

Genic capture and resolving the lek paradox

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The genic capture hypothesis offers a resolution to the question of how genetic variation in male sexually selected traits is maintained in the face of strong female preferences. The hypothesis is that male display traits are costly to produce and hence depend upon overall condition, which itself is dependent upon genes at many loci. Few attempts have been made to test the assumptions and predictions of the genic capture hypothesis rigorously and, in particular, little attention has been paid to determining the genetic basis of condition. Such tests are crucial to our understanding of the maintenance of genetic variation and in the evaluation of recent models that propose a role for sexual selection in the maintenance of sex. Here, we review approaches to testing the link between genetically determined condition and levels of sexual trait expression and consider the probable importance of deleterious mutations.

The 'LEK PARADOX' (see Glossary) has long haunted the study of sexual selection. If females prefer certain male traits that indicate VIABILITY, then the increased mating success of males bearing them should rapidly exhaust genetic variation for viability and drive the traits to fixation. This is the paradox [1–4]: female choice depletes genetic variation, thus leaving little room for choice to result in genetic benefits, and yet the genetic benefits to offspring are the explanation for that choice.

The lek paradox is, in fact, just a prominent example of one of the major unresolved issues in evolutionary biology [5,6]: what maintains ADDITIVE GENETIC VARIANCE in fitness-related traits [7]? This question continues to be a source of debate [8,9], with two broad and complimentary explanations based either on fluctuating selection or on mutation–selection balance. Fluctuating selection arguments depend on the idea that the optimal phenotype varies in either space [10,11] or time, for instance because parasites are continually evolving to overcome host defences [12,13]. Mutation–selection balance arguments address the question of whether mutations can generate new genetic variation as quickly as it is eroded by selection. Here, we discuss recent theoretical developments that suggest that the condition-dependent nature of

sexual display traits mean that mutations can indeed maintain variation in the face of DIRECTIONAL SELECTION created by female mate choice.

Houle [14] argued that the relatively high genetic variance of fitness-related life-history traits could be explained by their dependence on many underlying physiological and morphological traits, such that they sum genetic variation over many loci. This multitude of loci provides a large mutational target [15] that is resistant to erosion through directional selection. Similar to life-history traits, sexually selected traits also have relatively high coefficients of additive genetic variation [4]. Pomiankowski and Møller [4] argued that this pattern could be explained if selection on sexual traits was an increasing function of trait size (e.g. [16]), because this would favour increased trait variance and select for an increase in the number and/or contribution of loci involved in trait expression. This mechanism has been criticized because, after initial spread, trait expression at any given level of condition is likely to be subject to stabilizing, rather than escalating, non-linear selection [2]. The hypothesis also fails to provide a mechanism for the positive genetic covariance between sexual trait expression and viability, required in 'GOOD GENES' models [17,18].

Andersson [19] suggested that the phenotypic quality of an individual will be influenced by most of its genome and, consequently, that the size of sexual ornaments will depend on the overall genetic quality of the individual rather than on a few major genes (see also [20]). Population genetic models of this concept show that the key to the origin and maintenance of the genetic variance in sexually

Glossary

Additive genetic variance: genetic variance associated with average additive effects of alleles. Causes offspring to resemble their parents.

Directional selection: selection that favours extreme trait values.

Genic capture: female preferences for costly male traits results in the evolution of a genetic covariance between condition and trait expression (condition dependence).

Good genes: models of sexual selection that assume extreme ornaments indicate the genetic quality of the bearer, defined as breeding value for fitness.

Lek paradox: persistent female choice for particular male trait values should erode genetic variance in male traits and thereby remove the benefits of choice; and yet choice persists. Most obvious in lekking species where females gain no material benefits or parental care from males.

Viability: the capacity of an individual to survive, grow and develop.

selected traits does lie in the number of loci involved in their condition-dependent expression [2,17,18]. Sexually selected traits are expected to show strong condition dependence because they are costly to produce. Crucially, the ability of a male to overcome the costs of trait expression [21] and reap the benefits of female preference depends upon his viability or 'condition'. This being so, any mutation that affects the overall condition of a male will consequently affect his sexually selected traits. Rowe and Houle [2] called this process GENIC CAPTURE and emphasized that it requires only that secondary sexual traits are costly and, furthermore, that condition has high genetic variance. The latter requirement is likely to be met because, as Andersson noticed [19,20], condition will be influenced by any allele that affects the ability of an individual to acquire and utilize resources. This will include alleles that have environmentally dependent effects on fitness, as proposed in the fluctuating selection arguments discussed above, and will also mean that the total number of loci affecting condition represent a large target for mutations [15]. Thus, condition should show large genetic variance and be closely associated with fitness.

Genic capture is the concept that a large proportion of the genome will become involved in determining the expression of sexually selected traits. This has been explicitly modelled in two ways: first, using a quantitative genetic approach [22] with deleterious mutations as a source of variance; and second, using an individual-based genetic simulation [23], allowing for changes in the environment to provide additional genetic variance in condition. Both models lead to the evolution of costly male sexual traits and female preferences (but see [24]). The models show that, if males can enhance their sexually selected traits by increased investment and if this is less costly to males with more resources to invest [21], then covariance between male display traits and condition evolves through sexual selection. The idea that condition is dependent upon a large proportion of the genome is taken as an assumption of these, and earlier models, but the theory makes several testable predictions (Box 1). Quantitative genetics provides approaches for examining the genetic basis of condition and condition dependence (Boxes 2,3).

Resource dynamics and the concept of condition

The common usage of the term 'condition' is as a summary of characteristics that reflect the general health and vigour of an individual. In early discussions of the potential for the expression of sexually selected traits to depend upon condition, the word was used almost interchangeably with phenotypic quality [25,26]. However, to clarify the predictions and assumptions of the genic capture hypothesis, we must define condition more narrowly as the amount of resources available for allocation to fitness-enhancing traits [23]. In attempting to measure condition, it is important to be aware that traits that reflect the health and vigour of the individual are condition-dependent traits, and not condition itself.

Discriminating between traits that are either a source of condition, condition itself, or condition-dependent invites characterization in terms of the acquisition,

Box 1. Predictions of the genic capture hypothesis

The fundamental prediction of good genes models of sexual selection, that offspring of preferred males will have higher fitness, is reasonably well supported [58] (but see [59]). Genic capture makes explicit the mechanism that is expected to lead to positive covariance between sexual traits and offspring fitness. It rests on the assumptions of condition dependence that arise from the costliness of sexual traits (predictions i and ii) and makes unique predictions (iii–vii). References are to works from which these predictions arise, although, frequently, they are not explicitly stated.

- (i) Expression of sexually selected traits should be strongly dependent upon condition [2,17,18,20,60].
- (ii) Individuals freed from the costs of producing sexually selected traits should have improved naturally selected fitness components [2,61].
- (iii) Condition should have a high coefficient of genetic variation [2].
- (iv) Sexually selected traits should be genetically correlated with condition [21].
- (v) Condition and condition-dependent sexually selected traits should be affected by many loci [2,17,18,20,60].
- (vi) By increasing the strength of selection on overall condition, sexual selection should enable populations to adapt more rapidly to changes in environment [23] or to purge genetic load [49,50].
- (vii) Traits that are more costly capture more condition-dependent variation [2,17].

storage and expenditure of resources. However, the crucial question is what net effect does that trait have on the resource dynamic? Non-reproductive traits are generally selected for their ability to increase resource acquisition ability, which requires keeping the individual healthy and alive. The notion of the net effect of many independent traits and, ultimately, many loci controlling net resource acquisition ability [27] is central to our understanding of the concept of genic capture. Storage of resources promotes the notion of a camel with its hump, but a physical 'resource pool' is not a necessary component of this hypothesis; the key is the ability to acquire resources to satisfy the demands of expenditure on condition-dependent traits. Reproductive traits constitute expenditure, because they have no role in resource acquisition but are selected to convert acquired resources into offspring.

Because expenditure on condition-dependent traits exerts a drain on available resources, condition-dependent traits should trade off under phenotypic manipulation. Nevertheless, these traits should be strongly phenotypically and genetically correlated to condition. Because they capture the same genetic variance in condition, genetic correlations between two condition-dependent traits can be positive but will depend on the relative genetic variances in resource acquisition and resource allocation [27].

Estimating condition from phenotypic traits

To test hypotheses about condition, it must be quantifiable. Species will differ in the way that resources are acquired, stored and spent, but knowledge of these parameters can be used to predict which traits are likely to be important determinants of condition in a particular species.

Phenotypic measures of condition can be divided broadly into two types: measures of resource acquisition ability and measures of the pool of resources. Resource acquisition ability can be quantified directly as parameters

Box 2. Quantitative genetic studies of condition and condition dependence

To date, most research has addressed the prediction that sexually selected traits respond to the manipulation of resource availability (reviewed in [38,62–64]), with the assumption that environmentally induced differences in male condition will be similar to genetically induced differences that could promote female choice. However, there are only a few studies in which the genetic variance in condition or in condition dependence has been investigated [21,65–69].

One approach to examining genetic variance in condition dependence is through investigation of genotype x environment (GxE) interactions (Box 3). In *Cyrtodiopsis dalmanni* stalk-eyed flies, there is an interaction between genotype and food quality that affects sexually selected male eye span [65,70], with evidence that genotype ranks are maintained across environments [65]. In sexually dimorphic stalk-eyed fly species, male eye span is more dependent on body length (which might reflect condition) than is female eye span [66]. These patterns have been cited as direct evidence for genic capture [66]. However, genic capture requires high genetic variance in condition [2], which was not found in this system, making it unclear how condition could maintain genetic variance.

In *Onthophagus taurus* dung beetles, there is high genetic variance for residual mass, but, more importantly, there is a genetic correlation between this measure of condition and courtship rate, a trait preferred by females [21]. This indicates that condition has a genetic basis and that courtship rate is a condition-dependent trait. In *O. taurus*, there is also a genetic correlation between residual mass and sperm competition traits [71].

In *Gerris incognitus* water striders, genital morphology displayed genetic variance and condition dependence, but there was no interaction between genotype and food treatment [67]. However, morphological traits generally scale positively with body size, so it is imperative that, in this type of study, a comparison is made between sexually selected traits and other traits [65]. In fact, in *G. incognitus*, the condition dependence of size was stronger than that of genital morphology [66], suggesting that genital morphology is not a trait that it would benefit females to pay attention to.

In *Ficedula albicollis* flycatchers, forehead patch size in males is dependent on fledgling residual mass [72]. This measure of condition has a genetic component [68,69], but no analysis has been presented of genetic correlations between condition and patch size, and there is no direct evidence that patch size is affected by a GxE interaction.

that show how efficiently the individual converts the environment into somatic tissue or activity. Most traits fall into this category (e.g. muscle efficiency). Traits that summarize the action of many such acquisition traits, particularly if measured under demanding conditions, are likely to provide the best estimates of resource acquisition ability. Such parameters might be growth rate (which encompasses all the traits involved in foraging, digestion and metabolic efficiency) or weight–energy balance under food restriction or during periods of enforced activity. This approach can be used with species that use recently acquired resources for breeding, and highlights the fact that it is not necessary to think of, or measure, condition only as the available resource pool, but also in terms of how efficient an individual is at acquiring resources.

Measuring the resources available to divert between competing components of fitness is rarely straightforward and the same careful consideration of acquisition, storage and expenditure must be made. When the expenditure on a trait is energy (e.g. in display or fighting), sugars are the fuel and fat the reserve of that fuel. In such cases, residuals of mass over some fixed morphological trait are a

Box 3. Genotype x environment interactions and condition-dependence

The insight of the genic capture hypothesis is that a large proportion of the genome is involved in determining condition [15,27]; hence, the ability of an individual to convert its environment into condition-dependent traits will have a large genetic variance [2]. Experimentally manipulating the environment (resource availability) of relatives will reveal their genetic ability to acquire resources and express condition-dependent traits. Such experiments enable us to measure the dependence that traits have on available resources and the extent to which condition dependence itself has genetic variance. Whether condition dependence has genetic variance will be revealed by the inspection of the genotype x environment (GxE) interaction.

Significant GxE means that individuals allocate resources to condition-dependent traits at different rates [65,67,73]. If the rank order of genotypes is maintained across environments, then some genotypes are always better and some always worse at producing condition-dependent traits across the studied environments (called ‘general vigour’ in life-history literature [74]). If, however, the genetic correlation between environments is weak, it suggests that a significant proportion of mutations that have neutral (or positive) effects in one environment will have deleterious effects in another, causing genotype reaction norms to cross; a situation where there is no ‘single best genotype’. Such a GxE interaction might maintain genetic variation where a single genotype cannot be most fit in all environments [75]. Provided that environments do not fluctuate too rapidly, females might still receive indirect benefits from choosing males with the highest levels of condition-dependent display within a given environment.

Because most mutations are deleterious and, furthermore, are likely to be more deleterious under stressful conditions, the pattern of GxE might reveal the signature of deleterious mutations [76]. For example, environmental stress should increase the variance in condition-dependent traits, and genotypes that were below average in benign conditions should perform very poorly under stress. Finally, a positive genetic correlation between environments might be achieved with or without a significant GxE interaction. The prevalence of these patterns will provide insights into the nature of good genes variation.

commonly used condition measure [21]. This is intuitively appealing because mass corrected for size is a good measure of the available reserves of fat from which to supply sugars. However, using residuals as a condition measure carries a few caveats [28,29]. Perhaps the most serious is the assumption that the variance that is unexplained by size actually does represent variance in the appropriate pool of resources. Unless empirically verified by manipulating residual mass [21], or correlating fat and residual mass [30–32], residual variance might instead reflect variance in shape or simply hydration. The use of residual mass also assumes that there is no relationship between the value of a unit of mass and body size [33]. If a unit of additional weight is less valuable to larger individuals, then the use of residuals will give a misleading impression of the resources available to individuals of different sizes.

In organisms that store resources in one life stage for use in the next, as in many insects, or that feed before, but not during the breeding season, as in some vertebrates, it might be possible to measure the resource pool directly (e.g. lipid content, fat-body mass or muscle mass) [33,34]. However, if energy stores can be replenished, they can be misleading; for example, in some passerine birds, fat scores are lowest in more dominant birds, because access

to food is predictable for high-ranking individuals [35]. Additionally, consideration must be given to the nature of the resources that are needed to express condition-dependent traits as these might come from different sources. For example, the fuel for energy-expensive activities is likely to be sugars, fed directly from digestion or reserves of fat, whereas the engine driving such activities is muscle bulk [34]. Other condition-dependent traits require synthesis of protein (e.g. orthopteran nuptial gifts [36,37]).

In estimating condition, consideration must be given to whether it is appropriate to either measure acquisition efficiency or the magnitude of the resource pool. That done, exactly what is being measured, how the resources will be used for the production of condition-dependent traits, the potential for changes in condition through feeding and the value of the pool to different-sized individuals, all require consideration.

Mutations and the genetics of condition

So far, studies of condition dependence have concentrated on phenotypic manipulations (Box 2; [38]). Empiricists should now focus on determining the genetic basis of condition itself, a process that will help define the very nature of 'good genes' (Box 3) [39]. One approach will be to examine the role of mutations in creating variance in condition. Although organisms might differ in the contributions of various mechanisms to their standing genetic variance for fitness [40], mutations are ubiquitous. They are predominantly deleterious and those with weak effects as heterozygotes can persist in populations for many generations [41]. How much variation in fitness can be attributed to advantageous mutation or to deleterious mutations will depend upon how well adapted an organism is to its environment. In situations where selection pressures resulting from environmental variation or intraspecific arms races are limited, standing genetic variance is expected to be dominated by the effects of deleterious mutations, in which case the concept of 'good genes' sexual selection would probably be more accurately described as 'absence of bad genes' selection. Estimates from *Drosophila* [8] and *Daphnia* [42] suggest that most standing genetic variance in life-history traits is due to the continuous influx and transient persistence of deleterious mutations.

Because they can persist as rare recessives, deleterious mutations contribute to inbreeding depression [43]. However, the contribution of overdominance (higher trait value in heterozygotes than in either homozygote) in causing inbreeding depression can sometimes be substantial [44], so simply demonstrating inbreeding depression for a trait of interest [45,46] cannot definitively show that the genetic variance in the trait is due to deleterious mutations. Nevertheless, greater inbreeding depression in sexually selected traits that are the subject of female choice compared with non-sexual traits is consistent with sexual trait expression being particularly sensitive to deleterious mutations. The contribution of rare recessives can be assessed more accurately using experiments that combine inbreeding with selection for the trait of interest [47]. This technique remains to be

tested in animals, although it has been used in plants [48], where the evidence suggests that, in *Mimulus*, the contribution of mutations to genetic variance in floral traits is negligible.

A unique prediction of the genic capture hypothesis is that mutations at most loci throughout the genome should affect the expression of sexually selected traits. There are several alternative empirical approaches to testing this prediction. For example, do mutations affecting male performance in sexual selection also cause general fitness decline? If mutations affecting resource acquisition create positive genetic covariances between condition and life-history traits, then condition-dependent sexual selection can be expected to remove deleterious mutations from populations. Recent models [49,50] have shown that such effects can alleviate the cost of producing males to the extent that sexual reproduction is advantageous. In particular, this requires that mutations decreasing male mating success also negatively affect female fecundity. Chippindale *et al.* [51] have recently shown that, in *D. melanogaster*, haplotypes that increase reproductive success in one sex decrease it in the other. This suggests that intersexual ontogenetic conflict [51] can oppose the process of decreasing mutational loads of populations [52]. Mutations occurring in populations at natural rates can be studied in mutation accumulation experiments, where selection against deleterious mutations is relaxed by enforcing monogamous mating and the equal contribution of the progeny of each female to the next generation. Such designs reveal fitness decline in the range of 0.1–2% per generation [41,53] so the decline can be substantial after only a few generations. The role of sexual selection in removing these mutations can be assessed by comparing the fitness decline in mutation accumulation lines with that in similar lines, where the equal contribution of the progeny of each female to the next generation is experimentally ensured, but where sexual selection is retained. A significant difference in fitness decline between sexually selected and non-selected lines would indicate that sexual selection is effective in removing deleterious mutations. An experiment on bulb mites using this design [54] did not detect any significant difference between lines with and without sexual selection. However, further studies are needed.

A similar approach can be used to examine the prediction that, by increasing the strength of selection on overall condition, sexual selection should enable populations to adapt more rapidly to changes in the environment. Lorch *et al.* [23] argue that, if changes in the environment frequently shift populations away from their present optimum, sexual selection might be more important in improving fitness of populations than mutation-based equilibrium models predict [49,50]. Holland attempted to test this prediction in *D. melanogaster* exposed to novel temperatures, but failed to find evidence that populations in which sexual selection was allowed to occur showed faster adaptation [55].

Finally, it might be possible to take advantage of detailed information about the genetics of sexual traits to examine how they are affected by mutations. For instance, individuals in a species in which quantitative trait loci

(QTL) mapping had established the location of genes with large effects on sexually selected and non-condition-dependent traits could be exposed to mutations through transposable element insertions or mutagens. The genic capture hypothesis would predict that sexually selected traits would show more sensitivity to mutations outside of regions known to contain QTLs for these traits than would non-condition-dependent traits. Species suitable for such experiments include *Drosophila* species that have complex and well studied courtship behaviours [56,57].

Conclusions

The genic capture hypothesis is based on clear assumptions and makes several specific predictions. Empirical tests of these assumptions and predictions will reveal the nature (good or bad) of genes that make mate choice beneficial and, more generally, the mechanisms maintaining genetic variation in natural populations. These studies will also have implications for answering questions about the maintenance of sexual reproduction, sexual conflict and inbreeding depression. Productive areas for future work are likely to include studies that manipulate genetic condition through mutation accumulation and induction or expression of deleterious mutations resulting from inbreeding. Such explicitly genetic approaches need to be combined with phenotypic measurements that encapsulate condition through multiple measures of how efficiently individuals acquire resources and convert them into future reproduction.

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