



Letter to the Editor

A Note on Errors in Grafen's Strategic Handicap Models

In two papers published in this Journal, Grafen (1990a,b) has provided an enlightening account of the strategic handicap principle. However, there are a number of mathematical errors in these papers, some of which are of potential biological significance. For readers not interested in the mathematical technicalities, I first outline the effects of the errors in Grafen's papers and their primary biological implications. Following this, I describe the errors in each of these papers in more mathematical detail and, where possible, indicate how they may be corrected. Some familiarity with Grafen's notation is assumed, though I have included page references to important concepts.

Contrary to his claim, the analysis of the model of sexual selection in Grafen (1990a) does not show that there is a unique pair of male signalling and female mating strategies. In fact, as the model stands, the possibility of a large or even infinite number of signalling ESSs has not been ruled out. If this worst case scenario was actually the case then an ESS strategy in a population would be prone to invasion by "nearby" ESS strategies due to finite population sizes and local effects. One might expect to see signalling strategies "drift" in such a population.

The problem with Grafen (1990b) is that his analysis of the ESS signalling strategies breaks down if signalling is cheap enough. This is because he has not shown that the solutions to the differential equations which define the signalling ESSs exist for all qualities. When this occurs, the optimal strategy for some individuals in the population is to produce a signal, a , of infinite magnitude. Of course, this does not make biological sense if the signal is a physical magnitude, such as the length of a tail or the loudness of a call—extreme exaggerations of

such signals will not be cheap. However, there are circumstances in which a signal level of ∞ can be interpreted sensibly by rescaling the a -axis. For instance, suppose that the signal was the proportion of an organism that is coloured black, the cost of the signal being, say, the energetic or survival cost of producing or obtaining the pigment, or an increased predation risk due to greater visibility. The proportion of an individual coloured, $c \in [0, 1]$ can then be related to an interval of infinite length $[a_{\min}, \infty]$ by a transformation such as:

$$c = 1 - \frac{1}{a - a_{\min} + 1}$$

Thus, $a = \infty$ is, in this case, the circumstance in which the signalling organism has produced the maximal possible signal—once the entire organism has been coloured the deepest black there is no further possibility of increasing the signal.

This observation provides a possible explanation for multiple signals. A population in which a range of individuals signal at the maximum possible level would be prone to the invasion of a second signal, as the higher quality individuals signalling at $a = \infty$ would be able to increase their fitness by distinguishing themselves from the lower quality individuals signalling at $a = \infty$. If this second signal was also cheap and bounded, there would remain the possibility of the invasion of a third signal, and so on. The strategic handicap principle asserts that a population signalling strategy (which relates signal level to an individual's "quality") is long-term evolutionarily stable only if for each individual the marginal cost of increasing the level of signal (or signals) would outweigh the marginal benefits that could be gained by doing

so. Thus, depending on the particular details of the situation, the evolutionary consequences of such a process of successive invasion of signals might be a stable collection of a number of individually bounded and cheap signals which are collectively expensive, or perhaps a potentially unbounded signal together with a number of cheap and bounded signals.

I now turn to a technical discussion of the errors in Grafen's papers.

GRAFEN (1990a): The problems in Grafen (1990a) primarily affect the uniqueness of the signalling equilibrium that he obtains. There are two main errors in this paper. The first is that Grafen neglects to consider absolute continuity and Lipschitz conditions [see e.g. Riesz & Nagy (1955) for definitions]. This is a recurrent problem throughout the paper, and to rectify it would require an almost complete reworking of Grafen's model. This is not done here, as Grafen's model turns out to be a special case of more general and less cumbersome results (Siller, 1997). However, the effects of this oversight can be easily seen where Grafen asserts the uniqueness of the solutions to the differential equations that arise in the process of solving his model.

The signalling ESS that Grafen obtains is a fixed point of a functional $M: C \rightarrow C$ defined by eqn (A4.3) (Grafen, 1990a, p. 508); precisely $M(A) = A^*$ where A^* is implicitly defined by the differential equation:

$$\frac{dA^*}{dq} = \frac{-1}{\alpha^2(q, A^*(q))} \frac{d}{dq} \ln \left(\frac{K(A, q)}{K(A, q_{\min})} \right) \quad \text{a.e.}$$

$$A^*(q_{\min}) = 0$$

where $\alpha^2(q, a)$ is the logarithmic derivative of α in a . M is not well defined for a number of reasons. First, for the usual uniqueness theorem of differential equations to apply (see e.g. Struble, 1962), $1/\alpha^2$ needs to be Lipschitz continuous in a for each q . Grafen has not made this assumption and thus M may not be guaranteed to be a function. Second, Grafen has implicitly assumed that any ESS of his model is absolutely continuous, as there can be an infinite number of continuous solutions to a differential equation that is defined only almost everywhere,

even if the equation satisfies conditions that guarantee only one absolutely continuous solution. This is a problem, as models similar to Grafen's can be constructed for which there exist continuous signalling ESSs which are not absolutely continuous (Siller, 1997).

The second problem in Grafen's (1990a) paper pertains to Lemma 9 in which he attempts a proof of the uniqueness of his signalling ESS. There are a number of mistakes in signs contained in the proof of this lemma, and once corrected, the uniqueness result no longer follows. The following is a repetition, using Grafen's notation, of the relevant section of the proof with corrections, starting from the ninth line of p. 514:

Taking logs before differentiating, we obtain

$$\frac{L'_i(A_i(q))}{L_i(A_i(q))} = -\alpha^2(q, A_i(q)),$$

and integrating with respect to a we obtain

$$L_i(a) \propto \exp \left\{ - \int_0^a \alpha^2[A_i^{-1}(a'), a'] da' \right\},$$

for $a \in [0, A_i(q_{\max})]$.

Let $n_i(q, a)$ be the derivative with respect to a of $\ln[\alpha(q, a)L_i(a)]$ for $i = 1, 2$, then

$$n_1(q, a) = \alpha^2(q, a) - \alpha^2(A_1^{-1}a, a)$$

$$n_2(q, a) = \alpha^2(q, a) - \alpha^2(A_2^{-1}a, a).$$

Consider some value of q where, without loss of generality, $A_1(q) < A_2(q)$. Because the A_i are strictly increasing and continuous, it follows that $A_1^{-1}A_1(q) > A_2^{-1}A_1(q)$. We also know that $\alpha^2(q, a)$ is increasing in q , so that:

$$\alpha^2[A_1^{-1}A_1(q), a] > \alpha^2[A_2^{-1}A_1(q), a].$$

It follows that:

$$n_1[q, A_1(q)] < n_2[q, A_1(q)],$$

and by definition $n_1[q, A_1(q)] = 0$. Hence

$$n_2[q, A_1(q)] > 0.$$

It is at this point that Grafen's proof fails. In his paper, the last inequality was reversed, which allowed him to obtain a contradiction observing the proof of Lemma 8 which showed that for $a < A_2(q)$, $n_2(q, a) > 0$. This is no longer a

contradiction, but is in agreement with the last inequality.

In conclusion, the proof of the existence of a signalling ESS in Appendix 4 of Grafen (1990a) is flawed as the functional of which any fixed point is an ESS is not well defined. Moreover, the proof of uniqueness (Lemma 9) is erroneous due to an odd number of sign errors. With some minor technical alterations, it is possible to obtain Grafen's existence result as a special case of a more general analysis of strategic handicap signals (Siller, 1997), but the proof is too long to include here. I have been unable to provide a proof or disproof of the uniqueness of the signalling equilibrium in Grafen's model, however but it is possible to construct models similar to Grafen's for which there are an infinite number of ESSs (Siller, 1997). Therefore, there is the possibility that there may be multiple ESSs to Grafen's model.

GRAFEN (1990b). There are two errors in the proof of the existence of a solution in the basic ESS model outlined in Appendix 2 of Grafen (1990b) which carry over into Appendix 4. These problems are trivial to rectify, but their existence is of potential biological significance.

The first problem, which has little bearing on the proof of the result as it may be circumvented, is that the differential equation:

$$P^{*'}(a) = -\frac{w_1[a, P^*(a), P^*(a)]}{w_2[a, P^*(a), P^*(a)]} \quad (1)$$

$$P^*(a_{\min}) = q_{\min} \quad (2)$$

may not have a solution for all advertising levels $a \in [a_{\min}, \infty)$, due to P^* asymptoting at some value of a . Consider the function:

$$w(a, p, q) = p + \exp(-a(1 + q^2)).$$

It satisfies all conditions prescribed by Grafen, namely: $w_1 < 0$, $w_2 > 0$, and:

$$\frac{\partial}{\partial q} \left(\frac{w_1(a, p, q)}{w_2(a, p, q)} \right) > 0,$$

for all a, p, q . Yet it is not true that a solution exists to the system of eqns (1) and (2) over the

entire interval $[a_{\min}, \infty)$, as the solution in a suitably small neighbourhood of a_{\min} is given by:

$$P^* = \tan(a - a_{\min} + \arctan(q_{\min}))$$

which "blows up" at $\pi/2 + a_{\min} - \arctan(q_{\min})$.

The second problem, which is in a sense the inverse of the first, is more critical. Grafen defines the ESS advertising function $A^*(q)$ to be the right inverse of the perception function P^* , but this may not exist if a asymptotes for some value of P^* . Consider:

$$w(a, p, q) = p + \frac{(\exp(q_{\min} - q) + 1)}{a - a_{\min} + 1} + q - q_{\min}.$$

This function satisfies all the given conditions, as well as satisfying the intuitive condition $w_3 \geq 0$ for the range of values of q that we are considering, but upon solving eqns (1) and (2) we see that the solution is given implicitly by:

$$(P^* - q_{\min}) \ln(\exp(q_{\min} - P^*) + 1) = 1 + \ln 2 - \frac{1}{a - a_{\min} + 1}$$

which asymptotes at the value of P^* given by:

$$(P^* - q_{\min}) \ln(\exp(q_{\min} - P^*) + 1) = 1 + \ln 2. \quad (3)$$

A solution to eqn (3) exists by the intermediate value theorem and is unique on $P^* \in [q_{\min}, \infty)$. Perhaps more simply, as the numerator of $-w_1/w_2$ is bounded above by 2, we may simply note that:

$$q_{\min} \leq P^* \leq q_{\min} + 2.$$

Thus, as $a \geq a_{\min}$, if the range of qualities extant in the population is large enough then no right inverse exists over the entire set of qualities. It is a sufficient condition for an inverse function to exist, no matter what the range of qualities, that:

$$-w_1/w_2 \geq \frac{\epsilon_1}{a - a_{\min} + \epsilon_2}, \quad \epsilon_1, \epsilon_2 > 0 \quad (4)$$

for all a, p, q . That is either $-w_1/w_2$ is bounded away from 0, or if it does go to zero in the limit as a tends to infinity, it must do so "slowly".

If a is interpreted as a physical magnitude, such as the length of a tail or the loudness of a call, then it is perhaps reasonable to assume eqn (4). A result in which the advertising function calculated by Grafen's differential equation

asymptotes at a quality of signaller less than q_{\max} , is the situation where individuals of high quality cannot advertise enough to distinguish themselves from individuals of lower quality. This circumstance may arise when there is a natural upper bound to the signal in conjunction with the cost of achieving this upper bound being small, such as in the pigmentation example described at the beginning of this note.

The obvious question to ask is: can an ESS pair of signaller/receiver strategies exist if the level of signal possible is bounded below the level that is necessary for the existence of a separating signalling equilibrium? Intuitively, one might expect that any such ESS would consist of a strictly increasing separating component for individuals of quality $[q_{\min}, q']$ and signallers of qualities $[q', q_{\max}]$ signalling at $a = \infty$. Receivers would be expected to treat signals $a = \infty$ as coming from an individual of some inferior quality $\hat{q} \in (q', q_{\max})$.

Under Grafen's assumption of "local flat extrapolation" (Grafen, 1990b, p. 542) there does not seem to be an ESS. If the two signal components are connected, then it is clear that a class of individuals (q'' , q') can do strictly better by marginally increasing their signal from $A^*(q)$ to ∞ . This incurs a small cost relative to the signalling benefit, as receivers would reward such signallers as if they were of the discretely higher quality \hat{q} . On the other hand, if the two components were disconnected, signallers of quality $q \in [q', q_{\max}]$ could do better by signalling marginally lower than $a = \infty$ as local flat extrapolation guarantees that their signal will be interpreted as if it had been $a = \infty$.

It can be shown (Siller, 1997) that if, alternatively, it is assumed that receivers sample a number of signallers and reward the individual that signalled highest, then a signalling ESS of the form outlined above may exist: signallers of high quality signalling at $a = \infty$, and signallers of low quality playing a strictly increasing signalling strategy bounded away from $a = \infty$. The reason for the discontinuity in the ESS signalling strategy is similar to the reason for the discontinuity in the ESS to Bishop & Cannings' (1978) Time Limited War of Attrition. Returning to the pigmentation example, such an ESS might be perceived by an external observer as a

dimorphic signal. However, as stated earlier in this note, such a situation would be unstable with respect to the invasion of an additional kind of signal.

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REFERENCES

- BISHOP, D. T. & CANNINGS, C. (1978). A generalized war of attrition. *J. theor. Biol.* **70**, 85–124.
 GRAFEN, A. (1990a). Sexual selection unhandicapped by the Fisher process. *J. theor. Biol.* **144**, 473–516.
 GRAFEN, A. (1990b). Biological signals as handicaps. *J. theor. Biol.* **144**, 517–546.
 RIESZ, F. & NAGY, B. SZ. (1955). *Functional Analysis*. New York: Frederick Ungar Publishing Co.
 SILLER, S. (1997). Strategically Determined Phenotypes and the Evolution of Signals. Ph.D. Thesis, Department of Plant Sciences, University of Oxford, U.K.
 STRUBLE, R. A. (1962). *Nonlinear Differential Equations*. New York: McGraw-Hill Book Company.

A Note in Response to S. Siller's Comments by A. Grafen

I welcome the corrections Siller (1998) makes in the preceding paper to the mathematical arguments in two of my own (Grafen, 1990a,b; references as in Siller's paper above). In one case (Grafen, 1990b), the corrections result in an interesting additional biological point, which Siller makes well, without detracting from the general thrust of the argument. In the other case (Grafen, 1990a), two main arguments, leading to results of existence and uniqueness, are called into question. Existence of a signalling equilibrium is fortunately provided as a special case of a much more general argument due to Siller (1997). Uniqueness of the signalling equilibrium remains an open question.

In defence of the original papers, I might say first, that to an important extent the results and their implications survive intact, even though some of the arguments unfortunately turn out to be incomplete or invalid; second, that Siller (1997) has chosen to rely on one technical

Lemma from Grafen (1990a); and third, the papers were sufficiently in the right direction that studying them led Siller (1997) to develop his own much more rigorous, as well as general and wide-ranging, results.

The general modelling philosophy underlying Grafen (1990a) was to produce a specific example to demonstrate how the handicap principle could work. Siller (1997) has succeeded, by working more abstractly, in construing an

argument that gives formal expression to biologists' informal reasoning about signalling. This is a much more powerful approach, and really raises the intellectual level of debate about signalling in biology.

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