

# A potential resolution to the lek paradox through indirect genetic effects

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Females often prefer males with elaborate traits, even when they receive no direct benefits from their choice. In such situations, mate discrimination presumably has genetic advantages; selective females will produce offspring of higher genetic quality. Over time, persistent female preferences for elaborate secondary-sexual traits in males should erode genetic variance in these traits, eventually eliminating any benefit to the preferences. Yet, strong female preferences persist in many taxa. This puzzle is called the lek paradox and raises two primary questions: do females obtain genetic benefits for offspring by selecting males with elaborate secondary-sexual characteristics and, if so, how is the genetic variation in these male traits maintained? We suggest that indirect genetic effects may help to resolve the lek paradox. Maternal phenotypes, such as habitat selection behaviours and offspring provisioning, often influence the condition and the expression of secondary-sexual traits in sons. These maternal influences are commonly genetic based (i.e. they are indirect genetic effects). Females choosing mates with elaborate traits may receive ‘good genes’ for daughters in the form of effective maternal characteristics. Recognizing the significance of indirect genetic effects may be important to our understanding of the process and consequences of sexual selection.

**Keywords:** lek paradox; indirect genetic effects; sexual selection; condition dependence; good genes; maternal effects

## 1. INTRODUCTION

Across many taxa, individuals go to remarkable lengths to select mates. Mate preferences are often costly, requiring time, energy and even risk of death (e.g. Hedrick & Dill 1993; Wickman & Jansson 1997; Byers *et al.* 2005). However, the fitness benefits of choosing a good mate presumably outweigh these costs. Recognizing the benefits gained by mate-choice decisions is crucial to our understanding of the process of sexual selection.

Females in many species discriminate among males based on the relative expression of secondary-sexual characteristics and often do not appear to receive any direct benefits for these mate-choice behaviours. This situation is most clearly seen in lek mating systems, where females approach a group of males (i.e. a lek), select a mate and leave with nothing but sperm. Because females receive no direct resources from mates, many researchers have surmised that these females must benefit from mate-choice behaviours by obtaining genetic benefits, i.e. ‘good genes’, for their offspring. Although female preference for good genes is intuitively appealing and would explain the observations of mate choice without direct benefits to females, population geneticists have argued that this idea may be problematic. Robertson’s corollary of Fisher’s fundamental theorem (Robertson 1966; see also Crow 2002) suggests that over time directional selection should erode the genetic variation for secondary-sexual traits, so that females will no longer profit from discriminating among males based on these traits and such female preferences should eventually disappear. Yet, females continually display strong preferences for males with

relatively elaborate traits. This situation has been called the ‘lek paradox’ (Borgia 1979; Taylor & Williams 1982; Kirkpatrick & Ryan 1991). Many researchers have explored the lek paradox and several have proposed promising resolutions (table 1). While the lek paradox describes only those situations where females do not receive direct, resource-based benefits from their mates (Andersson 1994), resolving the lek paradox will have broad implications across mating systems.

Of the many potential resolutions to the lek paradox, the ‘genetic capture hypothesis’ proposed by Rowe & Houle (1996), has received the most attention in recent years. This idea is based on two criteria: secondary-sexual traits exhibit condition dependence and condition has high additive genetic variance. The secondary-sexual traits are expected to ‘capture’ some of the additive genetic variance for condition (Rowe & Houle 1996; Tomkins *et al.* 2004). Indeed, existing evidence suggests that secondary-sexual traits are commonly condition dependent (e.g. Andersson 1994; Johnstone 1995; Cotton *et al.* 2004) and condition often has additive genetic variance (e.g. Rowe & Houle 1996; David *et al.* 2000; Kotiaho *et al.* 2001). Therefore, this hypothesis may be an important step towards resolving the lek paradox, based on the logic that females choosing mates with elaborate traits are selecting males with ‘good genes’ that can be passed onto offspring. However, the primary genetic influence on condition is often assumed to be *direct* additive genetic variance, i.e. genetic variation based within the focal generation. While the direct additive genetic variance is undoubtedly important, it is often not a primary determinant of the among-individual variation in condition (e.g. Griffith *et al.* 1999; Qvarnström 1999; Jia *et al.* 2000).

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Table 1. Some proposed resolutions to the lek 'paradox' (Borgia 1979; Taylor &amp; Williams 1982).

proposed resolution	references <sup>a</sup>
no cost to mate choice coupled with hidden non-genetic benefits	Reynolds & Gross (1990)
higher mutational input and selection for modifiers as a result of prolonged directional selection	Pomiankowski & Møller (1995)
genic capture through condition-dependent expression of traits	Rowe & Houle (1996)
lower variance in male-mating success than expected	Lancot <i>et al.</i> (1997)
mechanisms of sexual selection result in apparent balancing selection	Moore & Moore (1999)
genotype-by-environment interactions (context-dependent mate choice)	David <i>et al.</i> (2000); Jia <i>et al.</i> (2000)
mistake-prone mate choice	Randerson <i>et al.</i> (2000)
multivariate genetic variation orthogonal to direction of sexual selection	Hine <i>et al.</i> (2004)

<sup>a</sup> these studies each provide an idea or model that proposes to explain how genetic variation in sexually selected traits might be maintained in systems where males provide only genetic benefits to their offspring. There are a considerable number of empirical studies that have then tested many of these ideas.

Here, we extend the ideas of Rowe and Houle to include the capture of *indirect* genetic variance. Indirect genetic effects occur when genes expressed by one individual (in this case, the mother) have phenotypic effects in another individual (in this case, the offspring; Cheverud & Moore 1994; Moore *et al.* 1997; Wolf *et al.* 1997, 1999). Our idea is simple: mothers often influence offspring environments and variation among mothers in their influences can be genetically based. Offspring condition is often extremely sensitive to environmental influences (e.g. Griffith *et al.* 1999; Cotton *et al.* 2004; Garant *et al.* 2004) including those from mothers (Mousseau & Fox 1998a; Qvarnström & Price 2001). Thus, males with elaborate secondary-sexual traits might not honestly indicate superior additive genetic factors *directly* contributing to their condition, as is often envisioned. Instead, they may be signalling the additive genetic factors *indirectly* influencing their condition—factors from their mothers. Females choosing males with elaborate secondary-sexual traits may be receiving 'good genes' for daughters in the form of effective parenting characteristics.

In this paper, we will first discuss the condition dependence of many secondary-sexual traits and the importance of the environment to phenotypic variation in condition. We will next argue that offspring environments are often shaped by their mothers and these maternal effects may commonly have a genetic basis (i.e. they are indirect genetic effects). We present an adaptation of a previously published model (Wolf *et al.* 1997) to illustrate our arguments and to facilitate future empirical and theoretical studies. Finally, we discuss possible mechanisms for maintaining genetic variation in indirect genetic effects. Recognizing the indirect genetic benefits from mate-choice decisions may be an important step in resolving the lek paradox.

## 2. CONDITION AND THE ENVIRONMENT

Condition dependence is a key element of many sexual selection models (e.g. Darwin 1874; Fisher 1915; Zahavi 1975, 1977; Andersson 1982; Nur & Hasson 1984; West-Eberhard 2003). The secondary-sexual traits, such as ornaments and weapons, are expected to show strong condition dependence because these traits are important to fitness, yet costly to produce. Owing to the large costs involved, only those individuals of good condition will be able to produce the most elaborate traits (Andersson

1982; Kodric-Brown & Brown 1984; Nur & Hasson 1984; Zeh & Zeh 1988).

In common parlance, 'condition' is often used to indicate the general health and vigour of an individual. However, to clarify predictions and assumptions, studies of condition dependence generally define condition more narrowly as the quantity of resources available for allocation to fitness-related traits, including secondary-sexual characteristics (Lorch *et al.* 2003; Tomkins *et al.* 2004). Examining the correlations between estimates of individual condition with measurements of secondary-trait expression is one way of investigating the condition dependence of secondary-sexual traits for a particular group of animals (David *et al.* 2000; Kotiaho *et al.* 2001; Parker & Garant 2004). However, attempting to quantify condition should be undertaken with great care. Proxies for condition are often necessary because condition itself is difficult to measure directly. These proxies may or may not actually represent the condition, depending on species, environment and even life stage of an individual (Cotton *et al.* 2004; Hunt *et al.* 2004; Tomkins *et al.* 2004). However, useful proxies for condition may be deduced with a good understanding of the acquisition, storage and expenditure of resources by the particular research organism (Tomkins *et al.* 2004).

Some studies of the condition dependence of secondary-sexual traits skirt the problems of attempting to estimate condition. In these studies, researchers manipulate environmental variables experienced by groups of animals, assume that individual condition is affected in the process and then examine the relative expression of secondary-sexual characteristics among the groups (Cotton *et al.* 2004). These methods have been very useful in determining whether secondary-sexual traits of particular species are condition dependent, and they also inadvertently underscore an important quality of individual condition—that it is easily controlled by environmental forces.

Studies from a wide range of taxa show that the quality of environments experienced often has a large and even overwhelming influence on condition and the expression of secondary-sexual traits (Partridge & Endler 1987; Solberg & Sæther 1994; Ashley *et al.* 1998; Griffith *et al.* 1999; Lindström 1999; Post *et al.* 1999; Qvarnström 1999; Metcalfe & Monaghan 2001; Schmidt *et al.* 2001; Cotton *et al.* 2004; Garant *et al.* 2004; Kaňuščák *et al.* 2004; Jensen *et al.* 2006). For example, males of the field cricket, *Gryllus campestris*, use a long-range song to attract

females, and carrier frequency and chirp rate of these songs are the reliable indicators of male condition. Males that have encountered better nutritional environments in the laboratory have lower carrier frequencies and faster chirp rates (Scheuber *et al.* 2003a,b). Adult carrier frequency reflects juvenile condition, while chirp rate indicates adult condition. Females prefer males exhibiting lower carrier frequencies and faster chirp rates and rank males with low carrier frequencies, i.e. those who experienced good nutrition when they were young, over the males with fast chirp rates, i.e. those who have experienced good nutrition as adults (Scheuber *et al.* 2004). In many species, when females use secondary-sexual traits to select males for copulations, they may be more likely to choose mates who have experienced high-quality environments than males of top genetic quality. The implications of this undoubtedly common phenomenon have rarely been explored (for exceptions see David *et al.* 2000; Jia *et al.* 2000).

**3. WHAT DO SECONDARY-SEXUAL TRAITS ACTUALLY SIGNAL?**

In species where males provide only sperm, females should only display strong preferences for males in good condition when condition provides an honest signal of genetic quality. While condition is often largely shaped by the environment, some environmental factors may be predictable and genetically influenced (Cheverud & Moore 1994; Moore *et al.* 1997, 1998). Parents, mothers in particular, can have a tremendous influence on offspring environments (Mousseau & Fox 1998a). For instance, mothers influence offspring both pre- and postnatally through provisioning of food, growth factors and hormones, through selection of offspring habitat and by protecting the young (Cheverud & Moore 1994; Mousseau & Fox 1998b). In many species, the mother's phenotype is the single and most important environmental factor encountered by an individual during development (Mousseau & Fox 1998a). Maternal influences on offspring may be especially powerful when environments are generally stressful and offspring have limited access to resources (McAdam & Boutin 2003; Carter *et al.* 2004).

Maternal effects are defined as influences of maternal phenotype on offspring phenotype, beyond the direct genetic contribution (Mousseau & Fox 1998b). If these influences have a genetic basis in the mother, they constitute a type of indirect genetic effect. When indirect genetic effects are present, three main components contribute to an offspring's phenotype (i) additive genetic effects, (ii) non-genetic environmental effects, and (iii) indirect genetic effects (equation (5.4), figure 1; Wolf *et al.* 1998).

**4. ADVANTAGES OF MATING WITH A MALE WHO RECEIVED GREATER MATERNAL INVESTMENT**

As a twist to the traditional good-genes models of sexual selection, secondary-sexual traits might serve as honest indicators of the genetic contributions to condition via maternal effects. Elaborate traits may signal the genetic-based quality of parenting that a particular male experienced. A female choosing to mate with an elaborate male may produce daughters with 'good parenting genes' (figure 2).

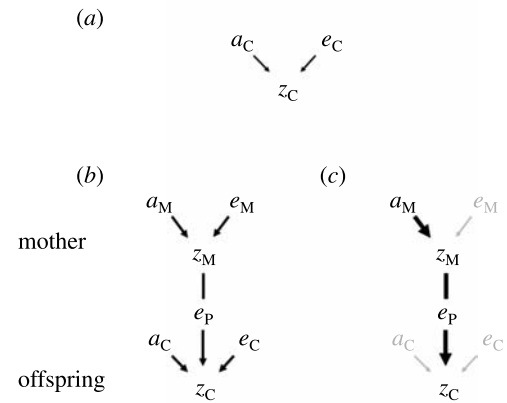


Figure 1. Illustration of additive genetic ( $a_C$ ,  $a_M$ ) and environmental ( $e_C$ ,  $e_M$ ,  $e_P$ ) contributions to phenotypes. (a) The condition of an individual ( $z_C$ ) reflects only additive genetic factors inherited from both parents and environmental influences. (b) A phenotype of the mother ( $z_M$ ), acts as an environmental influence ( $e_P$ , the maternal performance) on the condition of offspring ( $z_C$ ). (c) Illustrates indirect genetic effects influencing offspring condition. Here, offspring condition ( $z_C$ ) is largely determined by the environment provided by mothers ( $e_P$ ). The maternal effect is itself disproportionately influenced by additive genetic factors ( $a_M$ ). Modified from Moore *et al.* (1998).

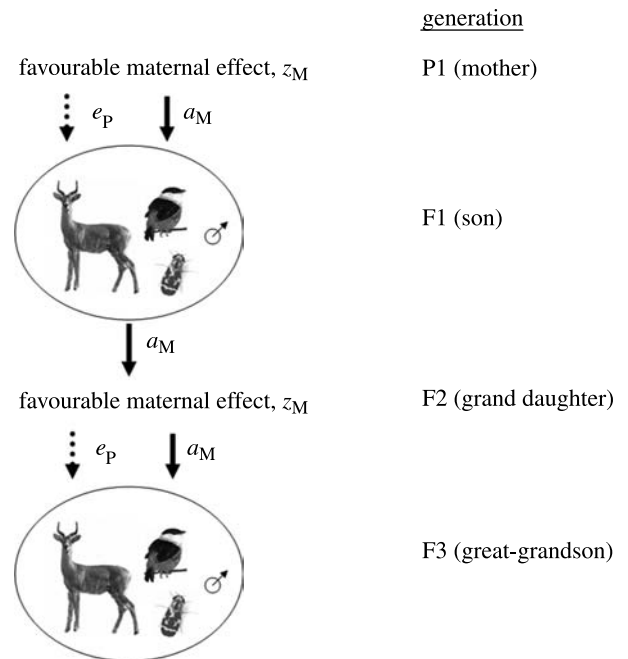


Figure 2. A hypothetical illustration of indirect genetic effects on secondary-sexual traits across four generations in three species that appear to have lek mating systems (the Uganda kob *Kobus kob thomasi*, white bearded manakin *Manacus manacus* and *Drosophila grimshawi*). In the P1 generation, a mother expresses characteristics ( $z_M$ ) which result in a favourable maternal effect ( $e_P$ ) on the condition of offspring. Sons in the F1 generation have not only received favourable parenting or other maternal effects, but they may also obtain 'good genes' ( $a_M$ ) for maternal characteristics when these characteristics have an additive genetic basis. While males may not express these genes themselves, their elaborate secondary-sexual traits may signal the potential genetic benefits for their daughters (the F2 generation). Phenotypes may 'skip' generations owing to the maternal source of additive genetic variance for the expression of condition and secondary-sexual traits.

The lek paradox describes only those situations where males do not provide resources to females and offspring. In these mating systems, males may inherit and pass-on genetic information for parenting but not express these genes themselves. While the lek paradox is best explored in such mating systems, insights into the lek paradox and possible indirect genetic benefits to mate choice might be gained by examining species with other mating systems. For instance, in the collared flycatcher, *Ficedula albicollis*, the size of the white forehead patch of males is a condition-dependent trait that predicts mating success (Gustaffson *et al.* 1995; Pärt & Qvarnström 1997; Qvarnström 1999; Griffith & Sheldon 2001). Maternal effects, including early timing of reproduction and smaller clutch sizes, are important for the production of elaborately ornamented sons (Qvarnström 1999). Highly significant components of variation in laying date and clutch size are attributable to additive genetic factors when measured in nature (Sheldon *et al.* 2003). Thus, indirect genetic effects probably play an important role in determining forehead patch size. Patch size, in turn, may signal these indirect genetic effects to potential mates. Female collared flycatchers mating with males with large forehead patches should produce daughters with maternal investment characteristics similar to their paternal grandmothers. To our knowledge, this prediction has not yet been tested. While females in this species may obtain both the direct, resource-based benefits from mates, as well as the genetic benefits for their offspring; the long-term, extensive pedigree data gathered from this species may provide an opportunity to specifically examine genetic benefits of mate choice.

The ubiquity of maternal influences on offspring phenotypes suggests that indirect genetic effects could be important players in the evolutionary process. However, more empirical studies of indirect genetic effects and their involvement in sexual selection are needed and will be facilitated by a formal framework to estimate the connections between indirect genetic effects, condition and the expression of secondary-sexual indicator traits. To this end, we adapt a previously published model to illustrate potential relationships among these variables. Ultimately, empirical research will be needed to determine the relative importance of direct and indirect genetic effects on secondary-sexual characters.

## 5. A MODEL OF MATE CHOICE FOR CONDITION-DEPENDENT INDICATOR TRAITS

Wolf *et al.* (1997) modelled how the indirect genetic effects arising from maternal or paternal care can directly influence a secondary-sexual indicator trait and result in mate choice for good parents. Here, we consider the case when maternal performance influences offspring condition, a potentially more common occurrence. We model maternal performance recognizing that researchers are not always able to identify the specific maternal traits that are influencing condition. Our approach assumes that maternal performance in one generation does not influence maternal performance in another (Falconer 1965; Cheverud & Moore 1994). Wolf *et al.* (1997) follow Kirkpatrick & Lande (1989) and relax this assumption, but their approach has the disadvantage of requiring that all maternal effects are known and measured. Thus, a further advantage of considering

maternal performance is that maternal effects can be manipulated experimentally without knowing their specific cause through, for example, cross fostering. This approach also facilitates the quantification of maternal performance. Refer to Cheverud & Moore (1994) for further discussion of the distinction between the models and the merits of each as well as descriptions of methods for measuring maternal performance.

We define the phenotypic expression of three traits: offspring condition,  $z_C$ ; maternal performance,  $z_M$ ; and a secondary-sexual indicator trait,  $z_I$ . Maternal performance effects are assumed to vary among mothers due to genetic variation among mothers, i.e. are heritable environmental effects. Following Rowe & Houle (1996), we argue that condition ( $z_C$ ) will be positively correlated with the indicator trait ( $z_I$ ) such that the correlation  $r_{C,I} > 0$  and when  $r_{C,I} = 1$ , they are the same trait. Thus, the correlation  $r_{C,I}$  measures the strength of honesty of signalling condition by an indicator trait. Maternal performance effects, if present, contribute to condition rather than the indicator trait directly.

Assuming the standard Mendelian rules of inheritance and polygenic influences on these continuous traits, we can define the phenotypes of these traits in terms of their additive genetic ( $a$ ) plus environmental and non-additive genetic ( $e$ ) components

$$z_I = a_I + e_I, \quad (5.1)$$

$$z_M = a_M + e_M. \quad (5.2)$$

Condition is slightly more complicated. As we have argued previously, offspring condition is expected to be influenced by maternal performance as well as genetic and other environmental effects. Thus, the model of the phenotype 'condition' includes maternal effects

$$z_C = a_C + e_C = z_{M,t-1}^*, \quad (5.3)$$

where the sub-subscript  $t-1$  indicates traits expressed in the previous generation (and those lacking  $t-1$  are expressed in the current generation) and the asterisk indicates that the individuals have survived selection in that generation (Arnold 1994). This equation highlights the distinction between different views of the contributions of additive genetic variance to condition (figure 1). Often, direct (within-individual) additive genetic variance for condition is predicted to be significant to condition,  $z_C$  and any indirect genetic effects on condition are ignored (figure 1a). Here, we emphasize that indirect genetic effects from parents can have an important influence on condition,  $z_C$  (figures 1c and 2).

To obtain the standard quantitative genetic description of a phenotype influenced by maternal performance, we substitute for the maternal performance trait,  $z_M$ , using the previous equations.

$$z_C = a_C + e_C + (a_{M,t-1} + e_{M,t-1}). \quad (5.4)$$

Central to honest-indicator models of sexual selection is the correlation between the secondary-sexual indicator trait (e.g. patch size in collared flycatchers) and condition, which can be described as

$$r_{C,I} = \frac{P_{CI}}{\sqrt{P_{CC} + P_{II}}}, \quad (5.5)$$

where  $P_{i,j}$  is the phenotypic variance (when  $i=j$ ) or covariance.

To consider the contributions of indirect genetic effects, we use the equations for the phenotypes above,

and solve for variances and covariances under standard quantitative genetic assumptions (Lynch & Walsh 1998)

$$P_{II} = G_{II} + E_{II}, \quad (5.6)$$

assuming no covariance between the environments of parents and offspring, and no genotype–environmental covariances. The phenotypic variance for condition is more complex, because it includes covariances between direct genetic and maternal effects

$$P_{CC} = G_{CC} + E_{CC} + (G_{MM} + E_{MM} + G_{CM}). \quad (5.7)$$

Here, we further assume random mating with respect to maternal and paternal performance within the same generation. The phenotypic covariance between the indicator trait and condition is

$$P_{CI} = G_{CI} + E_{CI} + \frac{G_{MI}}{2}. \quad (5.8)$$

Thus, the strength of the phenotypic correlation between condition and the indicator trait ( $r_{C,I}$ ) in the offspring generation is influenced by direct and indirect genetic effects, including the covariance between genes for maternal performance and genes for condition, and the covariance between the environmental influences on condition and the indicator traits. Equations (5.5)–(5.8) show that a genetic correlation between any aspect of the maternal performance and the indicator will result in an honest signal.

## 6. WHAT MAINTAINS ADDITIVE GENETIC VARIANCE FOR MATERNAL PHENOTYPES?

The lek paradox raises two primary questions: do females receive genetic benefits from discriminating among males and, if so, how is genetic variation for male traits maintained? We have argued that indirect genetic effects provide one possible source of genetic benefits to selective females. In these situations, directional selection pressures from females on males could result in the erosion of genetic variation for maternal phenotypes, favouring only those mothers who produce male offspring in good condition. However, empirical studies frequently reveal high additive genetic variance and moderate to high heritability in maternal phenotypes or their influences on offspring (e.g. Freeman-Gallant & Rothstein 1999; Van Tassell *et al.* 1999; Merilä & Sheldon 2000; Hunt & Simmons 2002; McAdam *et al.* 2002; Rauter & Moore 2002; MacColl & Hatchwell 2003; Sheldon *et al.* 2003; Wilson *et al.* 2005). How is this genetic variation in maternal phenotypes maintained? Evolutionary biologists recognize that various mechanisms may be responsible for maintaining additive genetic variance in the face of what appear to be strong directional selection pressures (Falconer & Mackay 1996; Roff 1997). Here, we will highlight two potential general mechanisms that might be particularly important in maintaining additive genetic variance for maternal characteristics.

Work by Randerson *et al.* (2000) suggests that genetic variation for an elaborate secondary-sexual trait can be maintained indefinitely due to occasional mistakes made by females in discriminating among potential mates (Neff 2000). Thus, the directional selection for maternal characteristics that produce sons with elaborate traits may not be as strong as we initially suspect. Mistakes in mate choice may be inevitable due to the environmental sensitivity of condition in males. Unpredictable or infrequent environmental variation may occasionally

obscure maternal influences on the condition of males. In addition, females may occasionally select suboptimal males (who received sub-optimal parenting) owing to the probable costs involved in finding the best mates, competing for mates or accurately assessing male quality (e.g. Dale *et al.* 1992; Hedrick & Dill 1993; Godin & Briggs 1996; Neff 2000; Randerson *et al.* 2000; Byers *et al.* 2005). In some cases, female searching behaviour and mate assessment may themselves be condition dependent, with females of poor condition unable or unwilling to invest in finding the highest quality mates (Hunt *et al.* 2005; Burley & Foster 2006). Work on flycatchers suggests that females may be socially or otherwise constrained in their selection of mates, and thus mate-choice ‘mistakes’ in this species may be common (Dale *et al.* 1992; Qvarnström *et al.* 2006).

Genotype-by-environment interactions (GEI) are another related mechanism that could explain the maintenance of additive genetic variance in maternal phenotypes. Previous work on GEI suggests that they, combined with environmental heterogeneity and gene flow (Gillespie & Turelli 1989), may be important in maintaining genetic variance in many traits (Sultan & Bazzaz 1993; Shaw *et al.* 1995; Charmantier & Garant 2005) including secondary-sexual characteristics (Qvarnström 1999; Jia *et al.* 2000; Rodriguez & Greenfield 2003; Welch 2003). GEI of mothers may result in maternal genotypes that are successful in one environment (producing attractive offspring of good condition) being relatively unsuccessful in another environment (producing unattractive offspring of poor condition). A small amount of gene flow between populations where different reaction norms are favoured is all that is needed to maintain additive genetic variance in maternal characteristics.

The maintenance of genetic variation is one of the main unresolved issues in evolutionary biology and many other mechanisms may be important. To most appropriately address this issue, researchers must understand the *source* of the additive genetic variation contributing to phenotypes. Previous studies addressing the maintenance of additive genetic variation in condition have generally focused on *direct* additive genetic variation, even though it may only be responsible for a small proportion of the total phenotypic variation in this trait. Future studies must also consider the maintenance of genetic variance in maternal phenotypes.

## 7. CONCLUSIONS

Mothers often differ significantly in the type and intensity of their influences on offspring and these differences can have striking implications for offspring phenotypes (Clutton-Brock 1991). High-additive genetic variance and moderate to high heritabilities for maternal characteristics appear to be common (Freeman-Gallant & Rothstein 1999; Van Tassell *et al.* 1999; Merilä & Sheldon 2000; Hunt & Simmons 2002; McAdam *et al.* 2002; Rauter & Moore 2002; MacColl & Hatchwell 2003; Sheldon *et al.* 2003; Wilson *et al.* 2005) and indirect genetic effects may create complex evolutionary dynamics. For instance, theoretical work suggests that traits with little or no direct additive genetic variance can still evolve if indirect genetic effects are present (Cheverud & Moore 1994; Moore *et al.* 1997). Additionally, when both direct and indirect genetic variances contribute to a trait, the

response to selection may be accelerated, slowed or even in the opposite direction from predicted (Kirkpatrick & Lande 1989; McAdam & Boutin 2004). An increasing number of researchers are recognizing the importance of examining the genetic basis behind maternal effects in natural situations (e.g. McAdam *et al.* 2002; Sheldon *et al.* 2003; Wilson *et al.* 2005). Further empirical research is needed to fully understand the implications of indirect genetic effects for evolutionary processes.

We suggest that indirect genetic effects may help to resolve the lek paradox. When secondary-sexual traits are tightly associated with condition and condition is significantly influenced by indirect genetic effects, females who choose males with elaborate secondary-sexual traits may obtain 'good genes' for their daughters in the form of effective maternal characteristics. Strong preferences by females for males with elaborate traits could result in the erosion of genetic variation for maternal phenotypes, favouring only those mothers who produce male offspring in good condition. However, additive genetic variance for maternal characteristics appears to be common, and could be maintained by a variety of mechanisms which have yet to be empirically explored in this context. By incorporating our understanding of the condition-dependent nature of secondary-sexual traits with investigations of indirect genetic effects, we may find important answers to the long-standing enigma of why males express such elaborate traits and why females prefer them.

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