ABSTRACT

The animal kingdom contains a spectacular diversity in colour signals used to indicate quality. The challenge of understanding this diversity lies in identifying and interpreting constraints on signals that maintain signal honesty. I used an integrative approach to measure the effects of potential signal modulators on whole-animal performance, ornaments, condition and immunocompetence in the lizard *P. i. wilhelmi*. This approach attempts to remove some of the uncertainty surrounding the validity of existing handicap models. First, I investigated seasonal changes in testosterone, corticosterone and carotenoids and compared these to seasonal changes in endurance, immunocompetence and body condition male *P. i. wilhelmi*. I also determined which colour patches were predictors of male quality by relating them to morphology, endurance, body condition and immunocompetence. I found some support for the immunocompetence handicap hypothesis so I tested whether testosterone was modulating ornaments and constraining signals through its immunosuppressive properties. I tested the immunocompetence-handicap hypothesis in male *P. i. wilhelmi* while also conducting parallel studies with free-ranging and captive-housed lizards to assess whether there were differences between the groups that could indicate exogenous factors influencing signalling in their natural environment. While experimentally elevated testosterone did affect endurance and the properties of their colour patches, immunosuppression was only evident in free-ranging lizards. To measure the extent of organisational effects in males I also manipulated testosterone in females and found no evidence of immunosuppression although testosterone did affect some aspects of colouration and endurance. Next, I tested the stress-linked immunocompetence handicap hypothesis by experimentally elevating testosterone, corticosterone, or both at the same time. I found that corticosterone had an isolated effect on one colour patch, and testosterone and corticosterone had opposing effects on endurance that were negated when both were elevated. Different colour patches were affected by either testosterone or corticosterone with little overlap, and the combination of the two had a different action to either hormone elevated in isolation. Finally, I tested the oxidative stress hypothesis of carotenoids as a limiter of signal output due to their requirement in the oxidative stress response. I found that supplemented

carotenoids vastly improved endurance, immune response and influenced different aspects of colouration to that of testosterone and corticosterone. My study examined four different hypotheses of constraints on signalling involving testosterone, corticosterone, interactions between testosterone and corticosterone and carotenoids in a consistent manner measuring multiple indices of quality as well as multiple colour signals. This study provides a unique integrative perspective on the roles played by each factor as well as prompting us to re-examine our approach to understanding constraints on signalling.