

## Corrigendum for the paper 'War and the evolution of belligerence and bravery'

Laurent Lehmann and Marcus W. Feldmann

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## Correction

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### Corrigendum for the paper ‘War and the evolution of belligerence and bravery’

Laurent Lehmann and Marcus W. Feldmann

In the paper ‘War and the evolution of belligerence and bravery’ (Lehmann & Feldman, 2008, which we will refer to as L&F), we used probabilities of identity by descent between pairs of homologous genes sampled in *sub-adult* individuals after migration (individuals sampled before stage (4) of the life cycle described on p. 2878 of L&F) in order to compute the invasion conditions of male belligerence and bravery. However, the formulation of the model requires that we should have used instead the probabilities of identity by descent between pairs of genes sampled in *adult* individuals (individuals sampled after stages (4) and (5) of the life cycle). In this corrigendum, we present the probabilities of identity by descent between adults and the corresponding corrected invasion conditions for belligerence and bravery.

#### 1. PROBABILITIES OF IDENTITY BY DESCENT

In order to evaluate selection on belligerence and bravery, we used eqn (A 6) of our appendix ( $Q_{ij} = (1 - m)^2 Q^J$ ), which is the probability of identity by descent between pairs of genes randomly sampled in two distinct sub-adult individuals (individuals sampled before stage (4) of the life cycle), one gene from an individual of sex  $i$  and the other from an individual of sex  $j$ , and where  $Q^J$  is the probability of identity between a pair of juveniles (individuals sampled after stage (1) of the life cycle).

However,  $Q_{ij}$  needs to be the average probability of identity by descent between pairs of homologous genes randomly sampled in two distinct adult individuals of sex  $i$  and sex  $j$  (individuals sampled after stages (4) and (5) of the life cycle), which is given by

$$Q_{ij} = [(1 - a\omega) + a\omega\{(1 - s_i)(1 - s_j) + s_i s_j\}](1 - m)^2 Q^J, \quad (1.1)$$

where the term in brackets is the effect of regulation (stage (4) of the life cycle) on the probabilities of identity, which was not accounted for in eqn (A 6) of L&F.

Equation (1.1) can be understood as follows. With probability  $1 - a\omega$ , the group where the two adults are sampled has not been conquered, in which case the probability of identity between the two individuals is  $(1 - m)^2 Q^J$ . With probability  $a\omega$ , this group has been conquered in which case the two adults descend from the same group before regulation with probability  $(1 - s_i)(1 - s_j) + s_i s_j$  (with probability  $(1 - s_i)(1 - s_j)$  from the conqueror group and with probability  $s_i s_j$  from the conquered group) and their probability of identity is then equal to that among sub-adults  $(1 - m)^2 Q^J$ .

Although we misinterpreted  $Q_{ij}$ , the equilibrium expression for  $Q^J$  (eqn (A 8) of L&F) was computed correctly because we took into account all events affecting the dynamics of  $Q^J$  over one iteration of the life cycle. Similarly, the inbreeding coefficient in adults  $F$  (eqn (A 7) of L&F) was also computed correctly as it is not affected by regulation. On substituting eqn (A 8) of L&F into equation (1.1), we obtain the equilibrium value for the probability of identity between two distinct adult individuals of sex  $i$  and  $j$  as

$$Q_{ij} = \frac{[(1 - a\omega) + a\omega\{(1 - s_i)(1 - s_j) + s_i s_j\}](1 - m)^2}{4N - (1 - m)^2 \left[ (4N - 1) - a\omega \left( (4N - 1)(s_f + s_m) - 2(N - 1)(s_f + s_m)^2 - 6s_f s_m \right) \right]}. \quad (1.2)$$

When the sexes have the same survival probability during regulation ( $s_m = s_f = s$ ), equation (1.2) reduces to

$$Q_{ij} = Q = \frac{\{1 - 2a\omega s(1 - s)\}(1 - m)^2}{4N - (1 - m)^2 (4N - 1)\{1 - 2a\omega s(1 - s)\}}, \quad (1.3)$$

which then gives relatedness  $R = 2Q/(1 + F)$  (L&F, p. 2881), after inserting eqn (A 7) of L&F, as

$$R = \frac{\{1 - 2a\omega s(1 - s)\}(1 - m)^2}{2N - (1 - m)^2 (2N - 1)\{1 - 2a\omega s(1 - s)\}}. \quad (1.4)$$

## 2 Correction. Belligerence and bravery

The main consequence of using equation (1.1) instead of eqn (A 6) of the appendix of L&F is that  $Q_{ij}$  is actually sex-specific, as can be seen from the numerator of equation (1.2). It follows that, first, eqns (3.1) and (3.3) of L&F are valid only when the sexes have the same survival probability during regulation ( $s_m = s_f = s$ ) with relatedness given by equation (1.4) instead of the incorrect eqn (A 9) of L&F, and, second, that eqns (3.2) and (3.4) have to be recalculated from tables 1 and 2, respectively, by using equation (1.2). The new invasion conditions are presented in the next section.

### 2. SELECTION ON MALE BELLIGERENCE

In the absence of sex-specific survival during regulation ( $s_m = s_f = s$ ) and substituting equation (1.4) into eqn (3.1) of L&F, we find that selection favours the male belligerence allele when

$$\frac{C_a}{aB_a} < \frac{2\omega(1-s)(1-m)}{N(1-(1-m)^2\{1-2a\omega s(1-s)\})}, \quad (2.1)$$

which holds for any population size. Corresponding invasion conditions for general  $N$  were omitted from L&F because the corresponding expressions evaluated with the probabilities of identity between sub-adults were too complicated. Instead, we presented only invasion conditions that assumed large  $N$  in the presence of sex-specific survival during regulation ( $s_m \neq s_f$ ) and where we omitted to take the factor in brackets in equation (1.1) into account.

In order to obtain the correct invasion condition for male belligerence under sex-specific survival, we substitute equation (1.2) into table 1 of L&F, and after summing up all the weighted changes in fitness, we find that selection favours the belligerence allele when group size is large (neglecting terms of order  $1/N^2$  this time) if

$$\frac{C_a}{aB_a} < \frac{2\omega x(1-m)\{1+a\omega(1-m)^2(s_f-s_m)(1-s_f-s_m)/2\}}{N(1-(1-m)^2\{1-2a\omega x(1-x)\})}, \quad (2.2)$$

where  $x = 1 - (s_f + s_m)/2$  as defined on p. 2881 of L&F. The only difference between this equation and eqn (3.2) of L&F is the term in the curly braces in the numerator, which makes the right-hand side somewhat smaller than in eqn (3.2) for otherwise similar parameter values, but this difference is very small for the parameter values given in the numerical results presented in figs 1 and 2 of L&F. But no qualitative differences are observed; that is, the right-hand sides of both equation (2.2) here and eqn (3.2) of L&F are positive or equal to zero for all combinations of parameter values.

### 3. SELECTION ON MALE BRAVERY

In the absence of sex-specific survival during regulation ( $s_m = s_f = s$ ), and substituting equation (1.4) into eqn (3.3) of L&F, we find that selection favours the male bravery allele when

$$\frac{C_\omega}{\omega B_\omega} < \frac{4(1-s)(1-m)}{N(1-(1-m)^2\{1-2a\omega s(1-s)\})}, \quad (3.1)$$

which holds for any population size. Again, no such result for general  $N$  was presented L&F, where we presented only the invasion condition assuming large  $N$  in the presence of sex-specific survival but with the probabilities of identity that omitted the factor in brackets in equation (1.1).

In order to obtain the correct invasion condition for male bravery in the presence of sex-specific survival during regulation, we substitute equation (1.2) into table 2 and after summing all the weighted changes in fitness, we find that selection favours the bravery allele if

$$\frac{C_\omega}{\omega B_\omega} < \frac{4x(1-m)\{1+a\omega(1-m)^2(s_f-s_m)(1-s_f-s_m)/2\}}{N(1-(1-m)^2\{1-2a\omega x(1-x)\})}. \quad (3.2)$$

The difference between this equation and eqn (3.4) of L&F is the same term in the numerator that distinguishes equation (2.1) above from eqn (3.2) of L&F.

## REFERENCE

Lehmann, L. & Feldman, M. W. 2008 War and the evolution of belligerence and bravery. *Proc. R. Soc. B* **275**, 2877–2885. (doi:10.1098/rspb.2008.0842)

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