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Journal:	*Journal of Evolutionary Biology*
Manuscript ID:	JEB-2014-00780.R2
Manuscript Type:	Research Papers
Date Submitted by the Author:	n/a
Complete List of Authors:	Roulin, Alexandre; Université de Lausanne, Departement Ecologie and Evolution; Jensen, Henrik; Norwegian University of Science and Technology, Centre for Biodiversity Dynamics, Department of Biology
Keywords:	Birds, Quantitative genetics, Sexual selection & conflicts

Sex-linked inheritance, genetic correlations and sexual dimorphism in three melanin-based color traits in the barn owl

A. ROULIN* & H. JENSEN†

*Department of Ecology and Evolution, University of Lausanne, Lausanne, Switzerland

†Centre for Biodiversity Dynamics, Department of Biology, Trondheim, Norway

Correspondence: Alexandre Roulin, Department of Ecology and Evolution, Biophore building, University of Lausanne, 1015 Lausanne, Switzerland. Tel.: +41 21 692 4189; fax: +41 21 692 4165; *e*-mail: Alexandre.Roulin@unil.ch

Short title: Heritability of sexual dimorphism

Abstract

Theory states that genes on the sex chromosomes have stronger effects on sexual dimorphism than genes on the autosomes. Although empirical data are not necessarily consistent with this theory, this situation may prevail because the relative role of sex-linked and autosomally inherited genes on sexual dimorphism has rarely been evaluated. We estimated the quantitative genetics of three sexually dimorphic melanin-based traits in the barn owl (*Tyto alba*), in which females are on average darker reddish pheomelanic and display more and larger black eumelanic feather spots than males. The plumage traits with higher sex-linked inheritance showed lower heritability and genetic correlations, but contrary to prediction these traits showed less pronounced sexual dimorphism. Strong offspring sexual dimorphism primarily resulted from daughters not expressing male-like melanin-based traits and from sons expressing female-like traits to similar degrees as their sisters. We conclude that in the barn owl polymorphism at autosomal genes rather than at sex-linked genes generate variation in sexual dimorphism in melanin-based traits.

Introduction

Sexual dimorphism refers to traits that are differentially expressed in the two sexes, which often results from selection favoring one sex to express a trait to larger values than the other sex. For instance, sexual selection can promote the evolution of showy male ornaments that confer mating benefits, whereas natural selection can favor camouflage in females (Lande, 1980; Andersson, 1994; Cuervo & Møller, 2000). Males can thus be positively selected to express an ornament to larger values and females selected to display the same trait but to reduced values (Bonduriansky & Chenoweth, 2009). Examples of so-called “sexually antagonistic selection” can also be found in other, non-ornamental traits and across different taxa (e.g. sexual size dimorphism in birds, mammals, insects; Preziosi & Fairbairn, 2000; Kruger, 2005; Lindenfors, 2002). However, in scenarios where selection acts differently in males and females, evolutionary change in trait expression is largely constrained because both sexes share most of their genome. When the genetic correlation between the sexes for an ornament is strong, selection exerted on one sex to be ornamented will affect the evolution of the ornament not only in this sex, but also in the other sex (Lande, 1987; Rhen, 2000; Poissant *et al*., 2009). Selection exerted on genetically correlated phenotypic traits will have similar constraining evolutionary effects. Indeed, counter-selected alleles encoding a sexually dimorphic trait can be maintained in a population owing to their positive effects on genetically correlated traits (Lande, 1980; Chenoweth *et al*., 2008; Gosden *et al*., 2012; Kirkpatrick, 2009). For instance, in the European kestrel (*Falco tinnunculus*) the degree of melanin-based coloration, a sexually dimorphic trait, is genetically correlated with body mass (Kim *et al*., 2013) implying that selection on body mass can affect the evolution of sexual dimorphism. The situation can be even more complex when selection exerted on traits in females constrains the evolution of the sexually dimorphic trait in males due to the genetic correlations among homologous and non-homologous traits across sexes (Jensen *et al*., 2008; Poissant *et al*., 2009; Harano *et al*., 2010). The allocation of genes on the sexual chromosomes may have evolved to alleviate this situation, as it is expected to decrease genetic correlations between the sexes and thereby allow each sex to express phenotypes to their optimal value. However, the relative role of polymorphisms at autosomally and sex-linked genes on sexual dimorphism (Reinhold, 1998) has rarely been considered in natural populations (Roulin *et al*., 2010; Husby *et al*., 2012; Larsen *et al*., 2014). This is a critical issue because, for instance, sex-linked and autosomally inherited components of phenotypic variation are not similarly sensitive to selection (Rice, 1984).

Sex-linked genes control the expression of secondary sexual characters because these genes can be expressed to higher levels in the homogametic than heterogametic sex (e.g. in birds males are homogametic ZZ and females heterogametic ZW) (Naurin *et al*., 2009). The exact role played by sex chromosomes and autosomes on sexual dimorphism is currently debated (Dean & Mank, 2014), further justifying studies on the quantitative genetics of sexual dimorphism. Depending on the genetic architecture, offspring sexual dimorphism can take several forms. The simplest situation is when only males express a secondary sexual character. In that case, the extent of offspring sexual dimorphism can depend on whether sons inherit alleles encoding an exaggerated or a small version of the sexually dimorphic trait (fig. 1a). When the two sexes express the secondary sexual trait, the extent of offspring sexual dimorphism may vary depending on the degree of resemblance between parents and their sons and daughters. When the resemblance between parents and sons is identical to the resemblance between parents and daughters (fig. 1b), the degree of sexual dimorphism (i.e. the lower trait expression in female offspring compared to their brothers) is of similar magnitude across families (value α in fig. 1b). When the lower trait expression in females differs between families, there might be specific situations where male offspring closely resemble their sisters (in fig. 1c when parents display a female-like version of the sexually dimorphic trait) and other situations where brothers and sisters are clearly different (in fig. 1c when parents display a male-like version of the trait). These effects may, furthermore, differ if we consider mothers and fathers (fig. 1d and e), for instance if polymorphic genes encoding sexually dimorphic traits are located on the sex chromosomes. In birds, for example, mothers pass on their single Z sex chromosome to sons but not to daughters, whereas males transmit a copy of the Z sex chromosome in both sons and daughters. Because genes located on sex chromosomes are predicted to result in higher phenotypic differences between males and females, we can expect a correlation between the degree to which phenotypic traits are coded by sex-linked genes and the degree of sexual dimorphism. Surprisingly, the current evidence for this prediction is rather limited (Dean & Mank, 2014).

Recently, quantitative genetic tools have been developed to estimate the extent to which polymorphism at genes located on the sex chromosomes and autosomes explain variation in phenotypic traits (Roulin *et al*., 2010; Husby *et al*., 2013; Larsen *et al*., 2014; Evans *et al*., 2014). This offers the possibility to examine the prediction that sexual dimorphism is positively associated with the extent to which polymorphism at sex-linked genes participate in the expression of the sexually dimorphic trait (Dean & Mank, 2014). To this end, we considered the barn owl (*Tyto alba*) because this bird displays three sexually dimorphic melanin-based plumage traits, with at least one trait showing sex-linked inheritance (Roulin *et al*., 2010; Larsen *et al*., 2014). Although members of the two sexes can express any phenotype, females are on average darker reddish than males (pheomelanin-based color trait) and display more and larger black spots located on the feather tips (two eumelanin-based color traits) (Roulin *et al*., 2001). These three melanin-based color traits are genetically correlated to a different extent in the two sexes (darker birds display more and larger black spots, particularly males) (Roulin *et al*., 2001; Roulin & Dijkstra, 2003). Because the three color-traits are already expressed in nestlings, we can perform powerful quantitative genetic analyses and compare the level of offspring sexual dimorphism with parental plumage traits. Our aim is therefore to measure the degree of offspring sexual dimorphism, estimate Z-linked and autosomal components of phenotypic variation, measure the phenotypic and genotypic correlations among traits within males and females, and measure the phenotypic and genotypic correlation between homologous and non-homologous traits among sexes. In traits for which sex-linked genes have a strong effect on trait expression, we predict heritabilities and genetic correlations to be lower (because females have only one copy of the Z sex-chromosome) but sexual dimorphism to be more pronounced than in traits for which the Z-linked component of phenotypic variation is lower.

Materials and methods

Study organism

The worldwide distributed barn owl shows pronounced variation in the expression of the three melanin-based color traits (reddish pheomelanic coloration and number and size of eumelanic black spots; Roulin *et al*., 2009). Although members of the two sexes can express these three heritable phenotypes in the range of any possible values, females are on average darker reddish and display on average more and larger black spots than males (Roulin *et al*., 2001). Spot size is positively selected in females and negatively selected in males, the magnitude of sexually antagonistic selection being population-specific (Roulin *et al*., 2010, 2011). Spot size is associated, particularly in females, with numerous phenotypic attributes such as growth, appetite, resistance to various stressful factors including free-radicals, pathogens and predators (Roulin & Ducrest, 2011; Van den Brink *et al*., 2012). The number of spots is associated with thermoregulation and sibling competition (A. Roulin unpubl. data) and pheomelanin-based coloration is involved in foraging, with differently colored individuals being adapted to different ecological conditions (Roulin, 2004a; Dreiss *et al*., 2012; Charter *et al*., 2012). Extra-pair paternity is rare in this species (Henry *et al*., 2013).

General method

Between 1996 and 2010, we studied barn owls in western Switzerland (46°49'N/06°56'E) in an area of 190 km^2 where 196 nest-boxes were available. Nestling sex was identified using sex-specific molecular markers (Roulin *et al*., 1999), whereas breeding females were distinguished from breeding males by the presence of a brood patch. Age of the breeding birds was known precisely if ringed as nestlings in previous years. For other individuals, we estimated age based on molt pattern (Taylor, 1993).

Melanin-based traits were reliably recorded (Roulin, 1999; 2004b). As feathers of each body part are similarly colored, a single person (AR) compared pheomelanin-based coloration of the breast, belly, flank and underside of the wings with eight chips ranging from -VIII for white to –I for reddish. A mean value over the four body parts was calculated. A 60 x 40 mm^2 frame was then placed on the breast and black spots were counted and their diameter measured to the nearest 0.1 mm. Mean spot diameter was used in the statistical analyses. At the age of 45 days, we can already record pheomelanin-based coloration, but not yet count and measure black spots, which were measured at 50-55 days. Thus, in a few cases, we could record only one plumage trait if these individuals disappeared from their nest (either because they died or left the nest prematurely) before we could record the other plumage traits. This explains discrepancies in sample sizes between plumage traits.

Offspring sexual dimorphism

From 1996 to 2010, plumage traits were measured in the two parents and in at least one daughter and one son in 431 families. This represents a sample of 1,099 female nestlings and 1,121 male nestlings, 259 different breeding males and 309 different breeding females. Because environmental effects on the expression of melanin-based traits are very weak in the barn owl (Roulin & Dijsktra, 2003; Roulin *et al.*, 2010), we pooled all offspring produced by a given pair in several broods produced in the same (barn owls can produce two annual broods) or different years giving a total of 400 families. We thus calculated mean daughters' and mean sons' pheomelanin-based reddish coloration, number of black spots and spot size in pooled families of 400 different breeding pairs. To compare the relative degree of sexual dimorphism in the three melanin-based plumage traits, we standardized plumage traits across the two sexes and the 400 different families (i.e. to calculate mean and standard deviations, we had 800 values for each plumage trait). For each plumage trait and family, offspring sexual dimorphism was defined as "standardized daughter value –

standardized son value”. Thus, larger values of offspring sexual dimorphism indicate that daughters are darker reddish than sons, or that daughters display more or larger black spots than sons. Note that if offspring sexual dimorphism is defined as “daughters’ value / sons’ value”, results are qualitatively similar. However, dimorphism defined as a difference rather than a ratio is more appropriate because ratios obtained with very small denominators tend towards infinity.

Statistical procedure

Animal model to derive quantitative genetic parameters

We used an estimate of the 1-year size of traits for all birds (fledglings and adults) because in a previous study, we showed that melanin-based plumage traits change with age in a sex-specific way (Dreiss & Roulin, 2010). This was done by estimating the relationship between age, in years, and trait size for all birds. In these models, we allowed for differences between sexes, effects of age, age^2, interactions sex*age and sex*age^2. Each of these parameters was included in the final model if *P*-values were smaller than 0.10. We then re-ran the model when also identity was included as fixed factor to derive individual intercepts because we often captured each individual in more than one year. The relationships found between age and plumage traits in these models were used to estimate 1-year trait size for all birds by summing the overall intercept of the model, the individual’s intercept and the sex-specific effect. To this value, we then added the (sex-specific) change in trait size from age 0 (i.e. intercept trait size) to age 1-year as given by the slope(s) for age, age^2, sex*age and/or sex*age^2. For birds measured as fledglings, the hatch year was known. For other birds, we used estimated age at first breeding to calculate their year of hatching.

Animal models are general mixed models, which utilize information from individuals with different levels of relatedness (i.e. not only parent-offspring) in a pedigree to estimate quantitative genetic quantities and various environmental effects (e.g. Lynch & Walsh, 1998; Kruuk & Hill, 2008; Charmantier *et al*., 2014). In the animal models, we estimated the proportion of variance due to differences among years (because this may explain some proportion of the trait variance; Roulin *et al*., 2010), and environmental maternal effects by including year and maternal identity as random factors, respectively. Birds from the same brood were assigned the same unique dummy mother ID's if their mother was missing, and birds without nest information were also assigned unique dummy mother ID's. Maternal environmental effects may be particularly important to control for in analyses of sex-chromosomal inheritance (Fairbairn & Roff, 2006). To avoid any bias due to differences in means and/or variance of traits between males (at least one plumage trait was measured in 1,703 individuals) and females (at least one trait measured in 1,922 individuals), trait sizes were standardized within each sex to have a phenotypic mean of 0 and phenotypic variance of 1 when estimating quantitative genetic parameters within and across sexes. The pedigree consisted of 4,343 individuals, 2,065 males and 2,278 females. Both parents were known for 70.4% of the individuals in the pedigree, only the mother for 5.1% and only the father for 0.3%. 1,047 individuals (i.e. 24.1%) in the pedigree had no known parents. Among the 334 individuals born before 1996 only 6 had one or two known parents. In contrast, among every cohort born 1996-2011 at least one parent was known for on average 80% of the individuals (range: 54-100%).

Additive genetic (co)variances, heritabilities and genetic correlations of reddish pheomelanin-based coloration, number and diameter of black spots was estimated by implementing a restricted maximum likelihood animal model using the VCE6 software (Neumaier & Groeneveld, 1998; Groeneveld *et al*., 2010). To estimate intra- and intersexual additive genetic (co)variances, and corresponding heritabilities and genetic correlations, we assumed that males and females represented two different environments and that each homologous trait in the two sexes in reality consists of two separate traits, one of which is expressed only in males and one of which is expressed only in females. Hence, male traits are missing in females, and *vice versa*. This is equivalent to estimating the additive genetic variances and covariances within and across two environments, which in our case are the two sexes (Roff, 1997).

To test whether heritability estimates were significantly different from zero, and whether estimates of genetic correlations between traits were significantly different from each other, or from zero or one, we calculated *z*-scores that were tested against a large sample standard normal distribution, following the procedure outlined in Jensen *et al.* (2003). Unfortunately, a likelihood ratio test cannot be carried out in VCE because the likelihood value calculated by VCE is different from the real likelihood as only the part of the likelihood required for optimization is computed (Groeneveld *et al*., 2010).

To examine whether any of the phenotypic variance observed in the reddish pheomelanin-based coloration, number and diameter of black spots was due to genes located on the Z-chromosomes (see Roulin *et al*., 2010; Larsen *et al*., 2014), we estimated autosomal and Z-chromosomal additive genetic variances by using Bayesian animal models and the INLA framework (Steinsland & Jensen, 2010; Holand *et al*., 2013; Larsen *et al*., 2014). These Bayesian animal models can currently only be used for single-trait models, and could hence not be used to estimate additive genetic covariances within and across sexes. In the Bayesian animal models, we followed the recommendations of Larsen *et al*. (2014): we standardized the data across both sexes instead of within each sex as above, we present the Z-chromosomal additive genetic variance for males, and we regard Z-chromosomal additive genetic variance to be present if the model with both Z- and autosomal additive genetic variance has a DIC which is at least 10 units lower than the model with only autosomal inheritance.

Relationship between offspring sexual dimorphism and parental phenotypes

We examined whether the degree of offspring sexual dimorphism is associated more strongly with maternal or paternal phenotypes. Offspring sexual dimorphism in pheomelanin-based coloration, number of spots and spot diameter were entered as dependent variable in separate linear mixed models, where the identities of the two biological parents were entered as random variables. Six independent variables were simultaneously introduced in the models, i.e. standardized (mean = 0, SD = 1) maternal and paternal pheomelanin-based coloration and number and size of black spots. Non-significant variables were backward removed starting with the least significant ones (threshold level was 0.05). However, all significant variables in the reduced model were already significant in the initial model.

Analyses on sexual dimorphisms were carried out with the software JMP (version n° 8, SAS software, Inc. Carey NC). All tests were two-tailed and *P*-values smaller than 0.05 considered significant.

Results

Quantitative genetics

For sexes combined, pheomelanin-based coloration was more strongly heritable (h^2 = 0.836) than spot diameter (h^2 = 0.668) and number of spots (h^2 = 0.570) (Table 1).

Hatch year explained approximately 8 and 6% of the variation in number and diameter of spots, respectively, but explained none of the color variation (Table 1). Mother identity explained between 1 and 5% of phenotypic variation (Table 1). When sexes were analyzed separately, we found a tendency that the heritability was higher in males than in females (Table 1); this difference was however not significant for any of the three traits ($P = 0.65$, $P = 0.13$, $P = 0.09$ for pheomelanin-based color, number and diameter of spots, respectively). These patterns nevertheless support Bayesian single-trait animal models showing significant Z-chromosomal additive genetic variance for both number and diameter of spots but not for pheomelanin-based coloration (Table 2).

The three plumage traits were positively correlated within males and females, both phenotypically and genetically (Table 3a). The genetic correlations were more strongly positive within males than within females ($P < 0.0001$, $P = 0.06$, $P < 0.0001$ for pheomelanin-based color, number and diameter of spots, respectively; Table 3a). Although phenotypic correlations were less strong than their associated genetic correlation, they were highly correlated (Spearman's correlation: $r_s = 1$, $n = 6$, $P < 0.0001$) (Table 3a), which is not surprising given that heritabilities were very high (Table 1, see also Hadfield et al. 2007).

The genetic correlations between sexes for homologous traits were very strong and only significantly lower than 1 for number of spots ($P = 0.002$, values in the diagonal of Table 3b). Genetic correlations between males and females for non-homologous traits ranged from 0.145 for male pheomelanin-based color and female number of spots up to 0.841 for male number of spots and female diameter of spots, and were significantly higher than 0 and lower than 1 (all P-values < 0.0027, values off the diagonal in Table 3b).

Offspring sexual dimorphism

Offspring sexual dimorphism was more pronounced in pheomelanin-based coloration than in the size of eumelanic spots (mean standardized values ± SE: 1.03 ± 0.04 versus 0.74 ± 0.05; paired *t*-test: $t_{399} = 6.07$, $P < 0.0001$), which was itself more pronounced than offspring sexual dimorphism in the number of eumelanic spots (0.54 ± 0.05; paired *t*-test: $t_{339} = 4.70$, $P < 0.0001$). In 367 of the 400 different breeding pairs (91.8%), sisters were on average darker pheomelanic than their brothers (sign test comparing sexual dimorphism with 0, M = 158.50, $P < 0.0001$); in 313 families (78.3%), sisters displayed on average larger black spots than their brothers (M = 113.50, $P < 0.0001$); in 267 families (66.8%), sisters displayed on average more black spots than their brothers (M = 67.50, $P < 0.0001$). In 229 families (57.3%), sisters were simultaneously on average darker pheomelanic and displayed more and larger eumelanic spots than their brothers (note that in some families females can be darker reddish than their brothers but not necessarily more spotted). Offspring sexual dimorphism in pheomelanin-based coloration was strongly correlated with offspring sexual dimorphism in both number and size of black spots, i.e. when sisters were darker reddish than their brothers, they also displayed more black spots (Pearson's correlations: $r = 0.48$, $n = 400$ families, $P < 0.0001$) and larger spots ($r = 0.45$, $P < 0.0001$). The correlation between offspring sexual dimorphism in both eumelanic traits (i.e. number and size of spots) was stronger than the relationships with offspring sexual dimorphism in the degree of pheomelanism ($r = 0.64$, $P < 0.0001$; when sisters displayed more black spots than their brothers, these spots were also larger). This is consistent with the genetic correlation analyses (Table 3).

Relationship between offspring sexual dimorphism and parental phenotypes

Standardized offspring sexual dimorphism was more often and more strongly associated with standardized maternal than paternal plumage traits (Table 4, Fig. 2). Furthermore, offspring sexual dimorphism in pheomelanin-based coloration was more strongly related to the homologous trait (i.e. pheomelanin-based coloration) of their parents than it was for number and size of black spots (Table 4, Fig. 2).

Offspring sexual dimorphism in pheomelanin-based coloration increased (i.e. daughters were darker reddish than sons) particularly when their mother and father were pale rather than dark reddish (Fig. 2 and 3a) and when their mother displayed small rather than large black spots (Table 4). Similarly, daughters displayed more black spots than sons particularly when their mother was pale rather than dark reddish and when the mother and father displayed small rather than large black spots (Table 4; Fig. 2 and 3b). Finally, daughters displayed larger black spots than sons when their mother was light rather than dark reddish and when the mother exhibited small rather than large black spots (Table 4; Fig. 2 and 3c).

Discussion

We identified the determinants of offspring sexual dimorphism in three heritable melanin-based traits in the barn owl. Quantitative genetic analyses showed that the three traits are heritable and genetically correlated within and across sexes (Tables 1, 2 and 3; Fig. 2 and 3). As expected, the trait with the lowest Z-linked component, reddish pheomelanin-based coloration, showed the highest heritability and genetic correlation between the sexes (Tables 1, 2 and 3). In contrast to prediction, this trait was a more strongly sexually dimorphic trait compared to eumelanin-based plumage traits (i.e. number and size of black spots), which showed a significant Z-linked component (Table 2; Fig. 3). Another important result is that the degree to which daughters are more pigmented (i.e. display a darker reddish coloration, more or larger black spots) than their brothers increases when their parents are less pigmented (Table 4, Fig. 2).

Heritability

Heritabilies tended to be smaller in female than in male barn owls (Table 1; Fig. 3), a situation that seems to contrast with other organisms (e.g. Jensen *et al*., 2003). The cause is probably that two of the plumage traits are partially encoded by polymorphic genes located on the Z sex chromosome (Table 2). Since females do not pass on their Z to daughters, this might reduce the magnitude of the heritability. Up to date, few researchers have demonstrated that genes located on sex chromosomes are responsible for variation in color traits using Mendelian genetics (Southern, 1946; Munro *et al*., 1968; Zann, 1996), parent-offspring regression (Potti & Canal, 2011) or animal models (Roulin *et al*., 2010; Husby *et al*., 2012; Evans *et al*., 2014; Larsen *et al*., 2014). A recent study in collared flycatchers (*Ficedula albicollis*) and zebra finches (*Taenipygia guttata*) has suggested that sexually selected traits are not more often encoded by polymorphic genes located on sex chromosomes than other morphological traits (Husby *et al*., 2012), but rather the expression of genes underlying sex-specific phenotypes could be controlled by sex hormones (something that is not taken into account in animal models). Although theory postulates that sex chromosomes play an important role in the evolution of sexual dimorphism, since their transmission is sex biased or sex limited (Rice, 1984), many sexually dimorphic traits are encoded by polymorphic genes located on autosomes (Mank, 2009; Mank & Ellegren, 2009).

In the barn owl, variation in the most sexually dimorphic plumage trait (pheomelanin-based coloration) did not show any significant Z-component in contrast to the two least sexually dimorphic traits (number and size of black spots) (Table 2). This suggests that sex-linked inheritance is not a prerequisite for sexual dimorphism. For both number and size of black spots, the slopes of the resemblance between father and sons and between father and daughters were of similar magnitude but not the intercepts (Fig. 3b,c). In contrast, the resemblance mother-sons was more pronounced than mother-daughters for the three plumage traits (Fig. 3) probably because the maternal Z chromosome is transmitted only to sons. As a consequence, the intensity of offspring sexual dimorphism was reduced when mothers displayed many and large black spots and when they were darker reddish (Table 4; Fig. 2), since they produced similarly spotted sons and daughters (absence of sexual dimorphism). This suggests that, in contrast to intuition (Rice, 1984; Mank, 2009), polymorphism at genes located on sex chromosomes does not necessarily increase the degree of offspring sexual dimorphism because at some specific parental trait values, parents produce similarly plumaged sons and daughters (Fig. 3).

Genetic correlations between plumage traits within sexes

The evolution of a given phenotype can result from selection being exerted on it directly but also on genetically correlated traits, as shown for the specific case of secondary sexual characters (Brooks & Endler, 2001; Jensen *et al*., 2008; Poissant *et al*., 2008). Genetic correlations between traits can evolve because selection exerted on the different traits is correlated (McGlothlin *et al*., 2005; Roff & Fairbairn, 2012). Correlational selection implies that functionally related traits should not be expressed independently from each other because individuals derive more fitness benefits from some specific trait combinations than other combinations. For instance, alternative foraging modes may require different combinations of characters (Sinervo & Svensson, 2002), e.g. foraging upon a given type of prey may necessitate a particular coloration to be cryptic which in turn requires specific morphological structures (Roulin & Wink, 2004). Mechanistically, genetic correlations can arise if a given gene regulates different traits (pleiotropy), if several genes encoding a given phenotype are physically linked (Johnston *et al*., 2010) or if these genes are in linkage disequilibrium due to e.g. non-random mating (Lynch & Walsh, 1998).

In the barn owl, we studied three melanin-based color traits that necessarily share part of the melanogenic biochemical cascade. As could be predicted, the strongest genetic correlations were between the two eumelanin-based plumage traits (number and diameter of black spots), mean of male and female genetic correlations being 0.794, twice as strong as the genetic correlation between number of eumelanic spots and pheomelanin-based coloration (0.348). Interestingly, genetic correlations were on average 1.6 times stronger in males than in females (Table 3), possibly as a consequence of Z-linked genes (Table 2), implying that the evolution of a given plumage trait should be particularly constrained by the evolution of the two other traits in males. This finding suggests that the three melanin-based traits may have a more redundant function in males than in females. Accordingly, in females (and to a lower extent in males) the size of black spots is related to behavior and physiology (Roulin & Ducrest, 2011), while pheomelanin-based coloration plays a role in the adaptation to local conditions (Dreiss *et al*., 2012), probably associated with predator-prey relationships (Charter *et al*., 2015).

Genetic correlations between the three plumage traits were all positive (Table 3), i.e. darker pheomelanic individuals displayed more and larger black spots. This suggests that the production of pheomelanin and eumelanin pigments is not traded off against each other. Therefore, the expression of the melanogenic genes that allow the production of the precursors of both melanin types may have an overwhelming effect on plumage traits compared to genes that trigger the expression of pheomelanin pigments at the expanse of eumelanin pigments. To test these scenarios measurement of gene expression is needed (e.g. Emaresi *et al*., 2013).

Genetic correlations between homologous traits in the two sexes

Each sex can evolve more rapidly towards its phenotypic optimum if the genetic correlation between the sexes is low rather than high (e.g. Chenoweth *et al*., 2007) as shown in a review of the literature (Poissant *et al*., 2009). This is particularly relevant in species in which a trait is the target of sexually antagonistic selection where males are positively selected and females negatively selected (or *vice versa*). When the genetic correlation between the sexes is high, positively selected males will not only produce sons having a selective advantage but also counter-selected daughters, and the other way round with positively selected females (Foerster *et al*., 2007; Mills *et al*., 2012). In such a situation, selection should favor the breakdown of the inter-sexual genetic correlation, a process that may, however, take many generations (Lande, 1987). As a consequence, males who inherit the counter-selected female-like version of a sexually antagonistically selected trait (and females who inherit a counter-selected male-like trait) may evolve compensatory strategies to reduce the cost of sexually antagonistic selection (e.g. Abbott *et al*., 2013).

In the barn owl, we found evidence for the hypothesis that spot size is sexually antagonistically selected (positive selection in females and negative selection in males; Roulin *et al*., 2010, 2011). Although some of the underlying genes are located on sex chromosomes (Roulin *et al*., 2010; Larsen *et al*., 2014; Table 2), the genetic correlation between males and females for spot size is very strong (0.963; Table 3b) implying that small-spotted fathers will produce counter-selected daughters. Furthermore, if the absolute strength of negative selection exerted in males is weaker than positive selection in females, males will evolve away from their phenotypic optimum, as we could demonstrate in Switzerland (Roulin *et al*., 2010). This may explain why offspring sex ratio is correlated with parental spot diameter; the probability of producing sons being higher when both parents displayed a male-like plumage (i.e. small spots) and lowest when at least one of the parent displayed a female-like plumage (i.e. large spots). Furthermore, male-like females and female-like males produced sons and daughters with a high survival prospect, respectively (Roulin *et al*., 2010). These two compensatory mechanisms may have evolved as a consequence of the very strong genetic correlation between the sexes for spot size.

Interestingly, the degree of offspring sexual dimorphism was related to parental phenotype (Table 4, Fig. 2), implying that some parents produce daughters and sons that closely resemble each other while other parents produce very distinct daughters and sons. For the three plumage traits, the degree of sexual dimorphism decreased with parental melanism, i.e. when parents (particularly mother) were darker reddish or displayed more and larger black spots, sons resembled their daughters to a larger degree than when their parents were pale reddish or lightly spotted (Table 4). From a proximate of view, a potential explanation is that a gene of major phenotypic effect (such as *MC1R*) determines the amount of pigments produced in the two sexes and another gene of minor phenotypic effect (such as those of the melanocortin system) is responsible for the slight over-expression of melanin in females compared to males. In that case, when parents possess a mutation of the gene of major phenotypic effect that triggers the expression of a large amount of melanin pigments, feathers become saturated in melanin implying that the gene of minor phenotypic effect will have hardly any effect on sexual dimorphism.

With respect to spot size, sons and daughters differed the most when their mother displayed small rather than large black spots. Because this trait is sexually antagonistically selected (Roulin *et al*., 2010), the resulting intralocus genetic conflict may be particularly strong when mothers are large-spotted, since they will produce counter-selected large-spotted sons. As can be seen in fig. 3c, large-spotted mothers produce sons and daughters who are similarly spotted, whereas small-spotted mothers produce offspring displaying spots at the size that is typical for their sex (i.e. large-spotted daughters and small-spotted sons). This finding is particularly interesting as it suggests that positive selection on female spot size is associated with more intense intralocus genetic conflict, whereas negative selection on male spot size is associated with a reduced genetic conflict. This further suggests that mutations that increase the expression of larger spots are associated with more intense genetic conflict, whereas mutations that suppress the expression of large spots are related to a reduced conflict. It would be particularly interesting to identify the genes involved in the expression of large black spots but also to determine whether they are ancestral or derived (i.e. if barn owls were originally large- or small-spotted).

Genetic correlations between non-homologous traits within and across the sexes

Genetic correlations between non-homologous traits have been shown to reduce the rate of adaptation (Teplitsky *et al*., 2014a,b). In contrast, a study in the house sparrow (*Passer domesticus*) showed that indirect selection had a larger contribution to the predicted evolution of a melanin-based trait in males than direct selection (Jensen *et al*., 2008). Of particular interest was the finding that selection exerted on female morphology can affect the evolution of male ornamentation. This reinforces the idea that a particular trait cannot be considered independently from other phenotypic characters. This statement is not trivial because the importance of natural selection on the evolution of sexually selected traits may be considerable, but the role played by indirect selection exerted on genetically correlated traits in males and females is rarely studied or even discussed (see reviews in Jensen *et al*., 2008 and Teplitsky *et al*., 2014a,b).

Acknowledgements

We thank A.M. Holand for help with running the INLA analyses. The Swiss National Science Foundation (grants n° PPOA-102913 and 31003A_120517), Foundation De Giacomi and Herbette, and the Research Council of Norway (grants no. 221956 and 223257 to HJ) supported this study financially. We are grateful to two anonymous reviewers for useful comments.

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Table 1. Quantitative genetics of plumage traits in the barn owl. Estimates of the proportion of variation in pheomelanin-based coloration, number and diameter of black spots due to additive genetic effects (i.e. the heritability, h^2), maternal environmental effects and year of hatching. Estimates ± SE are from a model where both sexes and all three traits were included. We first assumed sexes to be the same environment; estimates for sexes combined. We also report heritability of plumage traits of male and female barn owls separately. These estimates are from a model where males and females were assumed to be two different environments, i.e. that females had missing values for male traits and vice versa. Both male and female traits were included in the same model. Variation in trait sizes due to any effects of year of hatching and maternal environmental effects were accounted for.

	Variance components – sexes combined			h^2 – sexes separately	
Trait	Hatch year	Mother ID	h^2	Males	Females
Pheomelanin-based colour	0.005±0.003	0.012±0.011	0.836±0.021	0.872±0.124	0.793±0.125
Number of black spots	0.077±0.021	0.040±0.012	0.570±0.030	0.716±0.136	0.500±0.040
Diameter of black spots	0.055±0.016	0.052±0.013	0.668±0.025	0.805±0.032	0.576±0.132

Table 2. Autosomal and Z-chromosomal inheritance of three melanin-based plumage traits in the barn owl. Additive genetic variances were calculated in one model assuming autosomal and Z-linked inheritance of the traits and another model assuming autosomal inheritance only. Z-chromosomal additive genetic variance is given for males (i.e. approximately twice that of females). Additive genetic variance estimates (Va) are posterior means and credible intervals are given in parentheses.

	Autosomal Va	***Z-chromosomal Va***	***Hatch year Vy***	***Maternal identity Vm***	***Residual Vr***	***DIC***
Pheomelanin coloration	0.524 (0.453; 0.607)	0.169 (0.104; 0.250)	0.003 (0.001; 0.008)	0.003 (0.000; 0.011)	0.136 (0.110; 0.167)	5618.161
	0.651 (0.593; 0.715)	**-**	**0.003 (0.001; 0.009)**	**0.003 (0.000; 0.011)**	**0.135 (0.108; 0.165)**	**5586.007**
Number of black spots	**0.154 (0.081; 0.272)**	**0.511 (0.411; 0.625)**	**0.053 (0.025; 0.101)**	**0.042 (0.021; 0.074)**	**0.320 (0.278; 0.365)**	**7845.770**
	0.548 (0.476; 0.628)	-	0.059 (0.028; 0.116)	0.035 (0.014; 0.065)	0.306 (0.262; 0.355)	7895.389
Diameter of black spots	**0.224 (0.161; 0.300)**	**0.454 (0.365; 0.563)**	**0.041 (0.018; 0.084)**	**0.030 (0.012; 0.059)**	**0.206 (0.171; 0.248)**	**6664.644**
	0.544 (0.481; 0.615)	-	0.046 (0.020; 0.093)	0.035 (0.014; 0.068)	0.208 (0.169; 0.254)	6758.495

The model with both autosomal and Z-chromosomal inheritance is regarded as significantly better if its DIC is >10 lower than DIC for the autosomal model only (Larsen *et al.*, 2014). Hatch year and maternal identity were included in the models as random effects and sex was included as fixed effect. The best model for each trait is given in bold.

Table 3. Phenotypic and genetic correlations between plumage traits (pheomelanin-based coloration, number and diameter of black spots) within males (above diagonal, in bold) and females (below diagonal) (a), and across-sex genetic correlations between homologous and non-homologous plumage traits in the barn owl (b). All phenotypic correlations are significant at $P < 0.001$. Estimates of genetic correlations (± SE) are from a model where males and females were assumed to be two different environments, i.e. females had missing values for male traits and vice versa. All male and female traits were included in the same model. Variation in trait sizes due to any effects of year of hatching and maternal identity was accounted for.

a) Phenotypic and genetic correlations between plumage traits within each sex

	Phenotypic correlation			Genetic correlation		
	Pheomelanin color	Number of black spots	Diameter of black spots	Pheomelanin color	Number of black spots	Diameter of black spots
Pheomelanin color	-	**0.369**	**0.418**	-	**0.501±0.023**	**0.557±0.067**
Number of black spots	0.182	-	**0.713**	0.194±0.041	-	**0.926±0.028**
Diameter of black spots	0.332	0.527	-	0.380±0.068	0.661±0.037	-

b) Genetic correlations across sexes in homologous and non-homologous traits

		Female trait		
		Pheomelanin color	Number of black spots	Diameter of black spots
Male trait	Pheomelanin color	0.996±0.014	0.145±0.035	0.346±0.041
	Number of black spots	0.543±0.026	0.903±0.031	0.841±0.053
	Diameter of black spots	0.591±0.025	0.710±0.035	0.963±0.019

Estimates in the diagonal refer to the genetic correlations between homologous plumage traits in related males and females (e.g. pheomelanin-based coloration in females vs. males [0.996±0.014]). Off-diagonal elements refer to the genetic correlations between non-homologous plumage traits in males and females (e.g. pheomelanin-based coloration in females vs. number of black spots in males [0.543±0.026]).

Table 4. Offspring sexual dimorphism in melanin-based traits (pheomelanin-based coloration, number and size of eumelanic spots) in relation to parental plumage phenotypes in the barn owl. Linear mixed models included the identity of the two biological parents as random variables and the three standardized paternal and maternal plumage traits as six independent variables. Non-significant terms are eliminated starting with the least significant ones. Significant terms are written in bold and estimates (± SE) are given. Sample size is 400 different breeding pairs. Offspring sexual dimorphism was defined as the difference between standardized daughters' and sons' plumage trait values. Negative estimates indicate a reduced offspring sexual dimorphism when parents are more melanic.

	Offspring sexual dimorphism in standardized melanin-based plumage traits		
	Pheomelanin-based color	Number of black spots	Diameter of black spots
Standardized paternal plumage traits			
Pheomelanin color	**$F_{1,184.5}$ = 13.72, P = 0.0003** **(-0.171±0.046)**	$F_{1,230.8}$ = 0.007, P = 0.93	$F_{1,201.4}$ = 0.005, P = 0.94
Number of black spots	$F_{1,203}$ = 0.58, P = 0.45	$F_{1,136}$ = 0.48, P = 0.49	$F_{1,242.7}$ = 0.11, P = 0.74
Diameter of black spots	$F_{1,164.6}$ = 0.03, P = 0.86	**$F_{1,158}$ = 4.19, P = 0.04** **(-0.081±0.039)**	$F_{1,170.3}$ = 0.09, P = 0.76
Standardized maternal plumage traits			
Pheomelanin colour	**$F_{1,285.3}$ = 24.16, P < 0.0001** **(-0.238±0.048)**	**$F_{1,274.6}$ = 24.49, P < 0.0001** **(-0.223±0.045)**	**$F_{1,310.2}$ = 17.49, P < 0.0001** **(-0.203±0.048)**
Number of black spots	$F_{1,305}$ = 0.90, P = 0.34	$F_{1,293}$ = 0.88, P = 0.35	$F_{1,319}$ = 1.23, P = 0.27
Diameter of black spots	**$F_{1,175.3}$ = 14.05, P = 0.0002** **(-0.183±0.049)**	**$F_{1,187.1}$ = 86.53, P < 0.0001** **(-0.429±0.046)**	**$F_{1,251.6}$ = 54.45, P < 0.0001** **(-0.370±0.050)**

For instance, the degree of offspring sexual dimorphism in pheomelanin-based coloration is negatively correlated with paternal and maternal pheomelanin-based coloration and the size of maternal black spots.

Figure legends

Fig. 1. Sons' and daughters' expression of a secondary sexual character in relation to parental trait values. In these examples, males express the sex-trait to larger mean values than females, and hence large values are denoted "male-like" and low values "female-like". (a) Complete sexual dimorphism (or sex-limited dimorphism): only males express the secondary sexual character and in this case males can express different values of the trait, whereas all females display the same "female-like trait". (b-d) The dimorphism is not sex-limited and offspring resemble each of their parents to varying degrees. (b) Sons and daughters similarly resemble their parents but females express the trait to lower values than males (by a value α). (c) Sons and daughters resemble their parents but to different values; females express the trait to lower values than males but the extent of the decreased expression (values α_1 and α_2) is correlated with parental trait value. (d, e) The values α_1 and α_2 can be different when comparing offspring phenotype with paternal (d) and maternal (e) phenotype. These phenotypic models cannot make any assumptions or predictions regarding the underlying genetic basis.

Fig. 2. Relationship between sexual dimorphism in offspring plumage traits in relation to parental plumage traits in the barn owl. Offspring' mean plumage trait values were standardized across the 400 different breeding pairs and for each pair daughters' standardized value was subtracted from the sons' standardized value so that sexual dimorphism in the three plumage traits had the same scale and could be compared. Parental plumage traits were also standardized within each sex. For each of the three plumage traits (i.e. pheomelanin-based coloration, number and size of black spots) standardized offspring sexual dimorphism was regressed on the standardized

homologous trait value of their mother and father, separately. For instance, the line "Maternal spot diameter" is for the relationship between standardized offspring sexual dimorphism in spot diameter and maternal spot diameter. Significant regressions are indicated with the symbols *** $P < 0.0001$ and * $P < 0.05$.

Fig. 3. Relationship between mean offspring and parental pheomelanin-based coloration (a), mean offspring and parental number of spots (b), and between offspring and parental spot diameter (c) in the barn owl. Regression lines are based on 400 different breeding pairs.

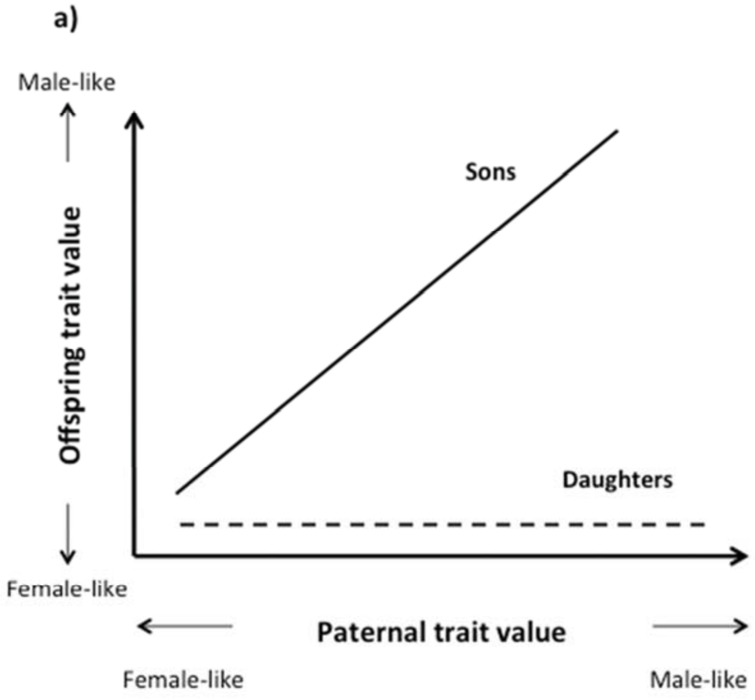

a)
Male-like
Offspring trait value
Female-like
Sons
Daughters
Paternal trait value
Female-like
Male-like

Fig. 1a.

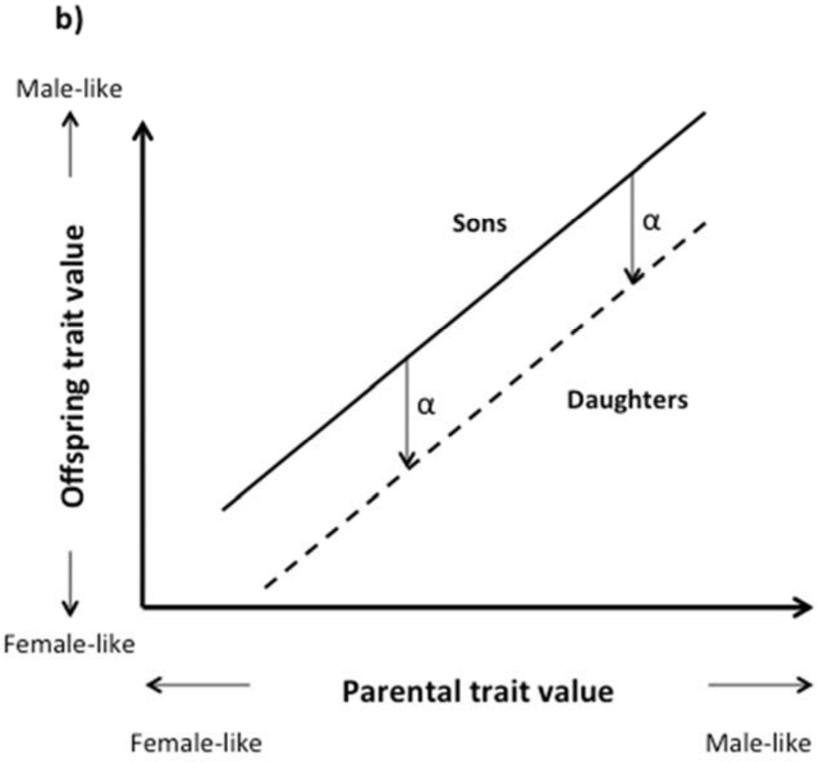
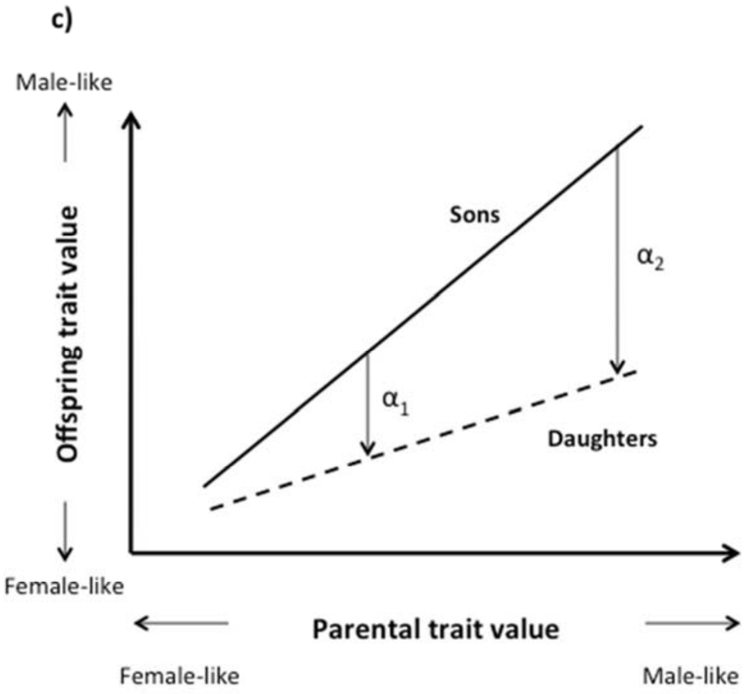

b)
Male-like
Offspring trait value
Female-like
Sons
α
α
Daughters
Parental trait value
Female-like
Male-like

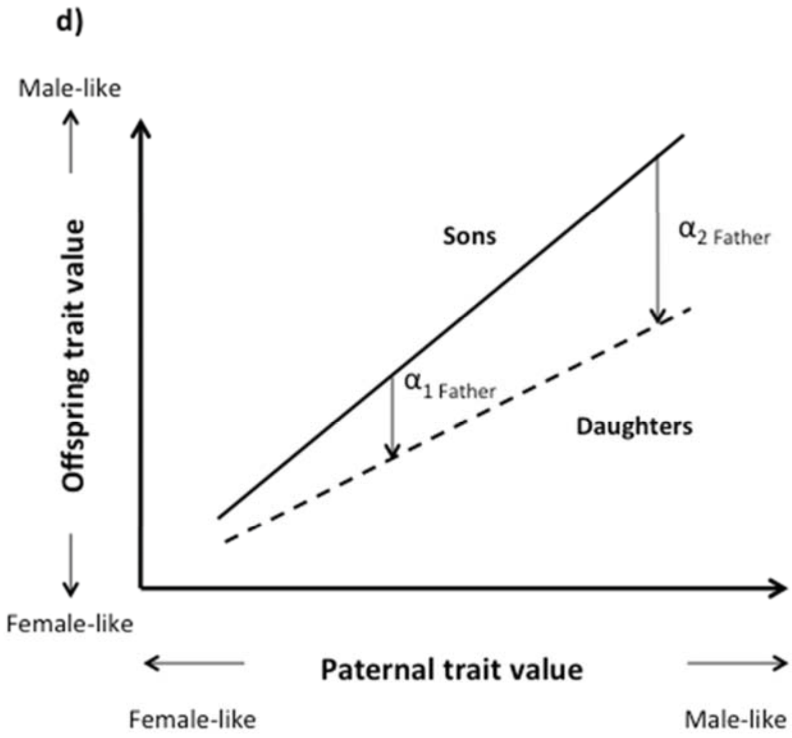
Fig. 1b.



786

787 **Fig. 1c.**

788



789

790 **Fig. 1d.**

791

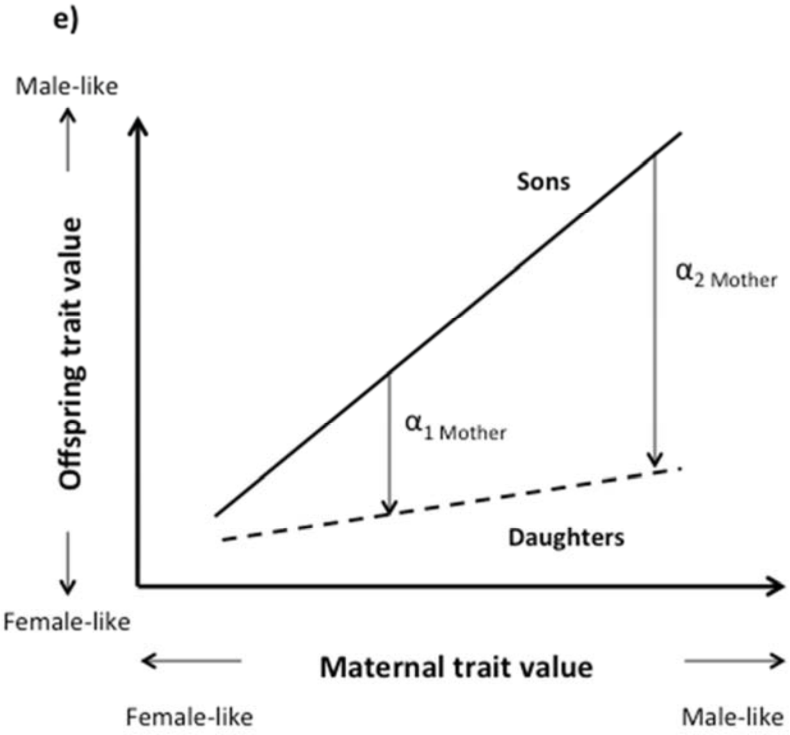

e)
Male-like
Offspring trait value
Female-like
Sons
$\alpha_{2\ \mathrm{Mother}}$
$\alpha_{1\ \mathrm{Mother}}$
Daughters
Maternal trait value
Female-like
Male-like

Fig. 1e.

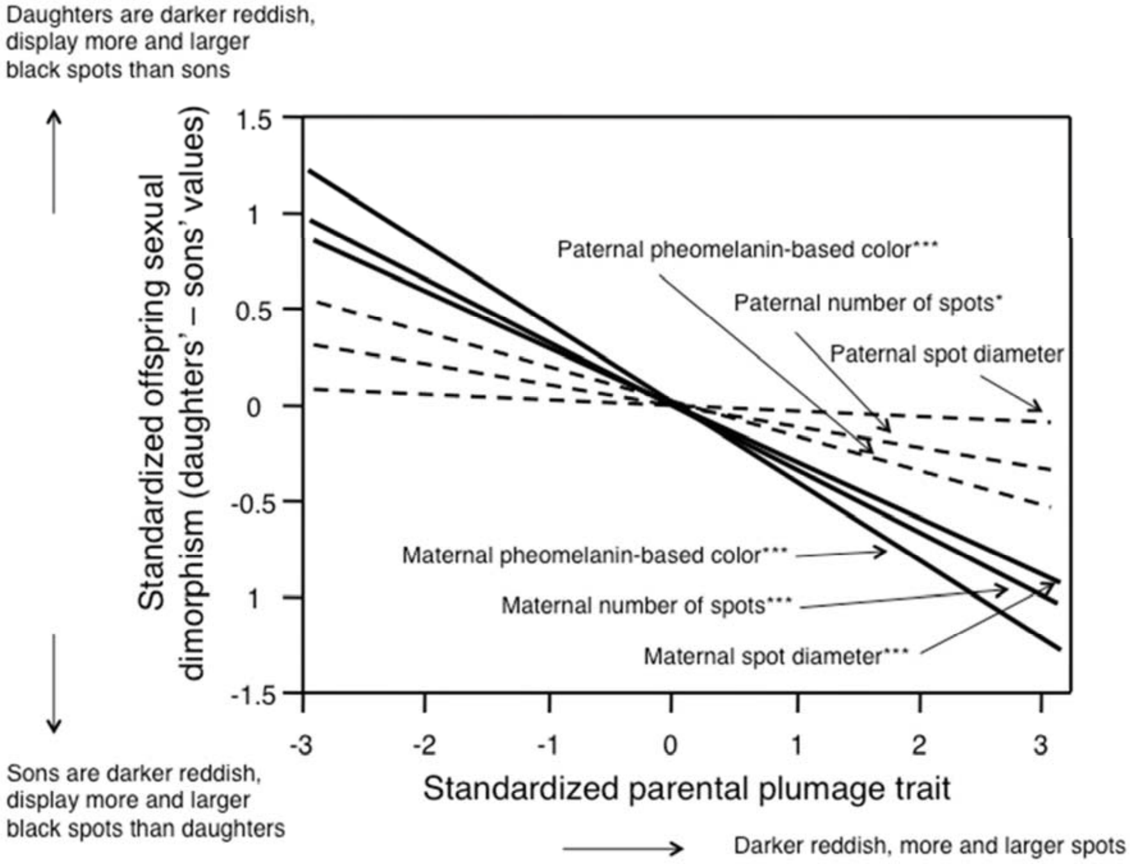

Daughters are darker reddish, display more and larger black spots than sons
Standardized offspring sexual dimorphism (daughters' – sons' values)
1.5
1
0.5
0
-0.5
1
-1.5
Paternal pheomelanin-based color***
Paternal number of spots*
Paternal spot diameter
Maternal pheomelanin-based color***
Maternal number of spots***
Maternal spot diameter***
-3
-2
-1
0
1
2
3
Standardized parental plumage trait
Sons are darker reddish, display more and larger black spots than daughters
Darker reddish, more and larger spots

Fig. 2.

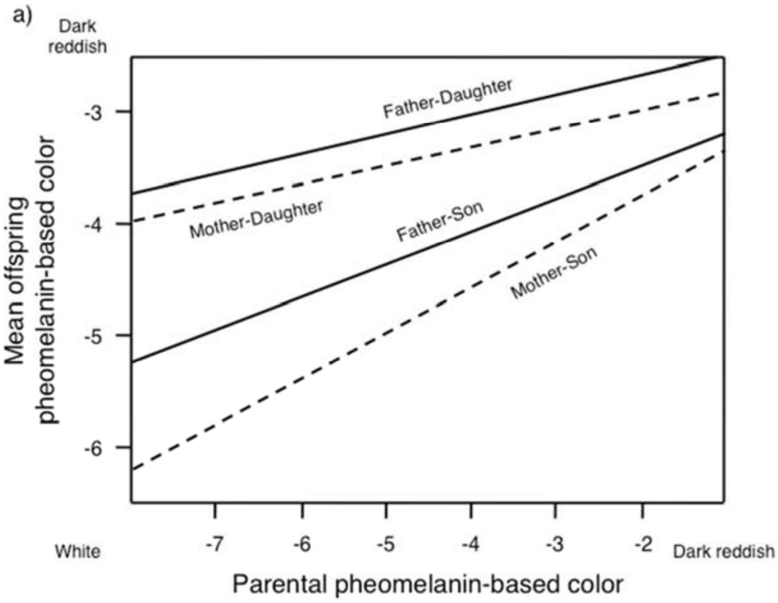

a)
Dark reddish
Father-Daughter
Mother-Daughter
Father-Son
Mother-Son
Mean offspring pheomelanin-based color
-3
-4
-5
-6
White
-7
-6
-5
-4
-3
-2
Dark reddish
Parental pheomelanin-based color

Fig. 3a.

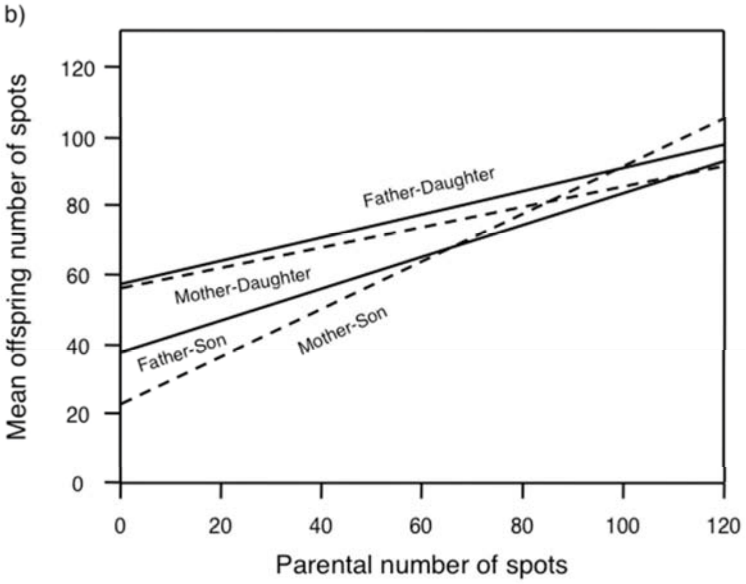
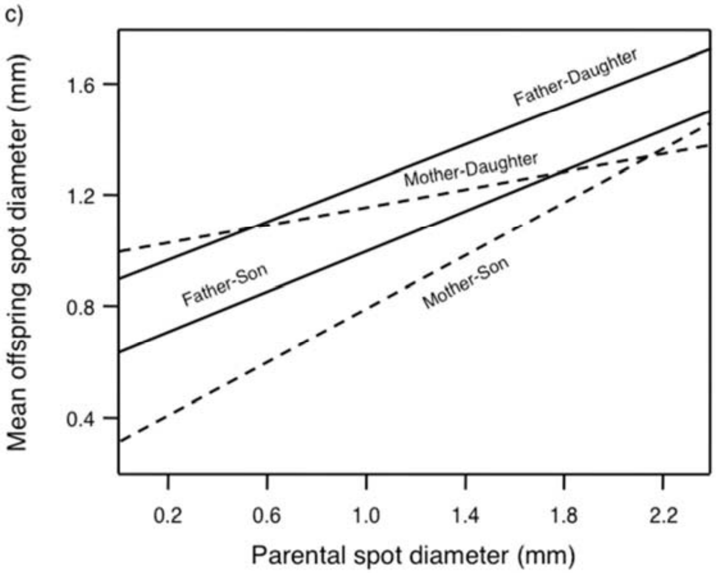

b)
Father-Daughter
Mother-Daughter
Father-Son
Mother-Son
Mean offspring number of spots
0
20
40
60
80
100
120
0
20
40
60
80
100
120
Parental number of spots

Fig. 3b.



804

805 **Fig. 3c.**