## CORRESPONDENCE

females paired with more-attractive males may produce more offspring<sup>6</sup>; and males with enlarged broods that increase parental investment are known to suffer higher parasite burdens<sup>7</sup>, show lower immunocompetence<sup>8</sup> and, most relevantly, produce smaller sexual ornaments the subsequent year<sup>9</sup>.

The trade-off between costly sexual ornaments and condition appears to exist. However, sexual ornaments that are produced and maintained in different ways may incur different kinds of maintenance costs that may influence the relationship between increased ornament and increased costs.

In a recent review<sup>10</sup>, we contrasted signals that were produced and fixed at one time, for example, nuptial plumage determined at moult, with signals that are produced through continued input of pigment, such as red skin patches or coloured secretions. This approach can be generalized to compare signals with production costs paid at one time during the seasonal cycle with those that impose cost over an extended period. Signals of the latter type include energy intensive displays or secondary sexual traits, such as the peacock's train, that have unavoidable continuing maintenance costs. The trade-off between signal and immune function may be stronger for the latter type of signal than the former. In fact, the evidence available for this trade-off5 is for a character that imposes continuing physiological costs on the bearer4. The sexual ornaments of birds produced during moult may nonetheless invoke such costs, paid in immunosuppression, if more-elaborately ornamented individuals suffer more harassment on feeding grounds or, alternatively, if resources that are required for immune defence are put directly into the ornament. However, generalizations from one type of sexual ornament - one that requires progressive payments - to another - one that is paid in a single instalment - should be made with caution.

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## Reply from B.C. Sheldon and S. Verhulst

Jacqui Shykoff suggests that (1) mechanisms mediating the fitness costs of sexual ornaments may differ between different types of ornaments, and (2), in particular, a trade-off with immunocompetence may be stronger for traits that have unavoidable continuing maintenance costs as compared with traits whose production is paid for in a single 'instalment'.

We agree wholeheartedly with the first point. In fact, we explicitly discussed the possibility that other mechanisms may be more important in mediating the costs of sexual ornamentation (p. 319 and Box 1 in Ref. 1). However, we are not convinced about the usefulness of the distinction made in Shykoff's second point. We are not aware of any direct evidence demonstrating that the costs of any ornament vary seasonally, or that the seasonal pattern of costs differs between ornaments of the two kinds suggested by Shykoff. If ornaments exist for which the costs are paid in a single instalment, the question remains through which mechanism is the honesty of such a trait maintained. In our view, a trade-off with immunocompetence seems just as likely a candidate for this type of trait, as for traits that have unavoidable, continuing maintenance costs. As we suggested in our review<sup>1</sup>, it is possible that a common mechanism enforces honesty of ornaments and mediates costs of reproduction. One should note that a

cost of reproduction is analogous to the idea of 'single instalment' ornaments, in that increased effort over a short period has demonstrable long-term fitness (and immunocompetence) consequences. Finally, Shykoff states that the only evidence for a trade-off between ornamentation and immune response has been obtained from a 'continuous cost' ornament. This is not surprising, since this is the only study so far published that has investigated this trade-off explicitly.

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# Reintroductions: challenges and lessons for basic ecology

Sarrazin and Barbault1 discuss the lack of scientific input into reintroduction programmes and suggest that a greater involvement by scientists will benefit conservation. We agree with this, but following our recent review of translocations in the UK2 we would sound a note of caution. Owing to lack of funds, most reintroduction projects cannot research the basic scientific questions raised by Sarrazin and Barbault and the 1995 IUCN guidelines3. Often a compromise is attempted by applying scientific generalizations in the hope that these will improve the chances of reintroduction success. Such general ideas include Minimum Viable Population (MVP) theory, or the theory that inbreeding and low genetic diversity decrease population viability. Generalizations are applied vaguely to a programme (e.g. collecting a lot of individuals from a large population), rather than using them as a basis for research before starting the translocation (e.g. estimating the best population size for success and sampling of genetic variation). We concluded that such use of scientific generalizations could introduce irrelevant restrictions to the project or even worsen the chances of success.

An example of the misuse and misinterpretation of a generalization is the misinterpretation concerning the prescription that the source population should ideally be closely related

genetically to the original native stock. This is encouraged in the IUCN guidelines3 to ensure that the reintroduced individuals are adapted to the local conditions. Without genetic analyses, conservationists often interpret this generalization to mean that only local stock should be used. However, proximity does not necessarily correlate with genetic relatedness or adaptation; even adjacent populations may be very different genetically and ecologically4, or distant populations may be well-adapted to conditions at the release site. For example, Scottish populations of the chequered skipper butterfly (Carterocephalus palaemon) were favoured by many as the sources for a reintroduction in southern England, because they were British. In fact, French populations were eventually used, because the project team found that these populations were much more similar ecologically (same food plant, habitat type, and so on) to the extinct populations than were the Scottish populations<sup>5,6</sup>. A further worrying trend has been the development of the idea that the use of non-local stock (i.e. from tens or hundreds of miles away) will have harmful effects on genetic biodiversity, characterized by such phrases as 'genetic contamination'7, 'introduction of alien genes'3 or 'erosion of genetic variation'8. These are nebulous concepts. In fact, the only palpable concerns are (1) that the population will not establish because of maladaptation or

(2) that resident populations will be affected by outbreeding depression. Either problem may or may not occur in each reintroduction project. For example, outbreeding with the reintroduced population may actually have positive effects on resident populations by reversing inbreeding depression.

The trouble with generalizations is that they are often not general. The general figures of 50 and 500 for MVPs are of little use<sup>9</sup>, and low genetic diversity is not necessarily correlated with low population viability<sup>10</sup>. If generalizations are used proscriptively rather than as a starting point for research then errors may be made or there may be unnecessary restrictions on an important programme of conservation. The challenge for scientists is to make useful contributions to reintroduction projects within severe budgetary limitations.

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# Reply from F. Sarrazin and R. Barbault

Bullock and Hodder underline two limitations affecting the involvement of scientists with reintroduction programmes: (1) limited funding for basic research, and (2) the misuse of general concepts in reintroduction planning.

We agree that too crude uses of general concepts may be misleading for reintroduction planning. But should those concepts not be considered at all? We claim that a direct and open-minded link between scientists and managers is necessary to take into account all advantages and limitations of up-to-date concepts when designing a local reintroduction and assessing its success. This would prevent the direct use of magic numbers which quickly evolve: for example, the  $N_a = 500$  rule recently changed to  $N_e = 5000$  according to Lande<sup>1</sup>. In this local context, the aim of modelling has to be to achieve precision in description and prediction. However, peer reviewed publications of results and more-basic modelling are also necessary to extract understanding of reintroduction processes from various local situations. The trade-off between precision, prediction and understanding

exists in reintroduction modelling as in any other modelling approach.

Concerning funding problems, the question is: in a limited funding context, should we neglect to use the best available tools to improve the success of a reintroduction? It is often said that among conservation actions, reintroductions are too expensive for a risky single-species approach. This money should therefore be efficiently dedicated to extinction avoidance of the future reintroduced population. It is primarily a matter of Population Viability Analyses (PVAs). When managers and population ecologists work together, PVA costs would remain low. In some fairly well-funded reintroductions of charismatic species, such PVAs have been done belatedly and have shown that the monitoring of released populations might be improved to assess reintroduction success<sup>2,3</sup>. An earlier involvement of population ecologists in these programmes would have helped to spend money in the field more efficiently.

Therefore, we consider that, in fact, Bullock and Hodder's comments can be seen as additional arguments for further involving scientists in reintroduction programmes.

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