

## Original Article

## Condition-dependent mate assessment and choice by peahens: implications for sexual selection

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Condition-dependent mate choice is thought to affect the strength and direction of sexual selection. Although there is ample evidence of this from studies that experimentally manipulate female condition, few studies to date have examined condition dependence of natural mate choice wherein females interact with a pool of available males. We examined mate assessment by free-living *Pavo cristatus* peafowl, focusing on 3 measures of the choosing female's condition: mass condition (scaled mass index), ectoparasite load, and white blood cell (WBC) count. Females with greater mass condition were more active on peacock leks, approaching and visiting males more often, and spending more time near the males they visited. Condition did not affect the total number of males visited or the probability that a female would visit a male that she had already approached. Peacock mating success is strongly correlated with the iridescent colors of the eyespots on their train, suggesting that color signals are a major focus of female choice. Here, we show that females in better condition (higher mass condition and lower WBC count) allocate a greater proportion of their visit time to the most iridescent males displaying on leks. Our results provide evidence of strong condition-dependent effects on female mate assessment and choice in the absence of experimentally induced stress. We suggest that condition-dependent mate choice may help maintain variation in sexually selected male color traits.

**Key words:** courtship, condition-dependence, iridescence, lek paradox, mate choice, mate sampling, peacock, sexual selection.

## INTRODUCTION

Mate assessment can have considerable costs (Byers et al. 2006; Dunn and Whittingham 2006; Kasumovic et al. 2007), and as a result, this behavior may often be condition-dependent. This condition-dependent plasticity in mate assessment and choice is thought to affect the strength and direction of sexual selection (Tomlinson and O'Donald 1996; Jennions and Petrie 1997; Cotton et al. 2006). Previous experimental studies manipulating females' nutrition, energetics, or condition during development have provided ample evidence for condition-dependent female choice. For example, female 3-spined sticklebacks (*Gasterosteus aculeatus*) and female guppies (*Poecilia reticulata*) that are stressed and/or depleted of energetic reserves also become less selective about their mates (Luttbegg et al. 2001; Syriatowicz and Brooks 2004). Similarly, in the stalk-eyed fly (*Cyrtodiopsis dalmanni*), nutritional stress can cause females to become less selective about their mates (Hingle et al. 2001a, 2001b). In

black field crickets (*Teleogryllus commodus*), females reared on poor diets are less selective about mates when they become adults (Hunt et al. 2005), although a similar diet manipulation experiment with house crickets (*Acheta domesticus*) did not significantly affect female mate preferences (Gray 1999). In the wolf spider *Rabidosa rabida*, both age and rearing diet can influence female mating behavior, such that young females reared on a restricted diet are considerably less likely to mate with courting males (Wilgers and Hebets 2012).

Other recent studies have reported similar condition-dependent effects in vertebrates. Woodgate et al. (2010) reared captive female zebra finches (*Taeniopygia guttata*) under nutritional stress and found that those females made fewer visits to courting males during mate choice trials than females reared with food available ad libitum. Holveck and Riebel (2010) used a brood size manipulation to alter zebra finch nutrition during development and found that females reared in large broods with low nutritional input preferred the songs of low-quality males as adults, unlike females reared in small broods. Finally, Lerch et al. (2013) clipped the wings of adult female canaries (*Serinus canaria*) to increase the costs of flight, and

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found that those females were less likely to prefer the rapid male song types that female canaries normally prefer.

Only a few studies have addressed the effects of naturally occurring variation in condition on mate choice in the absence of experimentally induced stress (Choudhury and Black 1993; Rintamäki et al. 1995; Bakker et al. 1999; Uy et al. 2001). In barnacle geese (*Branta leucopsis*) and black grouse (*Tetrao tetrix*), variation in female body mass (not corrected for skeletal size) is related to the number of males visited for courtship (Choudhury and Black 1993; Rintamäki et al. 1995). In satin bowerbirds (*Ptilonorhynchus violaceus*), however, Uy et al. (2001) found no evidence of a relation between female body condition and the number of males visited for courtship (with body condition defined as the residual of mass regressed on tarsus length). The only study to date to relate natural variation in condition to females' responses to male traits was Bakker et al.'s (1999) study of wild-caught 3-spined sticklebacks. After breeding sticklebacks for 1 generation in the lab, Bakker et al. (1999) found that females sired by males in the best condition (i.e., higher body mass per unit length) showed greater preference for male red throat color, suggesting a relation between the standing genetic variation influencing body condition and that influencing how females respond to male traits. The fact that this study is the only one to demonstrate this relationship in the absence of experimentally induced stress is surprising, given considerable interest in the topic (Cotton et al. 2006). Importantly, however, the 2-choice test of female proximity to model male sticklebacks used by Bakker et al. (1999) does not address natural mate choice, which we define as the outcome of females interacting a pool of available mates.

Here, we studied whether condition influences mate choice in a large free-living population of peafowl (*Pavo cristatus*). Native to India, peafowl are lek-mating birds; groups of males (peacocks) maintain display court territories in open areas (leks) that females (peahens) visit for courtship and copulation. Peahens will often view the courtship displays of several different males over a period of days before mating (Petrie et al. 1991, 1992). Because courtship and copulation take place in open habitats, it is relatively easy to observe these interactions, especially in introduced populations where peafowl are habituated to human presence. Previous studies have identified train plumage iridescence as a major focus of mate choice in peafowl (Loyau et al. 2007; Dakin and Montgomerie 2013). We have also documented extensive variation in female condition and behavior in North American free-living populations of this species (Dakin 2011). Thus, the goal of this study was to test whether variation in female condition and health is related to variation in mate assessment behavior and whether this also affects the outcome of mate choice for sexually selected male color traits.

## MATERIALS AND METHODS

### Field methods

We conducted fieldwork in 2009 (February–April) and 2010 (January–April) at the Los Angeles Arboretum in Arcadia, CA, USA. Peafowl were introduced to Arcadia in the 1880s (Bell 2010), and since then the population has grown to more than 200 birds. All birds in this population are free-living, and courtship and copulation occur on leks, as has been described in wild populations in India (Hillgarth 1984; Harikrishnan et al. 2010). There are several leks in close proximity in the Arcadia population, where 16–20 adult males display (1–6 males per lek) during the breeding season. Each male maintains a court of approximately 2–3 m<sup>2</sup>. Starting in

early to mid March, females visit these leks and observe male courtship displays, with peak courtship activity occurring in late March. We captured birds in 2009 ( $n = 20$  males, 13 females) and 2010 ( $n = 20$  males, 35 females) prior to the start of male lekking activity and marked them with numbered leg bands. In 2010, we caught 13 of the males and 2 of the females that we had marked in 2009.

At the time of capture, we removed feather eyespots from the train of each male to measure eyespot colors (see Male Color Traits for details). We also measured the body mass ( $\pm 0.01$  kg) and both left and right tarsus lengths ( $\pm 1$  mm) of each captured male and female. We used the average of the left and right tarsus lengths as an index of skeletal size. To quantify ectoparasite load, we plucked 5–10 body feathers from each of 3 (ulnar, breast, and back) feather tracts of each bird and stored them in paper envelopes that were sealed for 2–4 months prior to examination. A small blood sample was also taken from each bird by pricking the cutaneous ulnar vein, and then used to make blood smears on 2–4 glass slides so that we could assess hematological health.

### Observations

We observed females visiting males on leks using different methods in 2009 and 2010. In 2009 (16 March–7 April), we used a focal female approach, wherein 2 observers tracked individual females visiting males on leks between 07:00–12:00 and 16:00–18:00 PST (peak lekking times of day; see also Petrie et al. 1991). To conduct these observations, we selected the first female that was seen walking toward a lek and followed her from a distance of approximately 20 m. While observing a focal female, we recorded which lek she was approaching, the identity of the adult male that she was closest to on the lek, and estimated whether she was within approximately 2 m of that male. We also recorded that male's train display behavior (i.e., whether or not his train was erect, and if it was erect, whether he was performing a wing-shaking display, a train-rattle display, or neither). The wing-shaking display is performed often when males have their trains erect, even if no females are present; in contrast, the train-rattling display is only performed when females are nearby and positioned in front of the male's erect train (see Dakin and Montgomerie 2009 for descriptions of these displays). We noted the time whenever there was a change in the distance to the closest male, in his display behavior, or in the identity of the closest male. We stopped watching a focal female when she left the vicinity of the leks for more than 5 min, at which time we selected a new focal female and followed her. Two observers conducted these focal female observations. We also noted all copulation attempts and successful copulations during these observation periods, as well as the identities of the birds involved.

In total, we conducted 123 observation periods in 2009 on 26 different females, comprising 8 that we had captured and marked, and 18 unmarked birds that could be identified based on their plumage. Total observation time was 121 h, with observation periods averaging 56 min (95% confidence interval [CI] 49–64, range 10–205 min,  $n = 123$ ). With every new observation period, we selected the first female that we spotted near the leks regardless of her identity, making no attempt to sample each female equally. Because female visits to the leks were relatively infrequent, observers did not have to choose between 2 females that were spotted simultaneously. Thus, the variation in the extent to which the 8 marked females were observed (range 15–1544 min; 1–23 observation periods) was the result of some females being more active on the leks than others and not biased sampling. In total, we observed 23 copulations involving 16 males in 2009, the majority (20/23)

of which involved unmarked females; only 1 marked female was observed copulating, and she did so 3 times.

In 2010 (15–27 March), 4 observers simultaneously and continuously observed 4 leks from 08:00–18:00 PST each day in an area where 11 males maintained display courts. During these continuous observations, we recorded the same behaviors described previously for our focal female observations. In total, we conducted 506 h of observations in 2010, during which 18 marked females visited the leks we observed. We recorded 19 copulations involving 11 males. The majority (17/19) of copulations involved marked females—only 4 marked females were seen copulating (3 copulated 4 times each, and one 5 times).

In both years, our observations did not include all courtship interactions during the breeding season for the females we studied because these females undoubtedly visited males on other leks and at times when we were not observing them. However, we consider that our sampling methods in both years provide a reasonable estimate of each female's level of involvement in mate assessment relative to other females in the population.

### Mate assessment behaviors

We used these observations to estimate the total number of males approached and visited by each female. We defined a “male approach” as any instance where a female came within 30 m of an adult male on a lek when that male had his train erect. If a female was within 30 m of  $\geq 1$  male with an erect train, we scored her as approaching the male closest to her. We defined a “male visit” as any instance where a female was in front of a male within 2 m of his erect train for more than 2 s while he performed the train-rattling display, thus clearly indicating that the female had experienced that male's courtship display. For each male visit, we also calculated the total amount of time ( $\pm 1$  min) that the female spent near the visited male (and not closer to any other male), as well as the total amount of time ( $\pm 1$  min) she spent  $\leq 2$  m from that male during his train-rattling display. We classified instances where a female made a male approach, but did not perform a male visit, as a “male skip.” Relations between measures of female mate assessment are shown in [Supplementary Table S1](#).

### Male color traits

In peafowl, the iridescence of the central blue–green region of the males' train feather eyespots strongly predicts male mating success ([Loyau et al. 2007](#); [Dakin and Montgomerie 2013](#)), where iridescence is defined as the amount of change in hue with changing light angle. Across peafowl populations, the most successful males tend to have the blue–green patch on their eyespots characterized by a greater change in *theta* and a minimal change in *phi* as the angle of incident light is shifted from 30° to 60° ([Dakin and Montgomerie 2013](#)), where *theta* and *phi* are measures of bird-perceived hue that account for birds' different sensitivities to different wavelengths of light (see [Stoddard and Prum 2008](#) for details).

In this study, we sought to address whether female preference for this aspect of iridescence is condition-dependent. To quantify the iridescence of captured males, we measured a 2-mm diameter spot on the left side of the blue–green region of a single eyespot feather sampled from the midline of the train ornament on each male (see [Dakin and Montgomerie 2013](#) for details). We used an Ocean Optics USB4000-UV-VIS spectrometer to measure light reflected from this spot, holding the measurement probe normal to the feather surface and the light source (Ocean Optics DH-2000 Deuterium Tungsten Halogen) at angles of 30° and 60° to right of

the feather surface, respectively. This configuration mimics the typical conditions under which females view peacock's train-rattling displays ([Dakin and Montgomerie 2009](#)). At each light angle, we took 2 measurements that were each the average 10 scans with a 100-ms integration time, repositioning the feather between these 2 repeat measurements, and then taking the average. Further details of these procedures are outlined in [Dakin and Montgomerie \(2013\)](#).

We used peafowl photoreceptor sensitivities reported by [Hart \(2002\)](#) to model the resulting color spectra in tetrahedral color space, calculating *phi* and *theta* for each male's blue–green patch at 30° and 60° light angles. *Phi* or hue latitude (the UV component of hue) is the vertical angle from the achromatic origin to the locus of a given color; *theta* or hue longitude (the non-UV component of hue) is the angular displacement around the base of the tetrahedral color space ([Stoddard and Prum 2008](#)). For each male, we estimated 2 iridescences: “*theta*-iridescence” as the absolute value of blue–green *theta* when illuminated at 30° minus blue–green *theta* at 60° and “*phi*-iridescence” as the absolute value of blue–green *phi* at 30° minus blue–green *phi* at 60°. Preferred males are those with high *theta*-iridescence and low *phi*-iridescence; of these 2 color traits, *theta*-iridescence is the best predictor of male mating success ([Dakin and Montgomerie 2013](#)).

We examined the condition-dependence of female preference for male color traits in 2 ways. First, we designated each female's most-visited male as her “preferred male,” evaluating preferred male eyespot iridescence in relation to female condition. In the case of ties for “preferred male,” we designated the male that the female had spent the most time visiting as her preferred male. All 5 marked females that were seen copulating did so with their preferred male. Second, for each female, we calculated weighted averages of *theta*- and *phi*-iridescences for all of the males that she female visited, weighting each male's iridescence value by the proportion of total time she spent visiting that male. We then evaluated females' weighted average *theta*- and *phi*-iridescences in relation to their condition.

### Female condition

Following [Hill \(2011\)](#), we used 3 different condition measures thought to reflect different aspects of health and physiological state: scaled mass index (SMI), white blood cell (WBC) count, and ectoparasite load.

We used [Peig and Green's \(2009\)](#) “SMI” as a measure of individual energy reserves or “mass condition,” estimating a scaling exponent from a reduced major axis regression of the natural logarithm of mass on the natural logarithm of tarsus length ( $n = 48$  female captures; note that 2 females were captured in both 2009 and 2010, and are each represented twice in this analysis). This scaling exponent (here 5.66) was used to estimate SMI, or the “standardized mass index,” each peahen would have at the median tarsus length (13.23 cm), given her actual body mass. SMI accounts for the fact that body mass and tarsus length are both subject to measurement error, and that they do not necessarily develop independently of one another, and performs better than other methods of estimating mass condition at predicting body composition and energetic reserves ([Peig and Green 2009](#)).

Elevated WBC counts are thought to indicate stress in birds ([Campbell 1995](#); [Ots et al. 1998](#)). In peafowl, previous studies have shown that the abundance of certain leukocyte types is related to male plumage development ([Møller and Petrie 2002](#); [Loyau et al. 2005](#); [Ros et al. 2009](#)). To quantify WBC count, we fixed blood smears in methanol and stained them with Giemsa, following

Campbell (1995). We examined at least 10 fields of view at  $\times 1000$  magnification on each slide (2–4 slides per female), counting the total number of leukocytes and erythrocytes. We then calculated WBC count as the number of leukocytes per 10 000 erythrocytes for each female (see Dakin 2011 for details).

Chewing lice (Ischnocera, Amblycera) are thought to be parasitic for avian hosts, and studies of other species have demonstrated that high loads of these lice can be energetically costly (Booth et al. 1993). To quantify ectoparasite load, we examined female body feathers under a dissecting microscope and counted the total number of chewing lice and eggs found. As an index of ectoparasite load, we determined the total number of chewing lice and eggs divided by the total number of feathers sampled from all 3 body regions sampled (breast, back, and ulnar).

The SMI for female peafowl was not significantly related to either their WBC count (Pearson correlation,  $r = -0.14$ ,  $P = 0.34$ ,  $n = 46$ ) or their ectoparasite load ( $r = 0.24$ ,  $P = 0.11$ ,  $n = 46$ ), nor was ectoparasite load significantly related to WBC count ( $r = -0.26$ ,  $P = 0.09$ ,  $n = 46$ ).

## Data analysis

We used R 3.0.1 (R Development Core Team 2013) for all statistical analyses.

In all, we studied 66 individually identifiable peahens (31 in 2009 and 35 in 2010), but we obtained data on the condition of only 26 of those females. Two of those females whose condition we measured were captured and observed in both years of the study, so we used their data from the first year only to avoid pseudoreplication and to obviate the need to include female identity in regression models. All subsequent analyses in this paper are based on those 26 females for which we had both observations of behavior on leks and measurements of their condition.

To test the relations between female condition and mate assessment behaviors, we used generalized linear models and an information-theoretic (IT) approach to model selection (Burnham et al. 2011) using the R package *MuMIn* (v 1.9.5). The IT approach allows for uncertainty in model selection and avoids the pitfall of overlooking effects that might be absent from the best model, and yet present in other models that fit the data equally well (Whittingham et al. 2006; Symonds and Moussalli 2011). For each response variable of interest, we fit all possible models entering our 3 measures of condition as predictors, as well as study year as a categorical variable to control for potential differences between years. We ranked the resulting model set by the bias-corrected Akaike information criterion ( $AIC_c$ ), a measure of goodness of fit penalized by model complexity. We considered models with  $\Delta AIC_c \leq 2$  relative to the best-fitting model in each set as the “top models.” Additional parameters in models with  $\Delta AIC_c > 2$  generally do not reduce model deviance by a sufficient amount to justify their inclusion and can thus be dismissed (Arnold 2010). We used the *model.avg* function in the *MuMIn* package to calculate an average of the top models in each set, and we report parameter estimates and 95% CIs for this averaged model as measures of effect size and estimate precision, respectively (Table 1). It is important to note that these results should not be interpreted as tests of null hypotheses, as this is incompatible with the IT approach. Instead, we focus our interpretations on effect size and model fit. As a measure of goodness of fit, we report maximum likelihood-based pseudo  $R^2$  values for the best-fitting model in each set (Cox and Snell 1989), which for Gaussian models is equivalent to  $R^2$  or the amount of variance explained. Further details on the structure of all top models in each set can be found in the Supplementary Table S2.

We assessed the fit of residuals for the full (saturated) model in each set to normality both visually and using the Shapiro–Wilk test. Only the residuals from the binomial model of number of visits per number of approaches differed significantly from normality ( $P = 0.04$ ; see Supplementary Figure S1). Preliminary analyses indicated that 1 female’s weighted average *phi*-iridescence was a significant outlier (Grubbs test,  $P = 0.03$ ), so we excluded this female from our analysis of weighted average *phi*-iridescence. This improved both model fit and the normality of residuals, but did not substantially change the estimation of predictors for that model set.

## RESULTS

### Female condition and activity on leks

Each peahen ( $n = 26$ ) made an average of 24.3 “male approaches” (95% CI 11.6–37.0) during our observations, “visiting” 41% (29–53%) of the males they approached and “skipping” the rest. On average, each of these females visited 3.2 (2.1–4.3) different males. There was no significant difference between study years ( $n = 8$  females in 2009 and 18 in 2010) in the number of male approaches ( $t$ -test,  $t = 0.91$ ,  $P = 0.37$ ), male visits ( $t = 0.91$ ,  $P = 0.37$ ), male skips ( $t = 0.90$ ,  $P = 0.38$ ), or unique males visited ( $t = 0.40$ ,  $P = 0.69$ ) per female. Nor was there any significant difference between study years in the proportion of male approaches that resulted in male visits ( $t = 0.03$ ,  $P = 0.97$ ) for each female studied.

The 22 peahens that made at least 1 male visit ( $n = 7$  in 2009 and 15 in 2010) spent on average 6.5 min (3.7–9.3) near the visited male and 2.0 min (1.5–2.4) viewing his train-rattling display. There was no significant difference between years in the amount of time females spent viewing visited males’ train-rattling displays ( $t = 0.75$ ,  $P = 0.46$ ). Females spent more than double the amount of time near the males they visited in 2009 (mean = 10.8 min [6.4–15.2] per visit) relative to 2010 (mean = 4.5 min [1.5–7.5] per visit;  $t = 2.4$ ,  $P = 0.02$ ); this may have been because in 2010, observations were made throughout the day including midday when females may be less motivated to engage in courtship (Petrie et al. 1991), whereas in 2009, observations were only conducted at peak lekking times. There was no significant difference between years in preferred male *theta*- ( $t = 1.54$ ,  $P = 0.16$ ,  $n = 22$ ) or *phi*-iridescence ( $t = 0.33$ ,  $P = 0.75$ ), nor in weighted average *theta*- ( $t = 1.54$ ,  $P = 0.16$ ) or *phi*-iridescence ( $t = 0.42$ ,  $P = 0.69$ ).

### Female condition and mate assessment

Females that most often approached males had significantly higher SMI (Table 1). In the best-fitting model of male approaches, this effect corresponds to a 6-fold increase in the number of males approached for females with the highest SMI, relative to those with the lowest. Females that most often approached males also had lower ectoparasite loads and WBC counts (Table 1). Although the 95% CIs for the parameter estimates for these other 2 effects overlapped with 0, the effect of WBC count in the best-fitting model corresponds to a 6-fold decrease in the number of males approached for females with the highest WBC count, compared with those with the lowest. SMI and WBC count together explain 26% of the variance among females in the best-fitting model of male approaches.

Females that visited males most often also had higher SMI (Table 1), and in the best-fitting model, this effect corresponds to a 9-fold increase in the number of males visited for females with the highest SMI, relative to the lowest. SMI and study year together

**Table 1**

**Peahen mate assessment and choice are influenced by condition. Parameter estimates are shown for the average of the top models ( $AIC_c \leq 2$ ) in each set, ordered by relative importance, a measure of the weight of evidence for that variable's inclusion in the model. Coefficient estimates are standardized to facilitate comparison. Effects that are significantly different from 0 based on 95% CIs are shown in bold; note that these are effect size estimates and they should not be interpreted as null hypothesis statistical tests. Maximum likelihood-based pseudo  $R^2$  values for the best model in each set are also given. Full details of all top models are provided in the Supplementary Materials**

Response	Predictors	Estimate	95% CI	Relative importance	Pseudo $R^2$
Male approaches ( $n = 26$ )	<b>SMI</b>	<b>0.017</b>	<b>0.003 to 0.031</b>	<b>1.0</b>	0.26
	WBC	-0.014	-0.030 to 0.002	0.53	
	Year	0.013	-0.002 to 0.028	0.37	
	Ectoparasites	-0.012	-0.027 to 0.004	0.14	
Male visits ( $n = 26$ )	<b>SMI</b>	<b>0.052</b>	<b>0.010 to 0.094</b>	<b>1.0</b>	0.27
	<b>Year</b>	<b>0.041</b>	<b>0.000 to 0.081</b>	<b>0.45</b>	
	WBC	-0.031	-0.074 to 0.011	0.23	
	Ectoparasites	-0.018	-0.046 to 0.009	0.09	
Male skips ( $n = 26$ )	SMI	0.024	-0.002 to 0.049	0.68	0.20
	WBC	-0.024	-0.051 to 0.003	0.47	
	Year	0.021	-0.005 to 0.046	0.16	
	Ectoparasites	-0.018	-0.046 to 0.009	0.09	
Number of males visited ( $n = 26$ )	SMI	0.364	-0.028 to 0.757	0.64	0.13
	WBC	0.005	-0.007 to 0.017	0.19	
Visits per approach ( $n = 26$ )	SMI	0.006	-0.005 to 0.018	0.24	0 (NA)
	WBC	0.005	-0.007 to 0.017	0.19	
	Ectoparasites	0.005	-0.009 to 0.019	0.16	
	Year	0.021	-0.005 to 0.046	0.16	
Average time near visited males ( $n = 22$ )	<b>SMI</b>	<b>0.056</b>	<b>0.015 to 0.096</b>	<b>1.0</b>	0.68
	<b>WBC</b>	<b>-0.071</b>	<b>-0.117 to -0.025</b>	<b>1.0</b>	
	<b>Year</b>	<b>-0.091</b>	<b>-0.134 to -0.047</b>	<b>1.0</b>	
	Ectoparasites	-0.032	-0.076 to 0.012	0.34	
Average time spent viewing visited males' displays <sup>a</sup> ( $n = 22$ )	Null				0 (NA)
	SMI	<b>0.468</b>	<b>0.142 to 0.794</b>	<b>1.0</b>	
Preferred male <i>theta</i> -iridescence ( $n = 22$ )	<b>WBC</b>	<b>-0.520</b>	<b>-0.868 to -0.172</b>	<b>1.0</b>	0.56
	Year	-0.212	-0.566 to 0.143	0.32	
	WBC	0.374	-0.059 to 0.806	0.806	
Preferred male <i>phi</i> -iridescence ( $n = 22$ )	<b>SMI</b>	<b>0.428</b>	<b>0.143 to 0.712</b>	<b>1.0</b>	0.14
	<b>WBC</b>	<b>-0.549</b>	<b>-0.809 to -0.288</b>	<b>1.0</b>	
Weighted average <i>theta</i> -iridescence <sup>a</sup> ( $n = 22$ )	<b>WBC</b>	<b>0.400</b>	<b>0.048 to 0.751</b>	<b>1.0</b>	0.63
	Ectoparasites	-0.337	-0.695 to 0.021	1.0	
	Year	-0.212	-0.566 to 0.143	0.32	
Weighted average <i>phi</i> -iridescence <sup>a</sup> ( $n = 21$ )	<b>WBC</b>	<b>0.400</b>	<b>0.048 to 0.751</b>	<b>1.0</b>	0.47
	Ectoparasites	-0.337	-0.695 to 0.021	1.0	

NA, not applicable because the best-fitting model is the null model.

<sup>a</sup>Only 1 top model so no averaging.

explain 27% of the variance among females in the best-fitting model of male visits. The influence of female condition on the number of male skips was similar, but somewhat weaker. Females with high SMI and low WBC counts tended to skip more males—together in the best-fitting model, these 2 variables explain 20% of the variance in male skips, although the 95% CIs for both effects overlapped with 0 (Table 1). Females with higher SMI also visited more males in total, with SMI explaining 13% of the variance in the best-fitting model, although this effect was also relatively weak and its 95% CI overlapped with 0 (Table 1). Condition did not affect the probability that a female would visit a male once she approached him (Table 1).

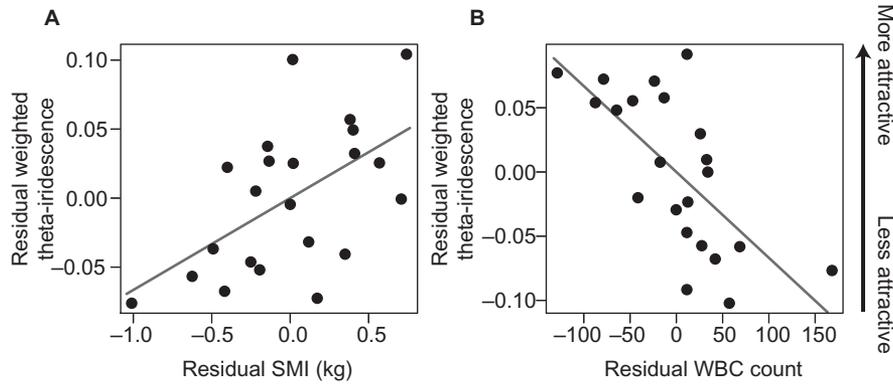
Females with higher SMI and/or lower WBC count spent more time with the males they visited. The effects of SMI and WBC count were retained together in all top models of time spent near visited males. The effect of SMI in the best-fitting model of time spent near males corresponds to a 3-fold increase for females with the highest SMI, compared with those with the lowest SMI. The effect of WBC count in that model corresponds to a 5-fold decrease over the observed range of WBC count values. The best-fitting model in this set explains 68% of the variance in time spent near visited males. Because the strong effect of study year in this model was likely the result of methodological differences, we also fit a model with the effects of SMI and WBC count alone to assess  $R^2$  for the model with only these two variables, and found that

SMI and WBC count explain roughly 34% of the variance in the amount of time females spent near visited males. Condition was not related to the average time females spent viewing visited males' train rattling displays (Table 1).

### Female condition and preferences for male traits

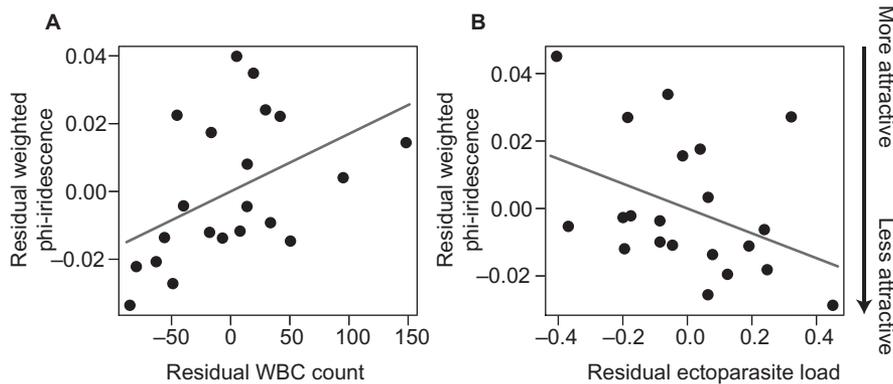
Females with higher SMI and/or lower WBC counts allocated more of their time to visiting males with higher *theta*-iridescence (Figure 1). The effects of SMI and WBC count were retained together in all top models of this response variable. This was true whether we evaluated female preference using either preferred male traits or the weighted average across all visited males (Table 1). Together, the effects of SMI and WBC count explain 56% and 63% of the variance in the best-fitting model of preferred male *theta*-iridescence and weighted average *theta*-iridescence, respectively (Figure 1).

Females with lower WBC counts tended to have preferred males with lower *phi*-iridescence, but this effect was relatively weak, explaining only 14% of the variance in the best-fitting model in this set (Table 1). The relation between female condition and the weighted average *phi*-iridescence of visited males was considerably stronger: females with lower WBC counts and/or fewer ectoparasites allocated more of their visiting time toward males with lower *phi*-iridescence (Figure 2). These effects explain 47% of the variance in the best-fitting model of weighted average *phi*-iridescence.



**Figure 1**

Partial regression plots from the best-fitting model of weighted average *theta*-iridescence (i.e., the average *theta*-iridescence of males visited weighted by the relative amount of time a female spent visiting each male). The model included 2 measures of condition as predictors: (A) SMI and (B) WBC count. *Theta*-iridescence is positively related to male mating success. Thus, on the *y* axis, higher values of weighted average *theta*-iridescence indicate a greater proportion of time allocated to visiting more attractive males.



**Figure 2**

Partial regression plots for the best-fitting model of weighted average *phi*-iridescence (i.e., the average *phi*-iridescence of males visited weighted by the relative amount of time a female spent visiting each male). The model included 2 measures of conditions as predictors: (A) WBC count and (B) ectoparasite load. *Phi*-iridescence is negatively related to male mating success. Thus, on the *y* axis, lower values of weighted average *phi*-iridescence indicate a greater proportion of time allocated to visiting more attractive males.

## DISCUSSION

Peahens in better condition approach and visit displaying males more often, and they spend more time near the males they visit. Peahens in better condition also allocate more of their visits to the most attractive peacocks (i.e., those with high *theta*-iridescence and low *phi*-iridescence of the blue-green region on their eyespot feathers; Dakin and Montgomerie 2013). These results provide compelling evidence that natural variation in mate assessment behavior is influenced by female condition. Only 3 previous studies have shown similar evidence of condition-dependent mate choice in the absence of experimentally induced stress: Choudhury and Black (1993), Rintamäki et al. (1995), and Bakker et al. (1999). Uniquely among these, our results show an association between a female's condition and her response to sexually selected male traits when choosing from a pool of potential mates (Dakin and Montgomerie 2013). In all cases, the directions of the effects we documented here indicate that females in better condition spend more time visiting the most attractive males (Figures 1 and 2), where attractiveness is quantified by the plumage color traits associated with peacock mating success across multiple populations (Loyau et al. 2007; Dakin and Montgomerie 2013). We also show that natural variation in condition explains a high proportion (>50%) of the variance in female preference in our study population (Table 1).

Of the 3 condition metrics used here, mass condition had the greatest influence on female mate assessment behavior (Table 1). One possible explanation for this is that females with greater mass condition have more energy to invest in lek visits. In support of this notion, Dunn and Whittingham (2006) have shown in tree swallows (*Tachycineta bicolor*) that clipping a female's wings (which may reduce foraging efficiency; Nooker et al. 2005) can reduce the probability that the female will mate with distant extrapair males, suggesting that energetic costs may constrain female mate assessment and choice. However, in our study, an alternative possibility that we cannot rule out is that early developmental conditions influence both female mass condition and activity levels in adulthood (Woodgate et al. 2010). Further experimental study is needed to evaluate causes of variation in female condition, including the relative roles of genetic variation, age, nutrition, and early developmental conditions, as well as how these factors influence mate choice in this and other species.

There are several possible mechanisms that could explain our results, and in particular the strong relations between female condition metrics and male color traits shown in Figures 1 and 2. Females in better condition may be more selective about which males they visit (Luttbeg et al. 2001; Hingle et al. 2001a, 2001b; Hunt et al. 2005). It is also possible that condition-dependent

variation in female sensory physiology, color perception, or cognition might drive differences in how females respond to male color traits (Ronald et al. 2012; Buchanan et al. 2013). Another hypothesis—that is not mutually exclusive—is that females in better condition may be better able to tolerate unwanted copulation attempts, or may be better able to tolerate aggressive interactions with other females (which occur more often near the most successful males; Petrie et al. 1992). Dominant females in the best condition may also limit other females' access to males directly via aggressive interactions. In other polygynous bird species, females have been shown to aggressively limit other females' access to preferred males or breeding sites (e.g., Kempenaers 1994; Sandell 1998; Bro-Jørgensen 2002), although this does not appear to be the case in black grouse (Karvonen et al. 2000), another lek-mating species where larger females visit a greater number of males (Rintamäki et al. 1995).

Alternatively, females in poor condition may actually prefer males with low *theta*- and high *phi*-iridescence; that is, they may prefer traits that are not preferred by most other females, and that are associated with reduced male mating success (Dakin and Montgomerie 2013). This type of preference reversal has been found in previous studies of sticklebacks (Bakker et al. 1999) and zebra finches (Holbeck and Riebel 2010). With our observational study, we cannot determine whether females in poor condition actually have reversed preferences, whether they are less selective, or whether they are less able to act on their preferences. Further study is needed to test this in peafowl and in other birds, where there is evidence that females in poor condition may be less responsive to male displays (Woodgate et al. 2010; Lerch et al. 2013) or have altered preferences (Holbeck and Riebel 2010).

Ever since Fisher (1930), the assumption in models of sexual selection has been that females would choose the best-quality male among those available, given the constraints of time and circumstance. Such adaptive female choice eventually erodes variation in both male quality and sexually selected signals (Borgia 1979; see Tomkins et al. 2004 for a review). More recently, behavioral ecologists have come to appreciate that there may be extensive variation in female choice due to mate choice copying (Dugatkin and Godin 1992), variation in mating opportunities (Noë and Hammerstein 1994), genetic compatibilities (Tregenza and Wedell 2000), or fluctuating environmental conditions (e.g., Chaine and Lyon 2008; Cornwallis and Uller 2010). If female health and condition also influence mate choice, then this variation in choice behavior could be another factor that maintains variation in both male quality and sexually selected traits (Tomlinson and O'Donald 1996; Jennions and Petrie 1997; Cotton et al. 2006). We showed here that peahens in the best condition allocate more of their visits to males with color traits that are also strongly related to male mating success (Dakin and Montgomerie 2013). Thus, our results link natural variation in female condition to mate assessment of a pool of courting males. Moreover, the strength of the effects we document suggests that condition-dependent mate choice may have a considerable impact on the outcome of sexual selection. It would be interesting to examine the effect of condition-dependent mate choice on the long-term outcome of sexual selection in this and other systems.

## SUPPLEMENTARY MATERIAL

Supplementary material can be found at <http://www.beheco.oxfordjournals.org/>

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## REFERENCES

- Arnold TW. 2010. Uninformative parameters and model selection using Akaike's information criterion. *J Wildl Manage.* 74:1175–1178.
- Bakker TCM, Künzler R, Mazzi D. 1999. Condition-related mate choice in sticklebacks. *Nature.* 401:234.
- Bell A. 2010. L.A. then and now: peacocks are one of Arcadia founder's legacies. *Los Angeles Times.* 2010 May 7, p. A38.
- Booth DT, Clayton DH, Block BA. 1993. Experimental demonstration of the energetic cost of parasitism in free-ranging hosts. *Proc R Soc Lond B.* 253:125–129.
- Borgia G. 1979. Sexual selection and the evolution of mating systems. In: Blum MS, Blum NA, editors. *Sexual selection and reproductive competition in the insects.* New York: Academic Press. p. 19–80.
- Bro-Jørgensen J. 2002. Overt female mate competition and preference for central males in a lekking antelope. *Proc Natl Acad Sci USA.* 99:9290–9293.
- Buchanan KL, Grindstaff JL, Pravosudov VV. 2013. Condition dependence, developmental plasticity, and cognition: implications for ecology and evolution. *Trends Ecol Evol.* 28:290–296.
- Burnham KP, Anderson DR, Huyvaert KP. 2011. AIC model selection and multimodel inference in behavioral ecology: some background, observations, and comparisons. *Behav Ecol Sociobiol.* 65:23–35.
- Byers JA, Byers AA, Dunn SJ. 2006. A dry summer diminishes mate search effort by pronghorn females: evidence for a significant cost of mate search. *Ethology.* 112:74–80.
- Campbell TW. 1995. *Avian hematology and cytology.* Ames (IA): Iowa State University Press.
- Chaine AS, Lyon BE. 2008. Adaptive plasticity in female mate choice dampens sexual selection on male ornaments in the lark bunting. *Science.* 319:459–462.
- Choudhury S, Black JM. 1993. Mate-selection behaviour and sampling strategies in geese. *Anim Behav.* 46:747–757.
- Cornwallis CK, Uller T. 2010. Towards an evolutionary ecology of sexual traits. *Trends Ecol Evol.* 25:145–152.
- Cotton S, Small J, Pomiankowski A. 2006. Sexual selection and condition-dependent mate preferences. *Curr Biol.* 16:R755–R765.
- Cox DR, Snell EJ. 1989. *Analysis of binary data.* 2nd ed. New York: CRC Press.
- Dakin R, Montgomerie R. 2009. Peacocks orient their courtship displays towards the sun. *Behav Ecol Sociobiol.* 63:825–834.
- Dakin R, Montgomerie R. 2013. Eye for an eyespot: how iridescent plumage ocelli influence peacock mating success. *Behav Ecol.* 24:1048–1057.
- Dakin R. 2011. The crest of the peafowl: a sexually dimorphic plumage ornament signals condition in both males and females. *J Avian Biol.* 42:405–414.
- Dugatkin LA, Godin JG. 1992. Reversal of female mate choice by copying in the guppy (*Poecilia reticulata*). *Proc Biol Sci.* 249:179–184.
- Dunn PO, Whittingham LA. 2006. Search costs influence the spatial distribution, but not the level, of extra-pair mating in tree swallows. *Behav Ecol Sociobiol.* 61:449–454.
- Fisher RA. 1930. *The genetical theory of natural selection.* Oxford (UK): Clarendon Press.
- Gray DA. 1999. Intrinsic factors affecting female choice in house crickets: time cost, female age, nutritional condition, body size, and size-relative reproductive investment. *J Insect Behav.* 12:691–700.
- Harikrishnan S, Vasudevan K, Sivakumar K. 2010. Behavior of Indian peafowl *Pavo cristatus* Linn. 1758 during the mating period in a natural population. *Open Ornithol J.* 3:13–19.
- Hart NS. 2002. Vision in the peafowl (*Aves: Pavo cristatus*). *J Exp Biol.* 205:3925–3935.

- Hill GE. 2011. Condition-dependent traits as signals of the functionality of vital cellular processes. *Ecol Lett.* 14:625–634.
- Hillgarth N. 1984. Social organization of wild peafowl in India. *World Pheasant Assoc J.* 9:47–56.
- Hingle A, Fowler K, Pomiankowski A. 2001a. Size-dependent mate preference in the stalk-eyed fly *Cyrtodiopsis dalmanni*. *Anim Behav.* 61:589–595.
- Hingle A, Fowler K, Pomiankowski A. 2001b. The effect of transient food stress on female mate preference in the stalk-eyed fly *Cyrtodiopsis dalmanni*. *Proc Biol Sci.* 268:1239–1244.
- Holveck MJ, Riebel K. 2010. Low-quality females prefer low-quality males when choosing a mate. *Proc Biol Sci.* 277:153–160.
- Hunt J, Brooks R, Jennions MD. 2005. Female mate choice as a condition-dependent life-history trait. *Am Nat.* 166:79–92.
- Jennions MD, Petrie M. 1997. Variation in mate choice and mating preferences: a review of causes and consequences. *Biol Rev Camb Philos Soc.* 72:283–327.
- Karvonen E, Rintamäki PT, Alatalo RV. 2000. Female-female aggression and female mate choice on black grouse leks. *Anim Behav.* 59:981–987.
- Kasumovic MM, Bruce MJ, Herberstein ME, Andrade MCB. 2007. Risky mate search and mate preference in the golden orb-web spider (*Nephila plumipes*). *Behav Ecol.* 18:189–195.
- Kempnaers B. 1994. Polygyny in the blue tit: unbalanced sex ratio and female aggression restrict mate choice. *Anim Behav.* 47:943–957.
- Lerch A, Rat-Fischer L, Nagle L. 2013. Condition-dependent choosiness for highly attractive songs in female canaries. *Ethology.* 119:58–65.
- Loyau A, Gomez D, Moureau B, Théry M, Hart NS, Saint Jalme M, Bennett ATD, Sorci G. 2007. Iridescent structurally based coloration of eyespots correlates with mating success in the peacock. *Behav Ecol.* 18:1123–1131.
- Loyau A, Saint Jalme M, Cagniant C, Sorci G. 2005. Multiple sexual advertisements honestly reflect health status in peacocks (*Pavo cristatus*). *Behav Ecol Sociobiol.* 58:552–557.
- Luttbegg B, Towner MC, Wandesforde-Smith A, Mangel M, Foster SA. 2001. State-dependent mate-assessment and mate-selection behavior in female threespine sticklebacks (*Gasterosteus aculeatus*, Gasterosteiformes: Gasterosteidae). *Ethology.* 107:545–558.
- Møller AP, Petrie M. 2002. Condition dependence, multiple sexual signals, and immunocompetence in peacocks. *Behav Ecol.* 13:248–253.
- Noë R, Hammerstein P. 1994. Biological markets: supply and demand determine the effect of partner choice in cooperation, mutualism and mating. *Behav Ecol Sociobiol.* 35:1–11.
- Nooker JK, Dunn PO, Whittingham LA. 2005. Effects of food abundance, weather, and female condition on reproduction in tree swallows (*Tachycineta bicolor*). *The Auk.* 122:1225–1238.
- Ots I, Murumägi A, Hõrak P. 1998. Haematological health state indices of reproducing great tits: methodology and sources of natural variation. *Funct Ecol.* 12:700–707.
- Peig J, Green A. 2009. New perspectives for estimating body condition from mass/length data: the scaled mass index as an alternative method. *Oikos.* 118:1883–1891.
- Petrie M, Hall M, Halliday T, Budgey H, Pierpoint C. 1992. Multiple mating in a lekking bird: why do peahens mate with more than one male and with the same male more than once? *Behav Ecol Sociobiol.* 31:349–358.
- Petrie M, Halliday T, Sanders C. 1991. Peahens prefer peacocks with elaborate trains. *Anim Behav.* 41:323–331.
- R Development Core Team. 2013. R: a language and environment for statistical computing R version 3.0.1. Vienna (Austria): R Foundation for Statistical Computing [cited 2013 June 22]. Available from: <http://www.R-project.org>.
- Rintamäki PT, Alatalo RV, Höglund J, Lundberg A. 1995. Mate sampling behaviour of black grouse females (*Tetrao tetrix*). *Behav Ecol Sociobiol.* 37:209–215.
- Ronald KL, Fernandez-Juricic E, Lucas JR. 2012. Taking the sensory approach: how individual differences in sensory perception can influence mate choice. *Anim Behav.* 84:1283–1294.
- Ros AFH, Correia M, Wingfield JC, Oliveira RF. 2009. Mounting an immune response correlates with decreased androgen levels in male peafowl, *Pavo cristatus*. *J Ethol.* 27:209–214.
- Sandell MI. 1998. Female aggression and the maintenance of monogamy: female behaviour predicts male mating status in European starlings. *Proc. R. Soc. Lond. B.* 265:1307–1311.
- Stoddard MC, Prum RO. 2008. Evolution of avian plumage color in a tetrahedral color space: a phylogenetic analysis of new world buntings. *Am Nat.* 171:755–776.
- Symonds MRE, Moussalli A. 2011. A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike's information criterion. *Behav Ecol Sociobiol.* 65:13–21.
- Syriatowicz A, Brooks R. 2004. Sexual responsiveness is condition-dependent in female guppies, but preference functions are not. *BMC Ecol.* 4:5.
- Tomkins JL, Radwan J, Kotiaho JS, Tregenza T. 2004. Genic capture and resolving the lek paradox. *Trends Ecol Evol.* 19:323–328.
- Tomlinson IPM, O'Donald P. 1996. The influence of female viability differences on the evolution of mate choice. *Heredity.* 77:303–312.
- Tregenza T, Wedell N. 2000. Genetic compatibility, mate choice and patterns of parentage: invited review. *Mol Ecol.* 9:1013–1027.
- Uy JA, Patricelli GL, Borgia G. 2001. Complex mate searching in the satin bowerbird *Ptilonorhynchus violaceus*. *Am Nat.* 158:530–542.
- Whittingham MJ, Stephens PA, Bradbury RB, Freckleton RP. 2006. Why do we still use stepwise modelling in ecology and behaviour? *J Anim Ecol.* 75:1182–1189.
- Wilgers DJ, Hebets EA. 2012. Age-related female mating decisions are condition dependent in wolf spiders. *Behav Ecol Sociobiol.* 66:29–38.
- Woodgate JL, Bennett ATD, Leitner S, Catchpole CK, Buchanan KL. 2010. Developmental stress and female mate choice behaviour in the zebra finch. *Anim Behav.* 79:1381–1390.