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War and the evolution of belligerence and bravery

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Tribal war occurs when a coalition of individuals use force to seize reproduction-enhancing resources, and it may have affected human evolution. Here, we develop a population-genetic model for the coevolution of costly male belligerence and bravery when war occurs between groups of individuals in a spatially subdivided population. Belligerence is assumed to increase an actor's group probability of trying to conquer another group. An actor's bravery is assumed to increase his group's ability to conquer an attacked group. We show that the selective pressure on these two traits can be substantial even in groups of large size, and that they may be driven by two independent reproduction-enhancing resources: additional mates for males and additional territory (or material resources) for females. This has consequences for our understanding of the evolution of intertribal interactions, as hunter-gatherer societies are well known to have frequently raided neighbouring groups from whom they appropriated territory, goods and women.

Keywords: war; belligerence; bravery; relatedness; genetic transmission; cultural transmission

> Courage, above all things, is the first quality of a warrior.
> (von Clausewitz 1832)

1. INTRODUCTION

War is costly in lives and resources, but has been a recurrent event throughout human history. There are two major classes of explanations for the existence of war (Fearon 1995). The first is irrationality: individuals within groups or states are controlled by leaders subject to pathological biases leading them to ignore the costs of war. The second is rationality, i.e. war occurs if its benefits to the group or the state exceed its costs. In the rational case, economists and political scientists often consider interstate or civil wars as a bargaining process. The reason for initiating the conflict is then to induce the other side to make an acceptable offer for the distribution of some resources among the disputants, in the presence of incomplete information about their power or inability to comply to a deal (e.g. Fearon 1995; Slantchev & Leventoglu 2007). Evolutionists have stressed that reproduction-enhancing resources (those that increase the survival or the fertility of individuals), which can be obtained by coercion, may have played a crucial role in human evolution (e.g. Durham 1976; Tooby & Cosmides 1988; Turchin 2003; Richerson & Boyd 2005).

War is an aggressive interaction between groups of individuals, and it would not be possible if the groups were unable to form cohesive units of cooperating individuals. Within-group cooperation is the basis of between-group conflict (Turchin 2003). Sun Tzu was perhaps the first to make this point by emphasizing that one of the most important covenants which must be fulfilled when going to war is the 'The Moral Law', which exhorts individuals within groups to be in complete accordance with their ruler, so that they will follow him, altruistically, regardless of their lives (Sun-Tzu sixth century BC). Pre-state societies are characterized by small group size and limited gene flow between groups, which leads to significant genetic relatedness between members of the same group, a necessary condition for genetically based altruism to evolve (Hamilton 1970, 1971, 1975). Hamilton (1975) further speculated that high relatedness within groups, coupled with the development of language allowing for sophisticated collective action, would result in the development of cohesive solidarity within groups (i.e. helping behaviours) and explosive hostility between groups.

In this paper, we investigate Hamilton's scenario with a population-genetic model of war between groups in a saturated environment (i.e. the population is at its carrying capacity), in an attempt to quantify analytically the selective pressure on within-group coalition and between-group hostility. To this end, we assume that males, who are almost always the warriors in humans and higher primates, express two individually costly traits. The first trait causes an actor to be belligerent, which increases the probability that the actor's group goes to war and tries to conquer another group. The second trait causes an actor to be brave, which increases the probability that its group wins a war and conquers another group. We investigate the coevolutionary dynamics of male belligerence and bravery in response to two independent types of reproduction-enhancing resources that can be sequestered by conquest: additional mates for males (at the expense of the opposing males) and additional territory (or material resources) for females (at the expense of the females in the opposing group).

Our model of warfare between small-sized, pre-state groups of individuals is not the first: Choi & Bowles (2007) used simulations to analyse this problem. They did not analyse the roles of life-history features such as group size and migration rates, which are well known to affect the evolutionary dynamics of genetically determined social traits in subdivided populations (Hamilton 1975; Cherry & Wakeley 2003; Whitlock 2003; Rousset 2004; Lion & Van Baalen 2007; West *et al.* 2008). The analytical model presented here allows us to investigate how such features shape the evolution of male belligerence and bravery. Our model also supposes that individuals are diploid and that there are two sexes, which allows us to show that

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male coalitional aggression can be an adaptation to the conditions of limiting resources for both sexes.

2. MODEL

(a) *Life cycle*

We consider a population consisting of an infinite number of groups, each with a finite number N_m of adult males and N_f of adult females. Groups are connected by random migration (Wright's 1931; infinite-island model of dispersal) and warfare occurs between groups. Events in the life cycle occur in the following order. (i) Adult mated females in each group produce a large number of juveniles. Juveniles mature and become subadults (pre-reproductive). (ii) Each subadult disperses independently of the others to a new randomly chosen group. Males disperse with probability m_m, while females disperse with probability m_f. All adult individuals die. (iii) War occurs between groups. With probability a, the subadult males in each group try to conquer another random group. This results in a battle between pairs of opposing groups: the attacker and the attacked groups, where the attacker wins the battle with probability ω. If the attacker group wins the battle, we call the attacked group conquered. If the attacker group loses the battle, it retreats. (iv) Density-dependent competition occurs in each group between individuals of the same sex, and exactly N_m males and N_f females reach adulthood in each group. In non-conquered groups, only subadults from that group compete against each other. In conquered groups, subadults from both the conqueror and conquered group compete against each other, and with probability s_i; an individual of sex i randomly sampled from a conquered group after competition is a member from that group before competition. (v) In each group (conquered or not), the N_m males mate randomly with the N_f females.

If $s_i < 1$, the conquered groups are partially repopulated by individuals from the conqueror group and $1-s_i$ represents the fraction of the individuals of sex i of the conquered groups that are replaced by the individuals of sex i from the conqueror group. In order to have low values of s_i (high fitness benefit for conquerors), one could, for example, assume that with probability k_i an individual of sex i in a conquered group is killed after conquest, in which case $s_i = (1-k_i)/(1-k_i+1)$, or that individuals from the conquered groups are more likely to die from resource exhaustion. The probability s_i could also be determined by a negotiation between the combatant parties.

In order to determine whether between-group belligerence and within-group bravery will spread (whether a and ω evolve), we introduce a two-locus (two-trait) model with additive gene action, with only two alleles segregating at each locus. We measure fitness in units of mated females. That is, fitness is defined as the expected number of adult mated females produced, through sons and daughters, by adult mated males and females (e.g. Taylor 1988*b*, 1992). The first locus controls the expression of belligerence, which causes its bearer to express hostility towards other groups by affecting the probability that the actor's group tries to conquer another group. We assume that the probability a, that a group attacks another group depends on the average phenotype of pre-adult males in that group, where the phenotype of each pre-adult male is itself determined by the genotype of its father. We thus postulate paternal control of the phenotypes of offspring. This assumption is introduced for mathematical convenience. An adult male bearing a single copy of a mutant 'belligerence' allele produces sons that increment the net probability that a group goes to war by $B_a/(2N_m)$ relative to that of homozygotes for the resident (wild-type) allele in an adult male. We also assume that belligerence is costly (in terms of time or energy) and that it reduces the chance that a pre-adult survives density-dependent competition. We assume that bearing a single copy of the mutant belligerence allele decreases the fitness of an adult male by $C_a/2$ units.

The second locus controls the expression of bravery of pre-adult males during warfare, which is again assumed to be under parental control. An adult male bearing a single copy of a mutant 'bravery' allele produces sons that increment the net probability that a group wins a war by $B_\omega/(2N_m)$, relative to that of homozygotes for the resident (wild-type) allele in an adult male. Bravery is also assumed to be costly (in terms of risk of injury or death) and bearing a single copy of the mutant bravery allele decreases the fitness of an adult male by $C_\omega/2$ units, whenever a battle occurs. Individuals bearing two copies of the resident allele benefit from the expression of bravery by other males but do not pay the cost.

(b) *Change in gene frequency*

The change in gene frequency induced by selection will depend on the covariances of genes within individuals (linkage disequilibrium) and between individuals within groups (relatedness). The dynamics of these two types of genetic associations will in turn depend on the strength of selection. For analytical tractability, however, we will neglect the effect of selection on genetic associations by evaluating the change in gene frequency under weak selection only. With this assumption, the change in the frequency of a mutant allele is computed to the first order in a parameter δ describing the strength of selection, which can be thought of as the largest of the four phenotypic effects on fitness (C_a, C_ω, B_a and B_ω). Any effect of selection on genetic associations (of order δ or higher) can then be neglected because this will produce changes in the gene frequencies to the second and higher order in δ. Consequently, it is sufficient to compute genetic associations under neutrality, which implies that the linkage disequilibrium will be zero at equilibrium but relatedness will build up (Roze & Rousset 2005, 2008). For this reason, we ascertain the direction of selection at a locus by assuming that there is no current polymorphism at the other locus (i.e. separation of time scale). Under weak selection, the change in the frequency p over one iteration of the life cycle of a mutant allele (either the belligerence or the bravery allele) can then be expressed as

$$\Delta p = p(1-p)S, \tag{2.1}$$

where the selection coefficient S on the mutant allele is frequency independent (Rousset 2004, pp. 108–109 and pp. 206–207). The selection coefficient S can be computed as an inclusive fitness effect, which is a relatedness-weighted sum of the changes in the fitness of a focal individual bearing the mutant allele due to the expression of the mutation by him and other actors in the population (Hamilton 1964, 1970). Since we have postulated an infinite-island model of dispersal, the relatedness between individuals from different groups is zero. We need only to

evaluate the changes in the fitness of a focal individual, resulting from the behaviours of all individuals in the focal group, who carry copies of the mutant allele which are identical by descent (including the effect of the focal individual on itself). For simplicity, we also assume that the migration rate and the number of adult individuals of each sex is the same ($N_m = N_f = N$, $m_m = m_f = m$).

(c) *Inclusive fitness effect*

In order to evaluate S explicitly, we need four distinct quantities (e.g. Taylor 1990; Taylor & Frank 1996; Frank 1998; Rousset 2004). First, we must evaluate how carrying the mutation changes the fitness of a focal mated male and a focal mated female through their effects on sons and daughters. Second, we need to weight the changes in the fitness of a focal adult of sex j by the frequency t_{ij} of the transmission of its genes to offspring of sex i ($i,j = m,f$). Third, we need to weight the changes in fitness to offspring of sex i by the reproductive value v_i of the individuals of sex i (i.e. the class reproductive value of sex i; but because we evaluate fitness in terms of mated individuals, the distribution of class reproductive values at that stage is actually proportional to the distribution of individual reproductive values, since the number of mated individuals of both sexes is equal on average). Since all individuals are diploid, we have $t_{ij} = 1/2$ for all i and j, which implies that the reproductive values of all males and females are the same ($v_m = v_f = 1/2$). Fourth, we need to weight the changes in fitness by the probabilities of identity by descent between homologous genes sampled within and between the classes of actors affecting the fitness of the focal individual: this measures the extent to which group members are likely to increment or decrement the fitness of the focal individual relative to that of an individual not carrying the mutation. To this end, we define Q_w as the probability (varying between 1/2 and 1) of identity by descent between two homologous genes sampled randomly with replacement from the same individual, and which is the same for both sexes (i.e. co-ancestry with self; see equation (A 4) of appendix). We denote by Q_{ij} the probability of identity by descent between a gene sampled in an adult of sex i and another homologous gene randomly sampled from a distinct adult of sex j from the same group (i.e. identity evaluated after dispersal). Finally, we define $Q^R_{mm} = (1/N)Q_w + (1 - 1/N)Q_{mm}$, as the probability of identity between two genes randomly sampled with replacement from the same group (because we assumed paternal control Q^R_{ff} never appears).

In order to evaluate the changes in fitness, we first derive the fitness of an individual from a focal group in a monomorphic population, i.e. in a population fixed for either the mutant or the wild-type allele. This entails that a and ω are the same for all groups in the population, and if $\omega > 1/2$, there is an advantage to attacking (offensive advantage). Owing to our assumption of constant population size, fitness must be equal to one, and it depends on four events. First, the focal group is not attacked (probability $1 - a$), in which case both males and females obtain one unit of fitness by reproducing in the focal group. Second, the focal group is attacked and wins the battle (probability $a(1 - \omega)$), in which case both males and females obtain one unit of fitness by reproducing in the focal group. Third, the focal group is attacked but loses the battle (probability $a\omega$), in which case males obtain s_m units of fitness and females obtain s_f units of fitness by reproducing in the focal group. Fourth, the focal group attacks another group and wins the battle (probability $a\omega$), in which case a male and a female from the focal group obtain, respectively, $1 - s_m$ and $1 - s_f$ units of fitness by reproducing in the conquered group. Summing up all fitness components, we have

$$1 - a\omega + a\omega s_i + a\omega(1 - s_i) = 1. \tag{2.2}$$

In the next two sections, we evaluate how this fitness is altered by the behaviour of the focal individual (bearing at least one copy of a mutant allele) and its group members, assuming that the effects on fitness are small. Expressing the belligerence allele will alter a while expressing the bravery allele will alter ω. For ease of presentation, we proceed in a rather heuristic way (e.g. Taylor 1988*b*, 1992; Taylor & Irwin 2000), but the following calculations can be validated more rigorously by writing down the fitness functions corresponding to the life cycle (e.g. Taylor & Frank 1996; Rousset 2004).

(d) *Male belligerence*

By producing belligerent sons, a focal male decreases directly his fitness by $C_a Q_w$, where Q_w gives the probability that the focal male produces belligerent sons. Since a belligerent son has a lower chance of surviving density-dependent competition (stage 4 of the life cycle), his behaviour decreases the intensity of competition among males in his group. This implies that by remaining in his natal group (philopatry) a belligerent son increases the chances that his philopatric brothers find an empty spot, which indirectly increases the fitness of the focal male. Similarly, when adult males in the focal group produce belligerent sons, the intensity of competition for the focal male's offspring remaining philopatric decreases, which indirectly increases the focal individual's fitness. The net indirect increase in the focal male's fitness due to all adult males in the focal group carrying the mutation, and concomitantly reducing the intensity of competition, depends on three events. First, the focal group is not attacked or it is attacked but it wins the battle (probability $1 - a\omega$), in which case the focal male gains indirectly $C_a(1 - m)^2 Q^R_{mm}$ units of fitness, where $(1 - m)^2$ is the probability that two philopatric males compete against each other (since neither migrated) and Q^R_{mm} measures the probability that males from the focal group express a gene identical by descent to that of a focal gene in the focal male and thus produce belligerent males. Second, the focal group is attacked but loses the battle (probability $a\omega$), in which case the focal's male indirect fitness gain is $C_\omega(1 - m)^2 s_m^2 Q^R_{mm}$, where $(1 - m)^2 s_m^2$ is the probability that two philopatric males from the focal group compete against the other in this case. Finally, the focal group attacks another group and wins the battle (probability $a\omega$), in which case the focal male indirectly gains $C_\omega(1 - m)^2(1 - s_m)^2 Q^R_{mm}$ units of fitness. Summing up all components weighted by their probabilities of occurrence, we find that carrying the belligerence allele indirectly increases the fitness of the focal male by $C_a(1 - m)^2(1 - 2a\omega s_m(1 - s_m))Q^R_{mm}$.

By producing belligerent sons, the focal male also increases the probability that his son's group goes to war (effect on a of the last term on the left-hand side of equation (2.2)). Since the number of pre-adult males is

Table 1. Weighted changes in fitness for the belligerence allele.

	changes in fitness	weight
through sons	$-C_a$	$\nu_m(t_{mm}Q_w + t_{mf}Q_{fm})$
	$C_a(1-m)^2(1-2a\omega s_m(1-s_m))$	$\nu_m\left(t_{mm}Q^R_{mm} + t_{mf}Q_{fm}\right)$
	$a\omega B_a(1-m)(1-s_m)$	$\nu_m\left(t_{mm}Q^R_{mm} + t_{mf}Q_{fm}\right)$
through daughters	$a\omega B_a(1-m)(1-s_f)$	$\nu_f\left(t_{fm}Q^R_{mm} + t_{ff}Q_{fm}\right)$
direct fitness cost	$c = 1/4[C_a(1-\{1-2a\omega s_m(1-s_m)\}(1-m)^2/N) - 2x\omega aB_a(1-m)/N]$	
indirect fitness benefit	$b = 1/4[2x\omega aB_a(1-m)(2N-1)/N - C_a(1-\{1-2a\omega s_m(1-s_m)\}(1-m)^2(2N-1)/N)]$	
	$x \equiv 1-(s_f+s_m)/2$	

assumed to be very large, we assume that the effect of a single pre-adult male on the probability that his group goes to war is negligible. This entails that we ignore the change in fitness to the focal male due to belligerent sons dispersing, but we take into account the effect of those remaining philopatric because they constitute a fraction $(1-m)/N$ of the focal group's males after dispersal. The net increase in the probability that the focal group goes to war due to all males in the focal group carrying the belligerence allele is $aB_a(1-m)Q^R_{mm}$. If the war is won, (probability ω) the focal male's fitness through sons increases by $(1-s_m)$ and through daughters by $(1-s_f)$.

So far, we have calculated the fitness costs and benefits that accrue to a mated focal male bearing at least one copy of the mutant allele. But we must also take into account the fitness costs and benefits that accrue to a mated female bearing at least one copy of the mutant allele. This is obtained by weighting all the gains and losses of fitness calculated for the focal male by Q_{fm} instead of Q_w and Q^R_{mm}. The coefficient Q_{fm} is the probability of identity by descent between a gene sampled in the focal female and a homologous gene sampled in her mate who controls the phenotype of her offspring. The overall accounting of fitness change is provided in the first four rows of table 1.

(e) *Male bravery*

By producing brave sons, a focal male directly decreases his fitness by $C_\omega Q_w$ when the focal group is attacked and wins the war. Since bravery increases the risk that the sons of the focal male die, the number of competing males in the focal group decreases, which translates into a higher chance that neighbours find an empty spot during density-dependent competition (stage 4 of the life cycle). The indirect increase in the focal male's fitness due to all adults males in the focal group producing brave sons, when the focal group is attacked and wins the war, is $C_\omega(1-m)^2Q^R_{mm}$. The loss in fitness for a focal male producing brave male offspring when the focal group is attacked but loses the war is $C_\omega s_m Q_w$, while his indirect fitness benefit is $C_\omega(1-m)^2 s_m^2 Q^R_{mm}$. Finally, when the focal group attacks another group and wins the battle, the focal male loses $C_\omega(1-s_m)Q_w$ units of fitness in the conquered group and indirectly gains $C_\omega(1-m)^2(1-s_m)^2Q^R_{mm}$ units of fitness. Summing up all components, we find that carrying the mutation directly decreases the fitness of the focal male by $aC_\omega Q_w$ and indirectly increases it by $aC_\omega(1-m)^2\left(1-2\omega s_m(1-s_m)\right)Q^R_{mm}$.

A focal male producing brave offspring also increases the probability that the male's group wins the war, whenever that group is attacked or it attacks another group, or both. As we did in the case of male belligerence, we assume that the effect of a single pre-adult male on the probability that its group wins a battle is vanishingly small. Hence, we ignore the gain in fitness due to the effect of bravery of dispersing males but take into account the effect of those remaining philopatric. The increase in mating success for the focal male's sons due to all males in the focal group expressing bravery, and thus increasing the chance that the focal group wins a battle, is $2a\omega B_\omega(1-m)(1-s_m)Q^R_{mm}$, which is obtained as follows. With probability $(1-m)$, the focal male's son remains philopatric and two events might occur. First, the focal group is attacked by another group, in which case the expression of bravery decreases the probability that the attacker group wins the battle (i.e. negative perturbation of ω in the middle term of the left-hand side of equation (2.2)). Second, the focal group tries to conquer another group, in which case the expression of bravery increases the probability that the focal group wins the battle (i.e. positive perturbation of ω in the last term of the left-hand side of equation (2.2)). For both events, the focal male obtains $(1-s_m)$ units of fitness through sons and $(1-s_f)$ units of fitness through daughters. As before, we must also take into account the fitness costs and benefits that accrue to a mated focal female bearing at least one copy of the mutant allele, and the overall accounting of fitness effects is recorded in the first four rows of table 2.

(f) *Hamilton's rule*

Summing up all the weighted changes in fitness, i.e. the first four rows of table 1 (or table 2), and recalling that v_i and t_{ij} are both equal to 1/2 for all i and j, produces the inclusive fitness effect S of the mutant belligerence (or bravery) allele. Because we assumed no sex-specific dispersal, all probabilities of identities between genes drawn from pairs of adults are equal ($Q_{ff} = Q_{fm} = Q_{mm} = Q$), and we use the symbol Q to denote them. With this, the inclusive fitness effect S depends only on two probabilities of identity, Q_w and Q (recall that $Q^R_{mm} = (1/N)Q_w + (1-1/N)Q$). We can now separate all the changes in fitness appearing in S into those factoring Q_w (collectively called $-c$) and those factoring Q (collectively called b). We can, therefore, write the inclusive fitness effect as $S = -cQ_w + bQ$, where $-c$ is actually the average net effect of the behaviour of a focal individual (averaged over male and female roles) on its own fitness, and b can be thought of as the net effect of the behaviour of the actor on the fitness of adult recipients, summed up over all recipients in the focal individual's patch. The net fitness cost, c, and fitness benefit, b, for belligerence and bravery are given in tables 1 and 2, respectively. Selection favours a mutant allele when $S > 0$, which can be reorganized and written as $Rb - c > 0$, where $R = Q_w/Q$ is the

Table 2. Weighted changes in fitness for the bravery allele.

	changes in fitness	weight
through sons	$-aC_\omega$	$\nu_m(t_{mm}Q_w + t_{mf}Q_{fm})$
	$aC_\omega(1-m)^2(1-2\omega s_m(1-s_m))$	$\nu_m\left(t_{mm}Q^R_{mm} + t_{mf}Q_{fm}\right)$
	$2a\omega B_\omega(1-m)(1-s_m)$	$\nu_m\left(t_{mm}Q^R_{mm} + t_{mf}Q_{fm}\right)$
through daughters	$2a\omega B_\omega(1-m)(1-s_f)$	$\nu_f\left(t_{fm}Q^R_{mm} + t_{ff}Q_{fm}\right)$
direct fitness cost	$c = 1/4[aC_\omega(1-\{1-2\omega s_m(1-s_m)\}(1-m)^2/N) - xa\omega B_\omega(1-m)/N]$	
indirect fitness benefit	$b = 1/4[4xa\omega B_\omega(1-m)(2N-1)/N - aC_\omega(1-\{1-2\omega s_m(1-s_m)\}(1-m)^2(2N-1)/N)]$	

relatedness between two adult individuals (Hamilton 1971; Michod & Hamilton 1980). The relatedness can also be expressed as $R=2Q/(1+F)$ (see equation (A 4)), where F is the probability of identity between the maternally and paternally inherited gene copies within an individual (note that Q and F are equivalent to Wright's (1951) F_{ST} and F_{IT}, respectively).

3. RESULTS

(a) *Selection on male belligerence*

Substituting c and b from table 1 into $Rb-c>0$ and rearranging, we find that selection favours the belligerence allele when

$$\frac{C_a}{aB_a} < \frac{2\omega x(1-m)\{1+R(2N-1)\}}{N(1+R)-(1-m)^2\{1-2a\omega s_m(1-s_m)\}\{1+R(2N-1)\}}, \tag{3.1}$$

where C_a/aB_a is the ratio of the marginal cost to a male of expressing belligerence to the marginal increase in the attack probability (cost-to-benefit ratio), and $x \equiv 1-(s_f+s_m)/2$ (varying between 0 and 1) is the average increase in fitness that a focal individual can gain through conquest. If one considers that belligerence is an evolving continuous phenotype z, then the marginal cost (C_a), the marginal benefit (aB_a) and the attack rate a could be modelled as explicit functions of z (e.g. Frank 1998; Rousset 2004); and equating both sides of equation (3.1) allows one, in principle, to compute the values of z that are candidate evolutionary stable strategies (Maynard-Smith 1982; Eshel 1983).

The invasion condition (equation (3.1)) highlights that the direction of selection on a belligerence allele is an increasing function of the relatedness coefficient between adult individuals within groups, which is a dynamic function of the parameters of the model (N, m, a, s_m and s_f). In order to ascertain the direction of selection in the absence of interactions between related individuals, which are sometimes considered to be negligible in social groups (Clutton-Brock 2002), one needs simply to set $R=0$ in equation (3.1). In this case, belligerence may invade, but it is not altruistic (*sensu* Hamilton (1964, 1970)) because the trait spreads only if it results in a net direct fitness increment, i.e. the belligerence allele spreads only if $-c>0$. Generally, correlated effects due to interactions between relatives cannot be neglected when migration is limited (unless population size is extremely large, in which case the genetic variance between groups vanishes), which then allows for the build up of relatedness ($R>0$), and eventually the evolution of altruistic belligerence. We present the equilibrium value of R as equation (A 9) of the appendix, which allows us to compute the invasion condition explicitly in terms of life-history features by inserting equation (A 9) into equation (3.1). The resulting inequality is complicated, but to the first order in $1/N$ (i.e. large group size), the belligerence mutant invades the population, and goes to fixation (see equation (2.1)), if

$$\frac{C_a}{aB_a} < \frac{2\omega x(1-m)\{1+2a\omega x(1-x)(1-m)^2\}}{N\left(1-(1-m)^2\{1-2a\omega x(1-x)\}\right)}. \tag{3.2}$$

The threshold cost-to-benefit ratio on the right-hand side of this inequality, below which the mutant allele can invade, is monotonically decreasing with group size (N) and the migration rate (m), and monotonically increasing with x. That is, the selective pressure on the mutant allele is stronger when males and females from the conqueror groups are more likely to populate the conquered group (e.g. higher killing rate of males, k_m, and females, k_f, from the conquered groups after conquest).

In figure 1, we plot the threshold cost-to-benefit ratio (right-hand side of equation (3.2)) as a function of x for various parameter values, and we see that when the migration rate is relatively small (e.g. $m=0.1$), belligerence can be selected for even in groups of large size (e.g. $N=50$), whenever the returns from the war are substantial. In figure 2, we compare this threshold cost-to-benefit ratio with the exact expression given by the right-hand side of equation (3.1) with and without taking relatedness into account, as a function of group size N. Figure 2 shows that interactions between related individuals substantially affect the selection pressure on belligerence even in groups of large size, and that the approximation to the threshold cost-to-benefit ratio given by equation (3.2) remains good even for small group size.

(b) *Selection on male bravery*

Substituting c and b from table 2 into $Rb-c>0$, we find that selection favours the bravery allele when

$$\frac{C_\omega}{\omega B_\omega} < \frac{4x(1-m)\{1+R(2N-1)\}}{N(1+R)-(1-m)^2\{1-2\omega s_m(1-s_m)\}\{1+R(2N-1)\}}, \tag{3.3}$$

where $C_\omega/\omega B_\omega$ is the ratio of the marginal cost of expressing bravery to the marginal increase in the probability of winning a battle. Bravery could also be modelled as an evolving phenotype z, in which case the marginal cost (C_a), the marginal benefit (ωB_ω) and the probability of winning ω could be complicated functions of the phenotype z expressed by the individuals from the attacker and attacked groups and their tactics. In this case, care should be taken in evaluating ωB_ω because this is actually the average marginal increase in winning a battle, namely the average over the marginal increase in the probability of winning a battle when a focal group is attacked (defence) and the marginal increase in the probability of winning a battle when the focal group attacks another group (offence). These effects may be

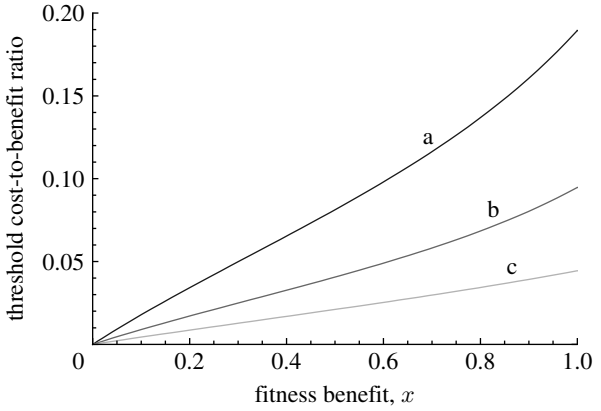

Figure 1. Threshold cost-to-benefit ratio for the mutant belligerence allele to invade the population as given by the right-hand side of equation (3.2) and graphed as a function of the average fitness benefits x for various parameter values ($x \equiv 1-(s_f + s_m)/2$). We have $a=0.2$ and $\omega=0.5$ for all curves, m$=0.1$ and $N=25$ for line a, m$=0.1$ and $N=50$ for line b and $m=0.25$ and $N=50$ for line c.

different but were assumed, here, to be the same. With both belligerence and bravery being continuous phenotypes, equations (3.1) and (3.3) could be used to compute candidate coevolutionary stable strategies.

Inserting equation (A 9) into equation (3.3), and keeping only the terms of leading order in $1/N$ (i.e. large group size), we find that the bravery mutant allele invades the population if

$$\frac{C_\omega}{\omega B_\omega} < \frac{4x(1-m)\{1+2a\omega x(1-x)(1-m)^2\}}{N\big(1-(1-m)^2\{1-2a\omega x(1-x)\}\big)}. \qquad (3.4)$$

The only difference between the right-hand side of this inequality and that of equation (3.2) is the factor 2 in equation (3.4), which replaces ω in the numerator of equation (3.2). Hence, the selective pressure on bravery is at least twice as strong as the selective pressure on belligerence, but it behaves qualitatively in exactly the same way. Therefore, bravery can also evolve in groups of large size, and the doubling of the selective pressure stems from bravery increasing the probability of winning a war when the focal group is attacked (defence), as well as when it attacks another group (offence).

5. DISCUSSION

We have provided a mathematical analysis of the selective pressure on costly male belligerence and bravery when these two traits are involved in tribal war occurring between small-scale, pre-state societies. We assumed that belligerence increases an actor's group's probability of trying to conquer another group, and that bravery increases the actor's group's ability to conquer the attacked group.

It has been repeatedly stressed that warfare in hunter-gatherer societies might be driven by the prospect of obtaining reproduction-enhancing resources from other groups (Durham 1976; Chagnon 1988; Turchin 2003; Richerson & Boyd 2005). Our results suggest that two very different types of reproduction-enhancing resources can drive the evolution of male belligerence and bravery. First, the two traits may evolve when only males from the conqueror groups obtain additional mates through conquest ($s_f=1$, $s_m<0$). In our model, this occurs when the males from the conqueror groups replace those from the conquered groups and then mate with conquered females.

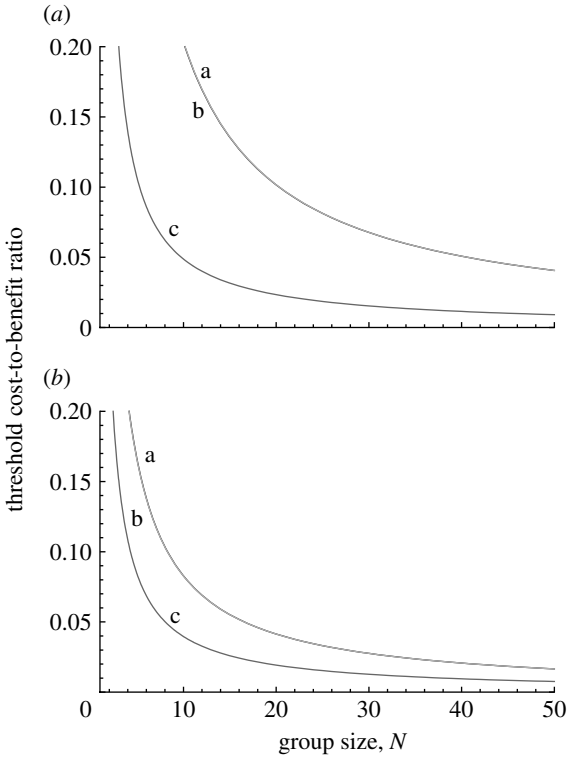

Figure 2. Threshold cost-to-benefit ratio for the mutant belligerence allele graphed as a function of group size N for $a=0.2$, $\omega=0.5$, $s_f=0.5$ and $s_m=0.5$, and two different values for the migration rate: (*a*) $m=0.1$ and (*b*) $m=0.25$. Line a (top lines) in (*a*) and (*b*) gives the right-hand side of equation (3.1). Line b (nearly indistinguishable from line a) gives the right-hand side of equation (3.2), which is the approximation to the right-hand side of equation (3.1) for large group size, but remains a good approximation even for small group size (with increasing values of a, the approximation becomes less accurate). Line c gives the right-hand side of equation (3.1) with $R=0$, i.e. by assuming that individuals within groups are not genetically related. This assumption markedly reduces the apparent selective pressure on belligerence.

Because males tend to be related within groups, this results in both direct and indirect fitness benefits to males that may offset their cost of expressing belligerence and bravery (equations (3.1) and (3.3)). Second, when females from the conqueror groups are likely to obtain more territories to reproduce, male belligerence and bravery can also evolve, even if the males obtain no fitness benefits by conquest ($s_m=1$, $s_f<0$). In our model, this occurs when females, who are likely to be related to the belligerent and brave males of their group, replace the females of the conquered group and subsequently produce offspring. This results in an indirect selective pressure on male belligerence and bravery, which again can offset the direct cost of expressing these traits in males (equations (3.1) and (3.3)). Although our formalization does not take into account all types of reproduction-enhancing resources that can be obtained by force (e.g. taking food, goods or slaves to the deme of the conqueror group), it demonstrates that male coalitional aggression can be an adaptation to the conditions of limiting resources for both sexes.

Because relatedness decreases with increasing group size (which decreases the coalescence rate within groups) and migration rate (which homogenizes the genetic composition of populations), the selective pressure on genetically determined belligerence and bravery also decreases

(equations (3.2) and (3.4)). This is a standard and general result, which has been repeatedly documented in the models considering the evolution of costly social behaviours in subdivided populations (e.g. Eshel 1972; Aoki 1982; Rogers 1990; van Baalen & Rand 1998; Taylor & Irwin 2000; Le Galliard *et al.* 2003; Gardner & West 2006; Lehmann *et al.* 2006; Lion & Van Baalen 2007). Despite the decrease in relatedness with larger population size, our results suggest that the selective pressure on male belligerence and especially male bravery can remain substantial even in groups of large size. For instance, with a migration probability of $m=0.1$, costly male bravery may evolve even when the number N of individuals of each sex in a group is as large as 50 (equations (3.2) and (3.4); figure 2), a figure that is larger than that is usually considered in the models for the evolution of costly social behaviours in subdivided populations.

This strong selective pressure can be explained by invoking two assumptions of our model. First, we assumed paternal control of the phenotypes of pre-adult males (which is plausible because group-level decisions tend to be made by the individuals from older age classes in human societies). Because a parent is less related to its offspring than the offspring is related to itself, a parent is more willing to 'sacrifice' an offspring than an offspring is willing to sacrifice itself when it is in control of its own phenotype. The selective pressure on male bravery is thus expected to decrease under offspring control, and could, theoretically, be halved. Nevertheless, it would still remain significant in groups of large size. The second important factor is that an actor expressing bravery has a dual effect on its group's members' fitness: on the one hand, bravery increases the actor's group's probability to resist group extinction (defence), and on the other hand it increases the probability that the actor's group conquers another group (offence), where these two effects do not directly increase the intensity of competition between the members of the actor's group. This situation is very different from that where the actor's behaviour augments the fertility of group members and thus produces higher local competition between group members, which, in turn, feeds back negatively on the evolution of the trait (Taylor 1992; Taylor & Irwin 2000; West *et al.* 2008). Because behavioural effects translate into a fitness benefit to all group members and no increase in competition between them, our life history easily promotes the evolution of costly social traits. Our formalization is, therefore, closely related to previous analytical models for the evolution of social behaviour, in which the actor's behaviour reduces the probability of environmental group extinction (Eshel 1972; Aoki 1982; Lehmann *et al.* 2006), the so-called selective extinction models, and those where whole groups compete against each other (Gardner & West 2006; Lehmann *et al.* 2006); the so-called budding or propagule dispersal models.

Our model is also closely related to the simulations of Choi & Bowles (2007) for the coevolution of helping and parochiality when warfare occurs between groups. In the setting used by these authors, interactions occur in each time period between randomly paired groups. The probability that war occurs between a pair of groups depends on the frequency of parochial individuals within groups (which can be thought of as belligerence in our model). The winning group, the one with the largest number of helpers (which can be thought of as bravery in our model), then has a higher chance to repopulate vacant breeding spots due to casualties in both combatant groups. Choi & Bowles (2007) carried out simulations with $N=26$ (haploid individuals) and $m=0.25$ and found that parochiality and helping might evolve, a result that is corroborated by our analytical model. However, in their discussion on the factors generating assortment between identical strategies, they suggest that kin selection is not important for their results. Our analytical formulation allows comparison of the intensity of selection with and without the effects of relatedness and how these depend on group size and migration rate. Hence, one can evaluate the level of belligerence and bravery that would evolve without relatedness, by direct effects on fitness alone (figure 2). Our results suggest that relatedness between group members plays a crucial role in accounting for the evolution of male belligerence and bravery. This is particularly the case when only females benefit from additional enhancing resources ($s_m=1$, $s_f<0$), and where the fitness benefits generating the selection pressure on both traits can accrue to males only indirectly. Our analysis thus reinforces Hamilton's (1975) conjecture that relatedness within groups can result in the development of within-group coalition and between-group hostility.

Although we assumed genetic inheritance of belligerence and bravery, these behaviours may also be inherited culturally (Cavalli-Sforza & Feldman 1981; Boyd & Richerson 1985), and our main results (equations (3.1) and (3.3)) apply to cultural transmission under specific conditions. If individuals express one of two cultural variants segregating in the population that directly affect reproduction (i.e. effects on Darwinian fitness; Cavalli-Sforza & Feldman 1981), and their transmission is unbiased, first vertically from parents to offspring and then horizontally or obliquely before or after the dispersal stage, then our invasion conditions also apply to culturally determined belligerence and bravery. In this case, $Q_w=1$ and Q_{ij} represent the probabilities of identity between the cultural variants carried by two individuals, one of sex i and the other of sex j, which may, in principle, remain positive in groups of any size (Lehmann *et al.* 2008). Consequently, under cultural transmission, male belligerence and bravery may evolve in large-scale societies.

In summary, our model has yielded two results. First, it has clarified the connection between relatedness, migration rate and population size for the evolution of male belligerence and bravery, and showed that genetically determined within-group coalition and between-group hostility may evolve in groups of large size ($N\sim 50$ of each sex), but cultural transmission of these traits may allow for their evolution in groups of any size. Second, we identified two independent types of reproduction-enhancing resources for males and females, which can drive intergroup conflict and should be taken into account when trying to understand its evolution. This is pertinent for understanding the possible benefits that allowed evolution of male coalitional strategies such as hunter-gatherers raiding neighbouring groups and capturing material resources and women by force (Chagnon 1988).

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APPENDIX A: PROBABILITIES OF IDENTITY BY DESCENT AND RELATEDNESS

Here, we compute the probabilities of identity between pairs of homologous genes randomly sampled within (Q_w) and between (Q_{ij}) adult individuals by standard methods (e.g. Karlin 1968; Taylor 1988*a*; Gandon 1999; Gillespie 2004; Rousset 2004). We evaluate these probabilities at equilibrium, neglecting time indices, and start by evaluating the probabilities of identity just after reproduction (stage 1 of the life cycle), i.e. at the juvenile stage.

By our assumption that individuals are diploid, the probabilities of identity between any pair of juveniles are the same, irrespective of their sexes. The probability of identity Q^J between two genes randomly sampled in two distinct juveniles can be decomposed as

$$Q^J = (1-a\omega)Q^J_{nc} + a\omega Q^J_c, \tag{A 1}$$

where Q^J_{nc} is the probability of identity between two homologous genes sampled in two distinct juveniles in a non-conquered group, while Q^J_c stands for the same probability in a conquered group. We express these two probabilities as functions of the identities within and between adults after dispersal and density-dependent competition (Q_w and Q_{ij}) by noting that with probability 1/4 the two genes are both of maternal and paternal origin, with 1/2 one gene is of maternal origin and the other is of paternal origin and with $1/N_i$ two randomly sampled juveniles descend from the same parent of sex i. In a non-conquered group, this gives

$$Q^J_{nc} = \frac{1}{4}\left[\frac{1}{N_f}Q_w + \left(1-\frac{1}{N_f}\right)Q_{ff}\right] + \frac{1}{2}Q_{fm} + \frac{1}{4}\left[\frac{1}{N_m}Q_w + \left(1-\frac{1}{N_m}\right)Q_{mm}\right]. \tag{A 2}$$

In a conquered group, a pair of adults share genes identical by descent after density-dependent competition only if this pair descends from the same group before competition. Hence,

$$\begin{aligned} Q^J_c = {} & \frac{1}{4}\left[\frac{1}{N_f}Q_w + \left(1-\frac{1}{N_f}\right)\{(1-s_f)^2 + s_f^2\}Q_{ff}\right] + \frac{1}{2}\{(1-s_m)(1-s_f) + s_m s_f\}Q_{fm} \\ & + \frac{1}{4}\left[\frac{1}{N_m}Q_w + \left(1-\frac{1}{N_m}\right)\{(1-s_m)^2 + s_m^2\}Q_{mm}\right]. \end{aligned} \tag{A 3}$$

In the above equations, we have

$$Q_w = \frac{1+F}{2}, \tag{A 4}$$

because with probability 1/2 the two genes under scrutiny are replicas of the same gene of an individual and are thus identical, while with probability 1/2 one gene is a replica of the maternally inherited gene and the other is a replica of the paternally inherited gene, in which case their probability of identity is F, which is the average inbreeding coefficient in an adult individual (i.e. probability of identity between the maternally and paternally inherited gene copies within an individual). At equilibrium, F in an adult individual is the same as the inbreeding coefficient within a juvenile of the next generation, which is equal to the average genetic identity between the parents of that juvenile, namely

$$F = (1-a\omega)Q_{fm} + a\omega\{(1-s_m)(1-s_f) + s_m s_f\}Q_{fm}. \tag{A 5}$$

When the dispersal rate is the same in each sex, the probabilities of identity between two genes sampled in two different adults will be the same, irrespective of the sexes of these individuals ($Q_{ff} = Q_{fm} = Q_{mm}$). These probabilities are then related to Q^J, according to the equation

$$Q_{ij} = (1-m)^2 Q^J, \tag{A 6}$$

which, on substitution into equations (A 2)–(A 5), allows us to solve equations (A 1) and (A 5) for F and Q^J explicitly

$$F = \frac{(1-m)^2\left(1-a\omega\{s_f(1-2s_m) + s_m\}\right)}{4N-(1-m)^2\left[(4N-1)-a\omega\left((4N-1)(s_f+s_m)-2(N-1)(s_f+s_m)^2-6s_f s_m\right)\right]}, \tag{A 7}$$

and

$$Q^J = \frac{1}{4N-(1-m)^2\left[(4N-1)-a\omega\left((4N-1)(s_f+s_m)-2(N-1)(s_f+s_m)^2-6s_f s_m\right)\right]}. \tag{A 8}$$

Under neutrality, the relatedness R between two individuals is given by the ratio of Q relative to Q_w (Hamilton 1971; Michod & Hamilton 1980). Using equation (A 4), this produces $R=2Q/(1+F)$, whose explicit solution can be obtained using equations (A 6)–(A 8), which yields

$$R = \frac{1}{2N-(1-m)^2\left[(2N-1)-a\omega\left((2N-1)(s_f+s_m)-N(s_f+s_m)^2+s_f^2+s_m^2\right)\right]}. \tag{A 9}$$

When $a=0$, all the above equations (equations (A 5)–(A 9)) reduce to the standard formulae (e.g. Taylor 1988*a*; Gandon 1999).

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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 ($Q_{ij} = (1-m)^2 Q^{\mathrm{J}}$), 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

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

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 $(1-m)^2 Q^{\mathrm{J}}$. 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 $(1-m)^2 Q^{\mathrm{J}}$.

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

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

When the sexes have the same survival probability during regulation ($s_{\mathrm{m}} = s_{\mathrm{f}} = s$), equation (1.2) reduces to

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

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

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

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

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

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

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

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

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

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

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

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

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