

Improved growth and survival of offspring of peacocks with more elaborate trains

Marion Petrie

Department of Zoology, University of Oxford, South Parks Road, Oxford OX1 3PS, UK

THERE is considerable controversy about what females gain from mate choice in a lekking species in which males provide no obvious resources. Females may gain direct benefits such as safe copulations or increased fertility by mating with particular males, or they may gain indirect benefits for their offspring¹⁻³. It is difficult to look for paternal effects on offspring performance because it is hard to control for any differences in the material and genetic contribution provided by the female and in the environment of the offspring during development; previous experiments have controlled for rearing environment but not maternal effects⁴. Here I report results from a controlled breeding experiment, with females allocated to males at random and all offspring reared under the same conditions, which show that the offspring of successful lek peacocks (*Pavo cristatus*) with the most elaborate trains grow and survive better under nearly natural conditions.

Observation at Whipsnade Park, UK, revealed that peahens show mate preferences in that they always reject some potential males as mates and mate with the male that has the most elaborate train⁵. The degree of train elaboration, measured as the total number of eye-spots visible in photographs, is a predictor of a male's mating success^{5,6}. Moreover, experimental reduction of the number of eye-spots in the train between years results in a decline in mating success for individuals⁶. This is evidence that females base their preference on some aspect of train morphology, although these data do not distinguish which of several possible attributes of the train females prefer, such as the overall symmetry of eye-spots in the train or the total area of eye-spots. To understand why a female preference for elaborate trains is maintained in this population, I looked to see whether there were any paternal effects on the growth of offspring. I removed males of known status from Whipsnade, and kept them in separate pens before assigning four breeding females randomly to each pen. The resulting offspring were reared under the same conditions and their growth monitored at regular intervals (Fig. 1).

The design of the experiment was to ensure that the main difference between the pens was the attractiveness of the males, but it is possible that during the random assignment of females chance differences were created between pens in the mean size of the females and this may subsequently contribute to any differences found between pens in offspring size. However, there were no significant differences between pens in any of the measured variables taken on females (ANOVA analysis of variance: body weight $F(7, 24)=0.32$, $P=0.94$; tarsus length $F(7, 24)=0.59$, $P=0.7$; condition (weight/tarsus; ref. 3) $F(7, 24)=0.57$, $P=0.77$; spur length $F(7, 24)=0.98$, $P=0.47$. Spur length of females increases with female age (M.P., unpublished results).

An analysis of variance was carried out on the size of the offspring at day 84 to see whether there was a significant effect of paternity on offspring growth. The potential confounding influences of hatch date and egg weight were removed by entering them as covariates in the analysis. There were significant differences between fathers in offspring weight, controlling for any differences due to hatch date or egg weight (main effect, father, $F(7, 324)=6.57$, $P<0.0001$; covariates: (1) hatch date, $F(1, 324)=124.73$, $P<0.0001$; (2) egg weight, $F(1, 324)=0.051$, $P>0.8$). Treating the offspring sexes separately, there were sig-

nificant differences between fathers in the growth of sons and daughters (daughters: main effect, father, $F(7, 165)=3.59$, $P<0.001$; covariates: (1) hatch date, $F(1, 165)=62.11$, $P<0.001$; (3) egg weight, $F(1, 165)=1.12$, $P>0.2$. Sons: main effect, father, $F(7, 146)=2.71$, $P<0.01$; covariates: (1) hatch date, $F(1, 146)=69.39$, $P<0.001$; (2) egg weight, $F(1, 146)=0.1$, $P>0.7$).

A multiple regression analysis was carried out to see whether growth differences between offspring were dependent upon any of the measured morphological variables of the father. A preliminary analysis of the data revealed that three variables were positively and independently correlated with the size of offspring at day 84. These were, father's tarsus length, father's train length and the size of the eye-spots in the father's train. These variables were entered into the multiple regression together with the hatch date which has a strong effect on offspring growth (later-hatched chicks being smaller than earlier-hatched chicks) and egg weight

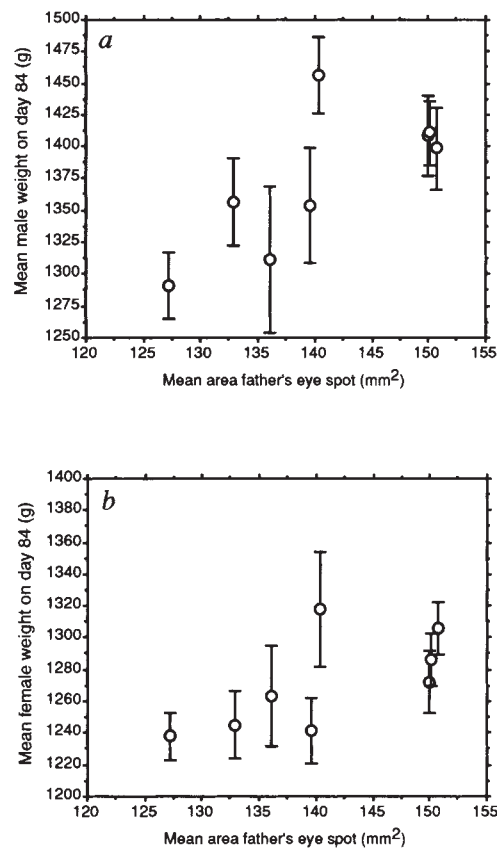


FIG. 1 The relationship between the mean weight (\pm standard errors) of offspring at day 84 and the size of the eye-spots in their father's train. *a*, This relationship for sons ($n=8$, $r=0.74$, $P=0.035$), and *b*, daughters ($n=8$, $r=0.66$, $P=0.077$) (all variables were log-transformed for calculation of regression statistics). Eight free-ranging full-trained displaying lek males whose mating success varied were removed from Whipsnade Park during February 1991 and transferred to a farm in Norfolk, UK. The peacocks were housed in separate pens and 4 naive adult peahens, known to be at least 2 years old, were measured and randomly assigned to each pen on 14 March. Pens were checked every day for eggs (eggs could not be assigned to a hen unless egg-laying was witnessed), which were labelled and removed. Groups of eggs originating from several different pens were placed under broody domestic chickens for incubation. Eggs were removed from the hens after 26 days and placed in a hatcher, where each egg had its own compartment. Hatched chicks were given an individual colour ring combination and were reared together under standard conditions with heat lamps and food and water *ad libitum*. Females produced 519 eggs and the growth of the surviving 349 offspring was monitored. Chicks were weighed and measured on days 0, 7, 14, 28, 42, 56 and 84.

TABLE 1 Results from a multiple regression analysis with the size of offspring at day 84 as the dependent variable and five independent variables ($F(5, 319) = 28.49, P < 0.0001$)

Independent variable	β	T	Significance
Mean area of 20 eye-spots in father's train	0.16	3.41	0.0007
Egg weight	-0.025	-0.54	0.59
Hatch date	-0.52	-11.05	0.0001
Father's tarsus length	0.047	0.89	0.37
Length of father's train	0.094	1.74	0.084

Train measures were made on shed feathers. The fathers in the pens started to shed their upper tail coverts between July and August; all the shed feathers were collected for each male. Several measures were taken on the trains of each bird: the total number of feathers, the weight of the train, the length of the longest feather and the mean size of 20 eye-spots. The area of the blue centre of each eye-spot was measured using a digital pad. This multiple regression only includes those measures that were positively and independently correlated with offspring growth. β , Regression coefficient.

(a potentially confounding variable); results are shown in Table 1. Males with larger eye-spots in their trains tended to have larger offspring after controlling for the other four variables. Figure 1a and b shows the positive relationship between the mean size of offspring produced in each pen and the size of eye-spots in the father's train for sons and daughters respectively.

Although there were no differences in the mother's phenotype between pens, it is possible that females produced larger or better-quality eggs in response to being mated to males with more elaborate trains and that this could account for the differences in growth. But the weight of an egg does not predict the size of offspring at day 84 (Table 1) and is controlled for statistically in all analyses which show paternal effects on offspring growth. Although it is theoretically possible that some differential maternal provisioning of the eggs, independent of egg size,

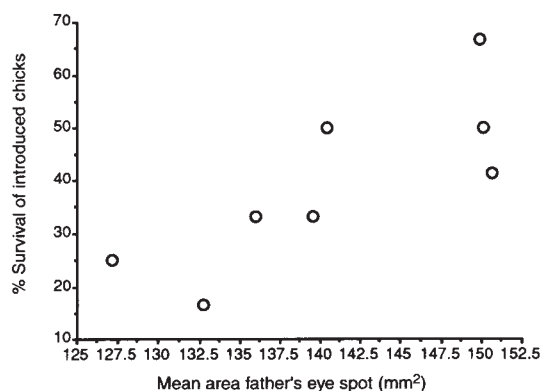


FIG. 2 The relationship between the proportion of offspring surviving introduction into Whipsnade Park and the size of eye-spots in their father's train ($n=8, r=0.79, P=0.018$). In January and February 1992, 12 offspring (7 males and 5 females) from each of the 8 males (3 from each of the 4 females per male) were introduced into Whipsnade Park. A matched sample of young were chosen from each pen so that there was no overall significant differences in hatching dates or weights (at day 84, $F(7, 95)=0.838, P=0.559$; at introduction $F(7, 95)=0.358, P=0.924$) of the offspring between fathers. Care was taken to release the offspring in batches of eight, consisting of one young of the same sex from each pen. There was a significant relationship between the proportion of sons surviving the introduction and the size of eye-spots in the father's train ($n=8, r=0.84, P=0.0094$) but not for the proportion of daughters surviving ($n=8, r=0.596, P=0.119$), but the sample of daughters for each male was small and there is a trend in the same direction.

could be responsible for larger trained males producing larger offspring, there is no evidence in any species⁷ that this sort of differential investment occurs. I tested to see whether there were any measurable differences in the quality of eggs laid for the different fathers in the following breeding season by measuring the lipid and protein content of two eggs laid by two different females for each male and found no significant differences between fathers in any of the measured variables (per cent lipid in yolk ($n=16$), mean was 64.73 ± 1.22 s.d., ANOVA $F(7, 15) = 0.85, P=0.57$; per cent protein in albumen, mean was 82.18 ± 1.842 s.d., ANOVA $F(7, 15)=0.33, P=0.92$; per cent protein in yolk, mean was 29.41 ± 0.62 s.d., ANOVA $F(7, 15) = 1.28, P=0.36$).

I released a sample of the offspring reared at the farm into Whipsnade Park (see Fig. 2 for details). Of the offspring introduced, 41% were present after 24 months. Several cases of mortality were reported and the condition of the corpses suggested that these were caused by fox (*Vulpes vulpes*) predation; other missing birds were presumed dead. Birds that were larger at the time of introduction were more likely to have survived their first year at Whipsnade. The mean weight of males that were presumed dead was 3.34 kg (s.d.=0.27), whereas that of surviving males was 3.54 kg (s.d.=0.21), $t=-3.12, P<0.003$; for females, the mean weight of those presumed dead was 2.67 kg (s.d.=0.24) whereas the mean weight of survivors was 2.85 kg (s.d.=0.18), $t=-2.27, P<0.03$. there was a significant positive correlation between the weight of the birds at introduction and their weight at day 84 ($n=95, r=0.61, P<0.0001$). The proportion of birds surviving for each of the eight fathers was dependent upon their mean weight at day 84 ($n=8, r=0.73, P=0.042$) and upon the size of the eye-spots in their father's trains (Fig. 2); however, multiple regression showed that neither of these factors significantly affected survivorship independently of the other (eye-spot size, partial $F=3.975, P=0.103$; mean weight, partial $F=1.96, P=0.22$).

The results show the offspring of highly ornamented males tend to grow better and that these advantages translate into differences in the chance of their subsequent survival under almost natural conditions. These data provide support for the idea that females may be gaining good 'viability' genes for their offspring when mating with attractive males and extend the previous evidence from lekking species which shows that preferred males are more likely to survive^{8,9}.

Norris⁴ has shown that male great tits (*Parus major*) with larger breast stripes, a trait preferred by females, produce more surviving sons. Cross-fostering experiments were used to control for differences in rearing conditions, but not for the possibility that higher quality females mate with preferred males; assortative mating of this sort has been shown to occur¹⁰. In this study random allocation of several females to each male controls for maternal effects on offspring performance. Although the evidence suggests that females may gain indirect benefits in the form of viability advantages, it does not exclude the possibility that females may also be gaining other advantages from their choice. □

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