | -0.013        | 0.069        | -0.149 to 0.127         |
| <b>(&gt;29 and <math>\leq 65</math> months)</b>  | <b>0.182</b>  | <b>0.080</b> | <b>0.028 to 0.336</b>   |
| <b>(&gt;65 and <math>\leq 112</math> months)</b> | <b>-0.179</b> | <b>0.072</b> | <b>-0.322 to -0.040</b> |
| <b>(&gt; 112 months)</b>                         | <b>0.124</b>  | <b>0.055</b> | <b>0.019 to 0.234</b>   |
| Sex (Female)                                     | -0.026        | 0.095        | -0.214 to 0.154         |
| Season (Spring)                                  |               |              |                         |
| Summer   | 0.086         | 0.107        | -0.122 to 0.294         |
| Autumn   | -0.018        | 0.192        | -0.378 to 0.372         |
| Winter   | 0.011         | 0.252        | -0.465 to 0.524         |
| PAC ( $\beta_w$ )                                | 0.045         | 0.047        | -0.046 to 0.142         |
| MAC ( $\beta_w$ )                                | 0.012         | 0.047        | -0.078 to 0.106         |
| PAC ( $\beta_B$ )                                | 0.016         | 0.048        | -0.075 to 0.114         |
| MAC ( $\beta_B$ )                                | -0.048        | 0.050        | -0.144 to 0.050         |

51 Random effect estimates (variance): Cohort ( $1.459 \cdot 10^{-2}$ ), Social group ( $2.134 \cdot 10^{-2}$ ), Year ( $5.414 \cdot 10^{-2}$ ),  
 52 Plate ( $6.777 \cdot 10^{-2}$ ), Row ( $1.606 \cdot 10^{-2}$ ), Individual ID ( $<1.000 \cdot 10^{-12}$ ), Mother ID ( $<1.000 \cdot 10^{-12}$ ), Father ID  
 53 ( $5.001 \cdot 10^{-9}$ ), Residual ( $8.511 \cdot 10^{-1}$ )



54 **Table S8** Additive genetic and environmental effects on relative leukocyte telomere length in  
55 European badgers of all ages, estimated using *ASReml-R*. Est. = fixed effect estimate, Prop. =  
56 proportion of variance explained, S.E. = Standard error,  $h^2$  = heritability. Age parameters refer to  
57 threshold model where Age 1 =  $\leq 29$  months old, Age 2 =  $> 29$  and  $\leq 65$  months old, Age 3 =  $> 65$  and  
58  $\leq 112$  months old and Age 4 =  $> 112$  months old. Variance components are:  $V_A$  = additive genetic,  $V_{PE}$  =  
59 permanent environment,  $V_{CO}$  = cohort,  $V_{YEAR}$  = year,  $V_{SG}$  = social group,  $V_{MAT}$  = maternal,  $V_{PAT}$  = paternal,  
60  $V_R$  = residual,  $V_{PLATE}$  = plate,  $V_{ROW}$  = row. Total phenotypic variance ( $V_p$ ) =  $3.970 \times 10^{-2}$ . Reference terms  
61 in brackets = reference level for factors. Significance of fixed effects was determined through Wald Z  
62 tests, and for random effects through twice the difference in log-likelihood. Significant parameters ( $p$   
63  $< 0.05$ ) are in bold.

| Trait: Relative leukocyte telomere length ( $n = 1248$ measurements; 612 badgers) |  |  |                            |                  |
|---|--|--|----------------------------|------------------|
| ASReml-R  |  |  |                            |                  |
|   | Est.   | S.E.   | F-value                    | p-value          |
| <b>Fixed effects</b>  |  |  |                            |                  |
| Intercept   | 0.4796   | $2.933 \times 10^{-2}$   |                            |                  |
| Age 1   | $-2.888 \times 10^{-4}$  | $6.920 \times 10^{-4}$   | 0.174                      | 0.677            |
| <b>Age 2</b>  | <b><math>2.156 \times 10^{-3}</math></b>                                     | <b><math>6.755 \times 10^{-4}</math></b>                                     | <b>10.18</b>               | <b>0.001</b>     |
| <b>Age 3</b>  | <b><math>-2.570 \times 10^{-3}</math></b>                                    | <b><math>8.358 \times 10^{-4}</math></b>                                     | <b>9.454</b>               | <b>0.002</b>     |
| <b>Age 4</b>  | <b><math>4.766 \times 10^{-3}</math></b>                                     | <b><math>2.036 \times 10^{-3}</math></b>                                     | <b>5.481</b>               | <b>0.019</b>     |
| <b>Season (Spring)</b>  |  |  | <b>3.627</b>               | <b>0.013</b>     |
| <b>Summer</b>   | <b><math>2.448 \times 10^{-2}</math></b>                                     | <b><math>1.123 \times 10^{-2}</math></b>                                     |                            |                  |
| <b>Autumn</b>   | <b><math>1.841 \times 10^{-2}</math></b>                                     | <b><math>1.799 \times 10^{-2}</math></b>                                     |                            |                  |
| <b>Winter</b>   | <b><math>-5.365 \times 10^{-2}</math></b>                                    | <b><math>2.521 \times 10^{-2}</math></b>                                     |                            |                  |
| <b>Random effects</b>   | <b>Est. (S.E.)</b>   | <b><math>h^2</math>/Prop. (S.E.)</b>   | <b><math>\chi^2</math></b> | <b>p-value</b>   |
| $V_A^a$   | $5.110 \times 10^{-9}$ ( $2.260 \times 10^{-10}$ )                           | $1.286 \times 10^{-7}$ ( $1.420 \times 10^{-8}$ )                            |                            |                  |
| $V_{PE}^a$  | $7.610 \times 10^{-9}$ ( $3.360 \times 10^{-10}$ )                           | $1.914 \times 10^{-7}$ ( $2.115 \times 10^{-8}$ )                            |                            |                  |
| <b><math>V_{CO}</math></b>  | <b><math>1.411 \times 10^{-3}</math> (<math>6.970 \times 10^{-4}</math>)</b> | <b><math>3.551 \times 10^{-2}</math> (<math>1.750 \times 10^{-2}</math>)</b> | <b>16.92</b>               | <b>&lt;0.001</b> |
| <b><math>V_{YEAR}</math></b>  | <b><math>1.161 \times 10^{-2}</math> (<math>4.230 \times 10^{-3}</math>)</b> | <b><math>0.292</math> (<math>7.632 \times 10^{-2}</math>)</b>                | <b>79.94</b>               | <b>&lt;0.001</b> |
| $V_{SG}$  | $1.494 \times 10^{-4}$ ( $2.163 \times 10^{-4}$ )                            | $3.761 \times 10^{-3}$ ( $5.458 \times 10^{-3}$ )                            | 0.700                      | 0.403            |
| $V_{MAT}$   | $5.086 \times 10^{-4}$ ( $5.612 \times 10^{-4}$ )                            | $1.280 \times 10^{-2}$ ( $1.414 \times 10^{-2}$ )                            | 0.544                      | 0.461            |
| $V_{PAT}$   | $1.974 \times 10^{-4}$ ( $3.658 \times 10^{-4}$ )                            | $4.968 \times 10^{-3}$ ( $9.214 \times 10^{-3}$ )                            | 0.412                      | 0.521            |
| $V_R$   | $2.585 \times 10^{-2}$ ( $1.142 \times 10^{-3}$ )                            | $0.651$ ( $7.189 \times 10^{-2}$ )   |                            |                  |
| <b><math>V_{PLATE}^b</math></b>   | <b><math>2.085 \times 10^{-3}</math> (<math>7.034 \times 10^{-4}</math>)</b> |  | <b>46.11</b>               | <b>&lt;0.001</b> |
| <b><math>V_{ROW}^b</math></b>   | <b><math>4.354 \times 10^{-4}</math> (<math>3.256 \times 10^{-4}</math>)</b> |  | <b>8.824</b>               | <b>0.003</b>     |

64 <sup>a</sup> Significance not tested because variance components were at boundary

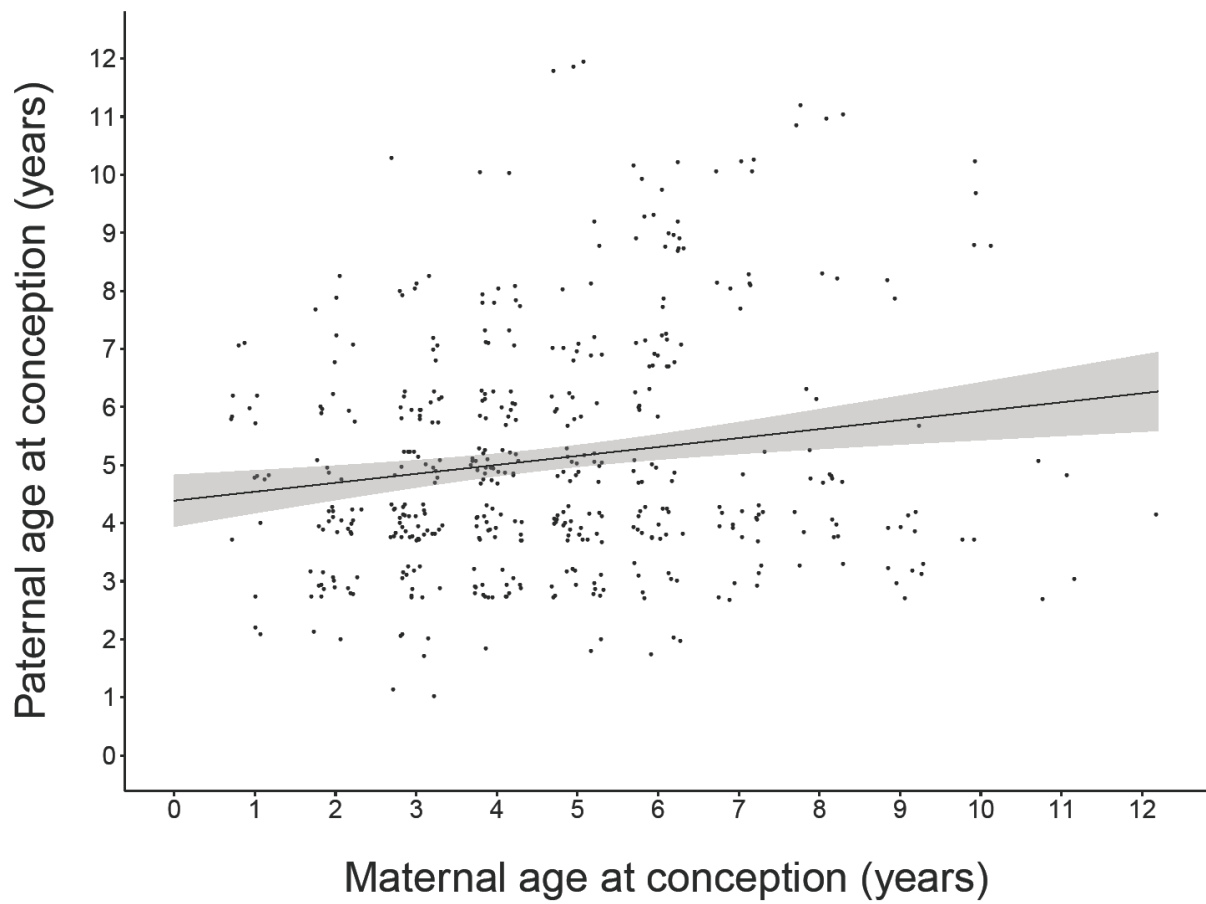
65 <sup>b</sup> Measurement error and not biological variance so no proportion and associated standard error  
66 provided

67 **Table S9** Additive genetic and environmental effects on relative leukocyte telomere length (Age  $\leq$  29  
68 months) in European badgers, estimated using *ASReml-R*. Est. = fixed effect estimate, Prop. =  
69 proportion of variance explained, S.E. = Standard error,  $h^2$  = heritability. Variance components are:  $V_A$   
70 = additive genetic,  $V_{PE}$  = permanent environment,  $V_{CO}$  = cohort,  $V_{YEAR}$  = year,  $V_{SG}$  = social group,  $V_{MAT}$  =  
71 maternal,  $V_{PAT}$  = paternal,  $V_R$  = residual,  $V_{PLATE}$  = plate,  $V_{ROW}$  = row. Total phenotypic variance ( $V_p$ ) =  
72  $3.910 \times 10^{-2}$ . Reference terms in brackets = reference level for factors. Significance of fixed effects was  
73 determined through Wald Z tests, and for random effects through twice the difference in log-  
74 likelihood. Significant parameters ( $p < 0.05$ ) are in bold.

| Trait: Early-life relative leukocyte telomere length ( $n = 837$ measurements; 556 badgers) |  |  |                            |                  |
|---|--|--|----------------------------|------------------|
| ASReml-R  |  |  |                            |                  |
|   | Est.   | S.E.   | F-value                    | p-value          |
| <b>Fixed effects</b>  |  |  |                            |                  |
| Intercept   | 0.4771   | $2.874 \times 10^{-2}$   |                            |                  |
| Age   | $1.120 \times 10^{-4}$   | $8.403 \times 10^{-4}$   | 0.018                      | 0.894            |
| <b>Season (Spring)</b>  |  |  | <b>2.933</b>               | <b>0.033</b>     |
| <b>Summer</b>   | <b><math>1.576 \times 10^{-2}</math></b>                                     | <b><math>1.398 \times 10^{-2}</math></b>                                     |                            |                  |
| <b>Autumn</b>   | <b><math>1.516 \times 10^{-2}</math></b>                                     | <b><math>2.408 \times 10^{-2}</math></b>                                     |                            |                  |
| <b>Winter</b>   | <b><math>-7.998 \times 10^{-2}</math></b>                                    | <b><math>3.150 \times 10^{-2}</math></b>                                     |                            |                  |
| <b>Random effects</b>   | <b>Est. (S.E.)</b>   | <b><math>h^2</math>/Prop. (S.E.)</b>   | <b><math>\chi^2</math></b> | <b>p-value</b>   |
| $V_A$   | $1.280 \times 10^{-4}$ ( $1.075 \times 10^{-3}$ )                            | $3.271 \times 10^{-3}$ ( $2.746 \times 10^{-2}$ )                            | 0.014                      | 0.906            |
| $V_{PE}^a$  | $8.770 \times 10^{-9}$ ( $5.560 \times 10^{-10}$ )                           | $2.240 \times 10^{-7}$ ( $2.569 \times 10^{-8}$ )                            |                            |                  |
| <b><math>V_{CO}</math></b>  | <b><math>1.945 \times 10^{-3}</math> (<math>1.138 \times 10^{-3}</math>)</b> | <b><math>4.970 \times 10^{-2}</math> (<math>2.862 \times 10^{-2}</math>)</b> | <b>11.13</b>               | <b>&lt;0.001</b> |
| <b><math>V_{YEAR}</math></b>  | <b><math>1.004 \times 10^{-2}</math> (<math>4.062 \times 10^{-3}</math>)</b> | <b><math>0.257</math> (<math>7.890 \times 10^{-2}</math>)</b>                | <b>40.45</b>               | <b>&lt;0.001</b> |
| $V_{SG}$  | $2.412 \times 10^{-4}$ ( $3.169 \times 10^{-4}$ )                            | $6.162 \times 10^{-3}$ ( $8.107 \times 10^{-3}$ )                            | 0.879                      | 0.348            |
| $V_{MAT}^a$   | $2.710 \times 10^{-9}$ ( $1.720 \times 10^{-10}$ )                           | $6.924 \times 10^{-8}$ ( $7.940 \times 10^{-9}$ )                            |                            |                  |
| $V_{PAT}^a$   | $2.360 \times 10^{-9}$ ( $1.500 \times 10^{-10}$ )                           | $6.024 \times 10^{-8}$ ( $6.907 \times 10^{-9}$ )                            |                            |                  |
| $V_R$   | $2.679 \times 10^{-2}$ ( $1.699 \times 10^{-3}$ )                            | $0.684$ ( $7.846 \times 10^{-2}$ )   |                            |                  |
| <b><math>V_{PLATE}^b</math></b>   | <b><math>1.771 \times 10^{-3}</math> (<math>7.239 \times 10^{-4}</math>)</b> |  | <b>19.49</b>               | <b>&lt;0.001</b> |
| $V_{ROW}^b$   | $1.942 \times 10^{-4}$ ( $2.461 \times 10^{-4}$ )                            |  | 1.319                      | 0.251            |

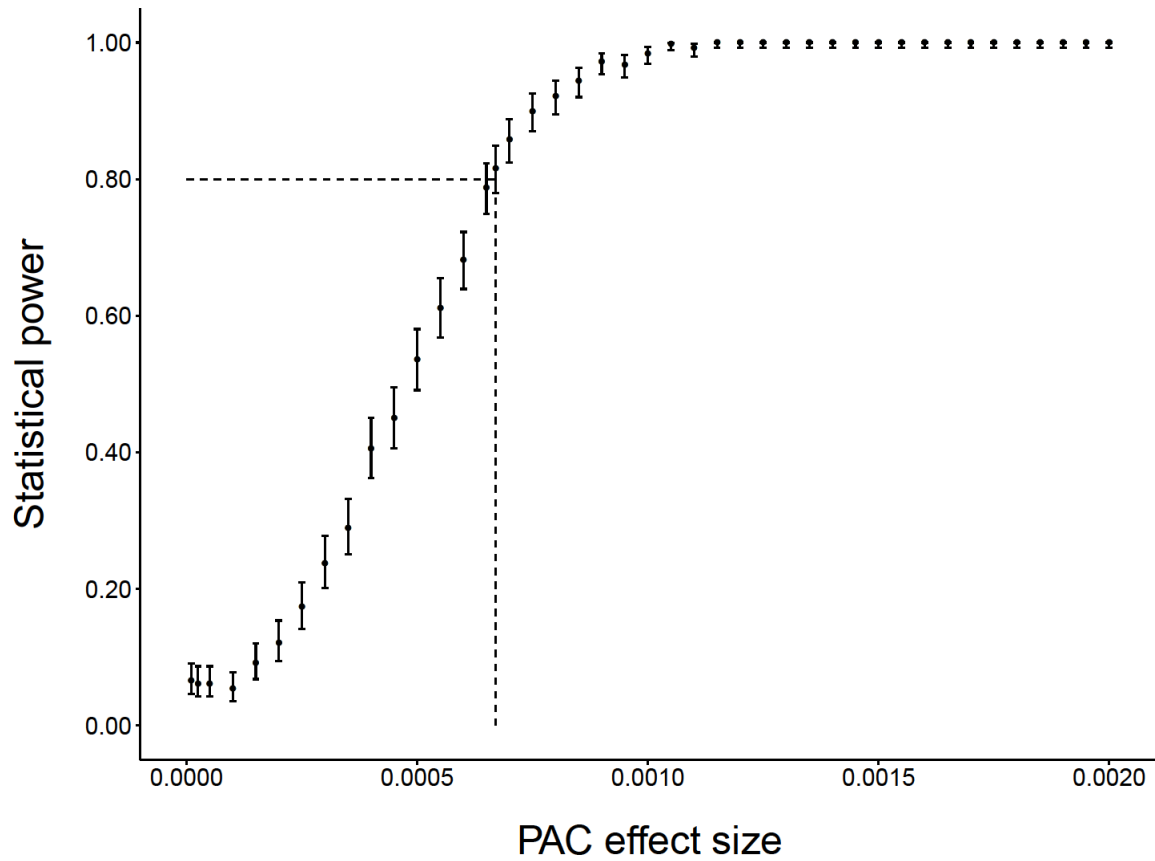
75 <sup>a</sup> Significance not tested because variance components were at boundary

76 <sup>b</sup> Measurement error and not biological variance so no proportion and associated standard error  
77 provided



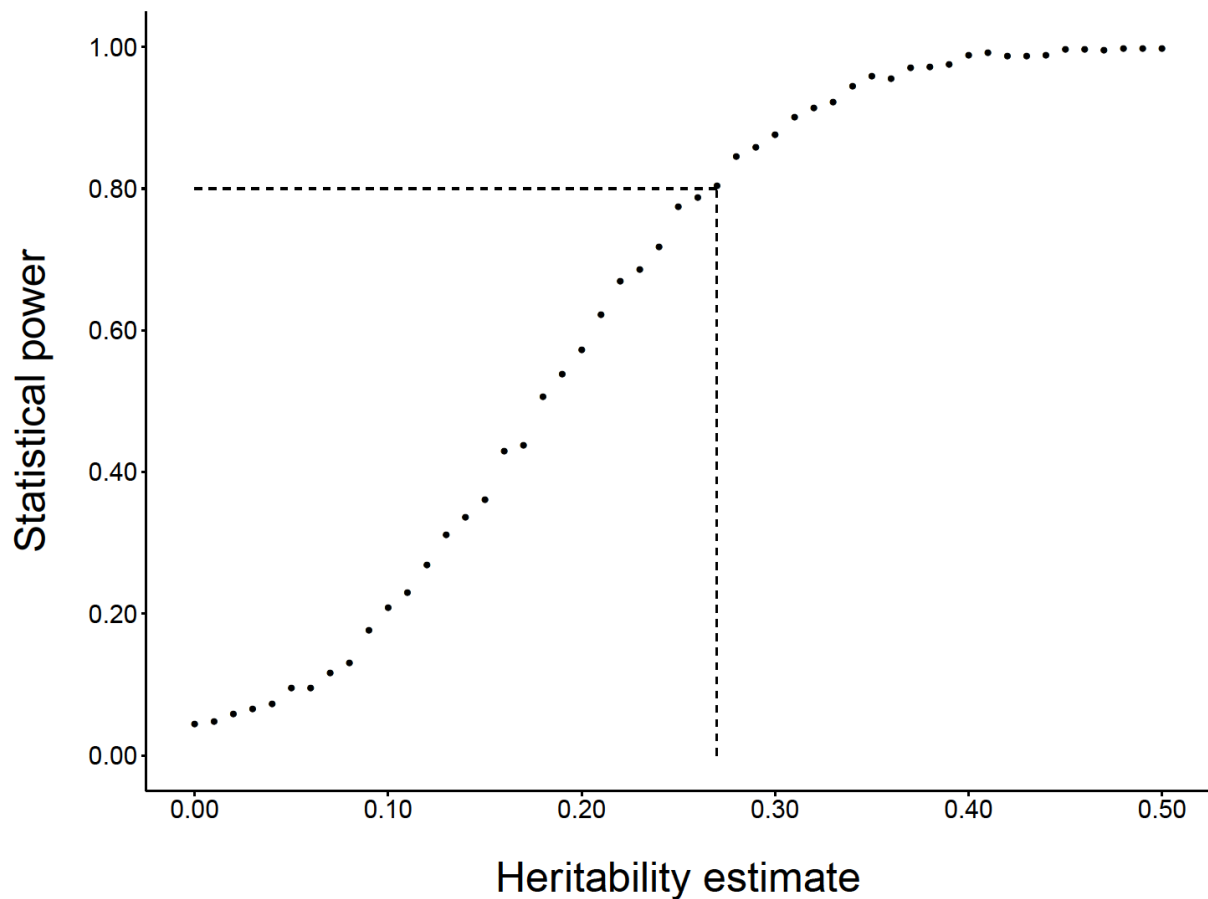
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79 **Figure S1** Scatterplot showing the correlation between paternal and maternal ages at conception for  
 80 badgers with relative leukocyte telomere length measures at any age ( $n = 471$  samples; 240 badgers).  
 81 Parental ages are integers, jittered for clarity on the amount of data.



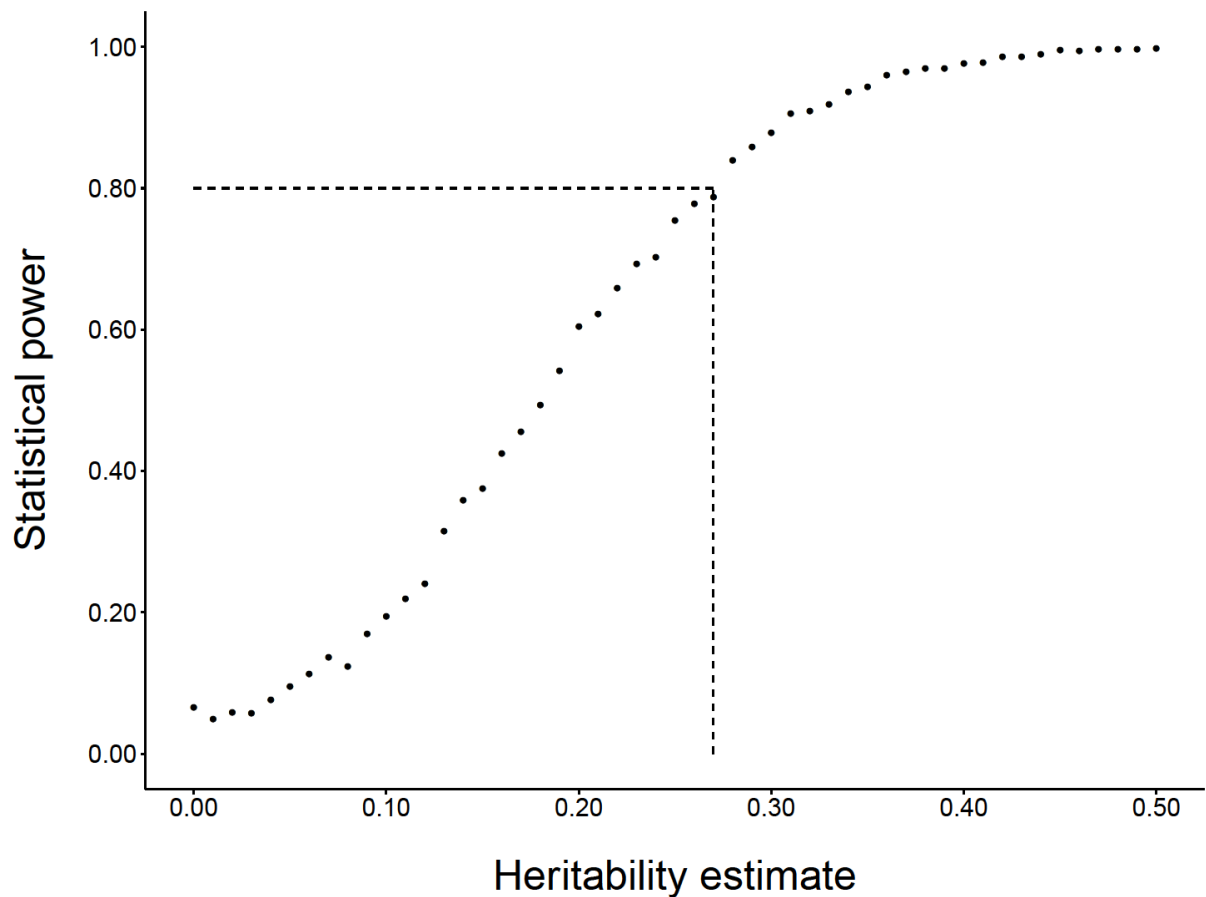
82

83 **Figure S2** Statistical power to detect paternal age at conception (PAC) effect sizes in our European  
 84 badger dataset using *simr* 1.0.5 (Green & MacLeod 2016). Point estimates and error bars show mean  
 85 power with associated 95% confidence intervals estimated from 500 simulations. Dashed line  
 86 represents  $\geq 80\%$  power to detect a PAC effect size of  $\geq 0.00067$ , with the specifications of our model  
 87 and structure of our data. This is similar to a correlation coefficient of 0.131 (where correlation  
 88 coefficient =  $(\beta_{\text{PAC}} * \text{SD}_{\text{PAC}}) / \text{SD}_{\text{RTLTL}} = (0.00067 * 24.57207) / 0.1254953$ ).



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**Figure S3** Statistical power to detect varying heritability estimates of telomere length in the European badger with our dataset ( $n = 1248$  measurements; 612 badgers) and pruned pedigree structure using *pedantics* 1.7 (Morrissey & Wilson 2010). Point estimates show mean power estimated from 1000 simulations. Dashed line represents  $\geq 80\%$  power to detect a heritability estimate of  $\geq 0.27$ , with the specifications of our model and structure of our data.



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**Figure S4** Statistical power to detect varying heritability estimates of juvenile telomere length ( $\leq 29$  months old) in the European badger with our dataset ( $n = 837$  measurements; 556 badgers) and pruned pedigree structure using *pedantics* 1.7 (Morrissey & Wilson 2010). Point estimates show mean power estimated from 1000 simulations. Dashed line represents  $\geq 80\%$  power to detect a heritability estimate of  $\geq 0.28$ , with the specifications of our model and structure of our data.

102 **References**

103 Green P., MacLeod C. J. (2016). simr: an R package for power analysis of generalized linear mixed  
104 models by simulation. *Methods in Ecology and Evolution*, 7, 493-498.

105 <https://doi.org/10.1111/2041-210x.12504>

106 Hadfield J. D. (2010). MCMC methods for multi-response generalised linear mixed models: the  
107 MCMCglmm R package. *Journal of Statistical Software*, 33, 1-22.

108 <https://doi.org/10.18637/jss.v033.i02>

109 Morrissey M. B., Wilson A. J. (2010). pedantics: an r package for pedigree-based genetic simulation  
110 and pedigree manipulation, characterization and viewing. *Molecular Ecology Resources*, 10,

111 711-719. <https://doi.org/10.1111/j.1755-0998.2009.02817.x>

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