

Comment on the Sloman/Waller exchange

May I butt in on the Sloman/Waller exchange and suggest that what they have both independently done is to rediscover sexual selection? They are both talking about a social process that increases the correlation between a favourable mutation and fitness. Darwin recognised this social process and he called it sexual selection. Sloman emphasises, rightly, that this social process may begin in childhood and it may exhibit positive feedback characteristics. Waller emphasises that the people not selected by the process may have a bad time, and he points out that the capacity (or, rather, obligation) to engage in the social process is genetically determined. These are additions to the theory which Darwin put forward in the Origin and subsequently elaborated in The Descent of Man and Selection in Relation to Sex.

Darwin made it clear that natural selection is based on differential ability to deal with the physical environment, including predator and prey relations with other species, but at the same time he recognised that selection occurs as a result of interactions with members of the same species. In the Origin of Species he wrote:

"This form of selection depends not on a struggle for existence in relation to other organic beings or the external conditions, but on the struggle between individuals of one sex, generally the males, for the possession of the other sex".

In 1871 Darwin published The Descent of Man and Selection in Relation to Sex which was devoted to a meticulous analysis of sexual selection. In this book he introduced the term for the first time, and he pointed out that sexual selection has two components. He wrote:

"Sexual selection depends on the success of certain individuals over others of the same sex, in relation to the propagation of the species; whilst natural selection depends on the success of both sexes, at all ages, in relation to the general conditions of life. The sexual struggle is of two kinds; in the one it is between individuals of one sex, generally the male, in order to drive away or kill their rivals, the female remaining passive; whilst in the other, the struggle is likewise between the individuals of the same sex, in order to excite or charm those of the opposite sex, generally the females, which no longer remain passive but select more agreeable partners. This latter kind of selection is closely analogous to that which man unintentionally, yet effectually, brings to bear on his domesticated productions, when he preserves during a long period the most pleasing or useful individuals, without any wish to modify the breed."

The capacity to "drive away or kill one's rivals" was not given a technical name until, in 1974 (1), Geoffrey Parker introduced the term resource-holding potential or RHP. Success in agonistic encounters raises RHP, so the genetically determined RHP management system acts as a deviation amplifying device. Human beings low in RHP suffer from low self-esteem and have increased liability to many forms of psychopathology.

Darwin included both types of sexual selection under the same heading, but did not give them separate names. Julian Huxley (2) introduced the term "intra-sexual selection" for the social process between members of the same sex, and he called mate choice "epigamic selection". Use of the term "intersexual selection" for mate choice has been rightly criticised by Helena Cronin (3). Epigamic selection is a powerful amplifying device; if women would only mate with men who can sing in tune, the musical ability of the population would rapidly improve. Darwin concentrated on epigamic selection, rather than on intrasexual selection, and so have most of the biologists who have followed him. This, and the rather clumsy name, have probably shielded intrasexual selection (and the mainly non-lethal forms of social competition which subserve it) from the biological enquiry which it deserves. Huxley (2) pays some attention to the fate of the unselected, pointing out that a significant proportion of adult birds fail to mate each year, and he wrote:

...defeat in combat has far reaching general effects, birds though physically uninjured sometimes dying as a result, if not promptly removed from contact with other birds, and even when physically recovered losing the impulse to mate for the rest of the season. Conversely, successful threat-displays promote both general and sexual vigour...

Huxley does not seem to have been aware of the work of Schjelderup-Ebbe, who had already published similar observations (4). Huxley also noted that when a male pelican's courtship display is rejected, its frontal protuberance shrinks and the nearby skin changes colour. This is likely to be part of a self-induced deviation amplification mechanism, as other

females can recognise him as a rejected suitor and ignore him, and thus his own physiological changes are reducing his fitness.

Intrasexual selection is what Sloman and Waller are talking about. The confusing thing about it is why anyone should choose to be unselected or de-selected - why isn't the tendency to go into one of Sloman's maladaptive cycles bred out of the population (which was Waller's original question)? There are two answers to this, one from ethology and one from behavioural ecology. The ethological answer is that social selection is mediated by agonistic behaviour, which has become ritualised, and is widespread in the animal kingdom, probably having evolved many times over. Because it is so common it must have some value, and the value is to prevent serious injury. The answer from behavioural ecology is an analysis of two alternative strategies which may be adopted in social competition: the "hawk" strategy which is one of escalation and fighting to the death, and the "dove" strategy which is one of de-escalation and giving way. Maynard Smith (5) applied game theory to the evolution of these strategies, and he showed that in certain conditions a pure hawk strategy is not stable, but is likely to be infiltrated and replaced by a mix of strategies. Either some of the players must be doves, or each player must play dove in a proportion of encounters. Note that this applies even if every member of the population starts with equal RHP. If there is genetic (or environmental) variation in RHP, then the game is different and the stable strategy is to assess the other and to play dove if one's RHP is less. This "Assessor" strategy is getting very close to Waller's comparator gene.

It is not generally realised that the rules of social selection changed about ten million years ago. The assessment is not now by the player himself (or herself) but by the group as a whole. We now have competition by attraction leading to "prestige" and "status" rather than competition by intimidation leading to dominance (6, and see my contribution to last September's ASCAP). This not only means that selection can be more rapid, but that any characters the group chooses can be selected for, rather than the "tough guy" attributes that give success in agonistic behaviour. This allows selection for task competence, linguistic ability, group loyalty and altruism. It probably also selected for "Parents choosing the bridegroom" so that what I have called "externally mediated sexual selection" (because the selectors are external to the competing or mating dyad) applied not only to intrasexual selection but also to epigamic selection or mate choice.

There are several important consequences of this change in the method of sexual selection:

1. Social attention holding power (SAHP) replaces RHP as the relevant self-concept.
2. The signals which raise and lower RHP and SAHP (which I have called anathetic and catathetic signals) are applied to the individual by the group as a whole rather than by the rival. Approbation and disapprobation have replaced submission and threat. These new signals convey the message, "you are good (bad)" rather than "you are more (less) powerful than me", and so have lost their implication of status difference between evaluator and the person being evaluated. Therefore they can be used both up and down the social hierarchy.
3. The social role of evaluator or judge has evolved.
4. Groups which allocate SAHP to individuals on the basis of qualities that make for group success are likely to outcompete groups that use other criteria.
5. Free-riders can be detected and allocated low SAHP, making group selection mathematically possible.
6. Groups which outlaw agonistic behaviour will outperform groups which do not.
7. Low self-esteem and depression, which are the fate of the unselected and de-selected, are now induced by the group as a whole, and they have come to be associated with group-relevant depressive emotions such as shame, guilt and humiliation in addition to the emotions which are aroused by losing an agonistic encounter.
8. Language is important for this new type of selection, because group members need to discuss each other's merits, and to give people "reputations".
9. Language is also important for attracting people and gaining SAHP.
10. With language the criteria for selection can be discussed by group members. Stories can be told about heroes who have the traits which the group values.
11. The positive feedback between the acquisition of language and the replacement of agonistic behaviour by social attraction has probably had a lot to do with the increase in human brain size over the past 3 million years. The change in the rules of sexual selection would have been the crucial factor. It is probably the only rule change since sexual selection itself evolved over 300 million years ago.

It is in no way denigratory to Sloman or Waller to suggest that they have rediscovered something that Darwin discovered 150 years ago. I wish I had done it myself.

Our contribution (7) has been to ask the question which Darwin never asked, "What happens to the people who are driven away?". Where are they? What do they look like? They cannot all be in prisons or psychiatric hospitals. They must be "out there" somewhere - or, more likely, "in here" with us (perhaps they are us!). Would they show up on a personality test? There is no suggestion in the personality literature that investigators have been looking for them. Could they be responsible for "Neuroticism/Negative

Affectivity" (8)?

And, once they have been driven away, what stops them from coming back? Do the "drivers away" stand constantly on guard ready to drive them away again? We have suggested (7) that the constraint which stops them coming back lies not in the drivers away but in themselves, in those who are driven away. We think they have some sort of "internal referee" which tells them, "You have not been selected, so stay away (or, stay down)", and this internal referee inhibits self-assertion and challenge behaviour, and causes them to have "subordinate self-perception", and we once called this internal referee the "yielding subroutine of ritual agonistic behaviour" but more recently we have called it the "involuntary subordinate strategy", and it consists of a lowering of those variables which cause a person to attack rather than submit, which are RHP, Resource Value and "sense of ownership", and it may manifest as a lifetime trait of low self-esteem, or as an episodic occurrence of a depressive state, depending on whether the individual feels unselected in the first place or is selected at first but then becomes de-selected.....but this is a train of thought with which ASCAP readers will by now have become familiar.

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#### References

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