The Royal Society

# Fisherian flies: benefits of female choice in a lekking sandfly

**T. M. Jones**[1,2], **R. J. Quinnell**[2]† **and Andrew Balmford**[3*]

[1]*Institute of Zoology, Zoological Society of London, Regent's Park, London NW1 4RY, UK*
[2]*Department of Medical Parasitology, London School of Hygiene and Tropical Medicine, Keppel Street, London WC1E 7HT, UK*
[3]*Department of Animal & Plant Sciences, University of Sheffield, Sheffield S10 2TN, UK*

We experimentally investigated the fitness consequences of female mate choice in order to test the relative importance of three competing but non-exclusive hypotheses for the maintenance of pronounced female mating preferences on leks: that females benefit directly; that they gain indirect Fisherian benefits by producing more attractive sons; or that they benefit indirectly because preferred males possess 'good genes' that confer increased viability on their sons and daughters. We allowed lekking female sandflies, *Lutzomyia longipalpis*, to choose between males of varying attractiveness to females, and monitored the consequences for their own survival and reproductive success as well as for their offspring. In contrast to the predictions of the direct-benefits model, we found no clear sire effect on the fecundity or survival of the females themselves; females mating with more attractive males did survive longer after oviposition, but never long enough to undertake a second batch of egg laying. We also found no evidence that females gained good-genes benefits in terms of enhanced offspring survival. However, we did find that generally attractive males fathered sons who were then chosen when they in turn formed leks. Although not completely precluding other benefits, our results indicate that Fisherian benefits are at least partly responsible for maintaining female choice at *L. longipalpis* leks. These findings indicate the importance of testing all putative benefits concurrently in exploring the maintenance of female mate choice.

**Keywords:** female choice; Fisherian benefits; good genes; direct benefits; lekking; lek paradox

## 1. INTRODUCTION

Why mate choice is most pronounced on leks—arenas where displaying males apparently offer discriminating females nothing but sperm—remains one of evolutionary biology's most enduring puzzles (Darwin 1871; Kirkpatrick & Ryan 1991; Andersson 1994). Three non-exclusive explanations suggest choice could increase female fitness directly (by helping females avoid males with low fertility or sexually transmitted diseases, for instance), or indirectly, either because male attractiveness is itself heritable (so choosy females produce attractive sons—the Fisherian process (Fisher 1930)) or because it signals heritable viability (so females acquire good genes for both their sons and daughters (Reynolds & Gross 1990; Kirkpatrick & Ryan 1991; Andersson 1994)).

There is now growing evidence for both direct and indirect benefits of mate choice in various lekking and non-lekking species (table 1). However, demonstrating that a particular benefit exists does not by itself mean that it plays the major role in maintaining female choice in a particular species. For example, if direct benefits are present, they are likely to have a much greater effect on female fitness than any indirect benefits (Price 1993; Kirkpatrick & Barton 1997). Thus evidence that indirect benefits underpin female choice would be most convincing if coupled with evidence of a lack of direct benefits. Moreover, discriminating between indirect-benefit models is potentially confounded by the fact that both Fisherian and good-genes models can accommodate heritability of male attractiveness (Balmford & Read 1991). In the former, it drives the initial evolution of the female preference (although it may not even be detectable nowadays (Grafen 1990)); in the latter, it can arise from a correlation between attractiveness and viability. Thus evidence for a Fisher effect is unambiguous only if coupled with the demonstration that good-genes benefits are weak or unimportant. Similarly, because (like good-genes models) Fisherian models predict that preferred traits will become costly and only expressed by high-quality males, then provided viability is heritable, choosy females might nowadays acquire good genes even if their preferences arose initially (and are largely maintained) by a Fisherian benefit (Balmford & Read 1991). These considerations mean that studies can best provide support for either indirect model if all three possible models are tested simultaneously, direct benefits are absent (or very limited), and one indirect benefit is relatively strong and the other weak or absent (for similar arguments, see Iwasa *et al.* 1991; Kirkpatrick & Ryan 1991; Andersson 1994). So far few studies have achieved this (but see Moore 1994; Whittier & Kaneshiro 1995).

Here we present the results of an experiment that attempts to test all three models simultaneously in a

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[*] Author for correspondence (`a.balmford@sheffield.ac.uk`).

† Present address: School of Biology, University of Leeds, Leeds LS2 9JT, UK.

*Received* 20 March 1998 *Accepted* 18 May 1998

Table 1. *Some tests of proposed benefits of female mate choice in lekking and other species*

(Most studies have looked for one benefit only, with most explicit tests of indirect models focusing solely on good-genes effects.)

| hypothesized benefit: | females with attractive mates predicted (Kirkpatrick & Ryan 1991) to have: | positive evidence from: | |
|---|---|---|---|
| | | lekking species | other species |
| direct | higher survival or fecundity | Borgia & Collis (1989); Robertson (1990); Bourne (1993); Able (1996) | many studies: see Johnstone (1995) |
| indirect: Fisherian | more attractive sons | no direct tests, but evidence of heritability of attractive traits: | |
| | | Wilkinson & Reillo (1994); Whittier & Kaneshiro (1995) | reviewed by Andersson (1994) and Pomiankowski & Møller (1995) |
| indirect: good genes | more viable sons and daughters | Petrie (1994) | Partridge (1980); Simmons (1987); Taylor *et al.* (1987); von Schantz *et al.* (1989); Møller (1990); Reynolds & Gross (1992); Norris (1993); Gilburn & Day (1994); Moore (1994); Hasselquist *et al.* (1996); Sheldon *et al.* (1997); Welch *et al.* (1998) |

lekking sandfly, *Lutzomyia longipalpis* (Diptera: Psychodidae). Phlebotomine sandflies of the *L. longipalpis* species complex form leks (Bradbury 1981) on or near their vertebrate hosts (Jones 1997); in the laboratory, these can be replicated (with or without a host) in small net cages (Jarvis & Rutledge 1992; Jones 1997). *L. longipalpis* leks are relatively mobile in space. Males exhibit territorial behaviour, defending areas approximately 2 cm in radius (Jones 1997). Male mating success within leks is highly skewed and largely determined by female choice (Jones 1997): females typically sample several males before mating with just one, and can readily terminate courtship by depressing their abdomens or moving away. Female choice is correlated with male production of a pheromone, which is thought to be dispersed by a wing-fanning display (Jones & Hamilton 1998). Females are haematophagous, requiring a bloodmeal for egg development. This process takes approximately three days, after which females lay a single batch of 40–60 eggs. Neither sex contributes to parental care.

Our experiment explored the consequences of a female's choice of mate in terms of her own fitness and that of her offspring. Females were permitted to mate freely in aggregations of five males that differed in their attractiveness to females, where attractiveness is defined as the number of females a male successfully mates with. We then tested the proposed benefits associated with each model (as summarized in table 1) by examining how the survival and reproductive success of the females and their offspring compared with the general attractiveness of their mate and their father, respectively.

## 2. METHODS

Experimental flies were obtained from a 22-generation captive colony originating from the Salvaterra district of Marajó, Brazil, and reared using standard culturing techniques at the Instituto Evandro Chagas, Belém (Killick-Kendrick *et al.* 1977; Jones 1997). Adults were maintained in small cages (15 cm × 15 cm × 15 cm) and provided with cotton wool swabs soaked in 30% sugar solution. Larvae were reared in Petri dishes (diameter 10 cm, height 1.5 cm) on a diet of dried liver powder. The population was maintained at *ca.* 500 adults by regulating the numbers of females feeding in each generation. Virgin flies were obtained by releasing adults into single-sex cages less than 12 h after emergence (Chaniotis 1967). Females were blood-fed on an anaesthetized host three days after emergence (Jones 1997, after Flecknell 1987).

Our experiment began with 25 trials in which we sequentially exposed ten virgin, blood-fed, 4-day-old females to caged leks consisting of five individually marked, 4–6-day-old males. Marking was achieved using fluorescent powders that have no detectable impact on a male's mating success or immediate survival (Jones 1997). Females were introduced singly, allowed to mate once, and then removed. The distribution of matings was highly overdispersed, with females exhibiting consistent preferences for particular mates (frequency distribution of males with 0, 1, 2, 3, 4 or >4 matings, compared with Poisson: $\chi^2_5=106.2$, $p<0.001$). Next, to augment the number of females that chose generally unattractive mates, we regrouped those males ($N=30$) that obtained the fewest matings (usually zero) in the first trials into six new five-male leks. Ten further virgin females were introduced singly to each of these new leks. The females again mated non-randomly ($\chi^2_5=12.6$, $p<0.05$). Conditions were thus similar in both sets of trials and all experimental females experienced mate choice.

To test the three hypothesized benefits of mate choice at leks (table 1), we maintained those experimental females that survived to oviposition, and compared measures of their fitness and that of their offspring with the overall attractiveness of the males that they chose (defined as the number of matings they achieved in the first round of trials). To avoid possible effects of sperm depletion, we excluded any females not among the first four mates of a given male (although this is in fact conservative, as male fertility declines only after six consecutive matings (Jones 1997; see also later)). After these exclusions, our sample consisted of 186 females.

### (a) *Direct benefits*

To test for potential direct benefits of mate choice, females were individually placed in small, glass, oviposition tubes at the same densities as those used in standard culturing (Jones 1997). They were then observed daily, and records taken of the time to oviposition, the number of eggs laid, and the time to death. A female's total survival was compared to the mating success of her mate in a generalized linear model with a fitted Weibull distribution, to allow for age-dependent survival (Pinder *et al.* 1978). The significance of each parameter was checked by stepwise deletion, adding significant terms (at $p<0.05$) back into the model before removing the next parameter (after Crawley 1993). More detailed measures of survival (between mating and oviposition, and survival from the start of oviposition) were compared to male mating success using parametric correlations, because the low numbers of days survived did not permit formal survival analysis. Likewise, variation in the numbers of eggs laid was analysed by correlation. In all cases, male attractiveness was set as the independent variable.

### (b) *Good-genes benefits*

Because of a lack of genetic markers for *L. longipalpis*, we were unable to assess offspring survival with trials using standardized, unrelated competitors (Partridge 1980; Taylor *et al.* 1987). We thus used a more conservative method to test whether females gained good-genes benefits from mate choice (see also Simmons 1987; Norris 1993; Moore 1994). We transferred their eggs to Petri dishes and compared the subsequent survival of families with paternal attractiveness. Eggs and larvae were monitored daily to record the numbers surviving to successive instars. Offspring of different females were kept separate until adulthood, so that we could compare their survival with the precise mating success of their fathers. To achieve this while still matching egg and larval densities to those seen in standard culturing, we switched to using smaller Petri dishes (diameter 5 cm, height 1.0 cm). Under these conditions, mean survival of our experimental progeny was comparable to that recorded for the parent colony (*t*-tests across the six developmental stages from egg to adult emergence: all n.s.). The proportion of larvae surviving each successive instar was calculated. Where data could be transformed to normality, these proportions were compared to paternal mating success using parametric correlations. Where transformation to normality was not possible, nonparametric correlation tests were done. As with tests for direct benefits, male mating success was set as the independent variable for all comparisons.

After adult emergence, we selected two sons and two daughters each from those females whose mates had achieved the highest, median or lowest number of matings in the first round of trials (means (±s.d.) of 4.9 (±0.2), 2.0 (±0.1) and 0.1 (±0) matings respectively, for high, average and low attractiveness sires). Offspring of males that could not be unambiguously assigned to one of these three categories were discarded. The culture conditions applied to all these adult offspring were the same as those experienced by their parents. One set of sons and one set of daughters were monitored daily to investigate survival of non-reproducing offspring. The second set of daughters was blood-fed at three days and allowed to oviposit, in order to test for possible sire effects on daughter fecundity; the final set of sons was used to look for Fisherian benefits (see below). The survival of all adult offspring and the fecundity of fed daughters were analysed in the same way as for their mothers. Because paternal identity was no longer known, the measures we obtained on offspring viability as adults were compared not with paternal attractiveness *per se*, but rather with the group to which their father belonged, which was entered as a categorical variable with three levels.

### (c) *Fisherian benefits*

We tested for Fisherian benefits by using the last set of sons to establish 38 three-male leks, each consisting of one son of a male of high, average and low attractiveness. Six fresh virgin females were introduced singly to each lek and allowed to mate; the resulting skew in mating success and female choice matched that seen in five-male leks (Jones 1997). The attractiveness of sons was assessed in the same way as that of their fathers. The proportion of matings obtained by a son was then analysed in a general linear model with a binomial error distribution, and with paternal group again as a categorical variable with three levels.

## 3. RESULTS

If females visiting leks gain direct fitness benefits from mate choice, those mating with generally attractive males should exhibit higher survival or fecundity than other females (Kirkpatrick & Ryan 1991). Our results suggest that this is not the case (for a detailed statistical breakdown, see table 2). There was no link between the total survival of females, or the time between mating and oviposition, and the mating success of their mates. We did find a difference in survival after oviposition: females mating with the most attractive males survived an average of one day longer than those that chose the least attractive males. However, as no females survived to undertake a second gonotrophic cycle, the biological significance of this result is unclear. There was also no evidence that females laid more eggs in response to choosing more attractive mates (table 2 and figure 1*a*), suggesting that there is no fecundity advantage to mate choice. These results were not biased by female mating order: the number of previous matings a female's chosen male had achieved did not influence her probability of survival ($\chi^2_1=0.38$, $N=186$, n.s.), or her fecundity ($r=0.10$, $N=186$, n.s.).

Although there was no evidence that females mating with generally attractive males increased their fitness directly, there was evidence of indirect benefits. When introduced to leks consisting of three sons, virgin females once again showed clear preferences for particular males ($\chi^2_3=12.7$, $p<0.01$). Moreover, in agreement with Fisherian models, the mating success of sons increased with the attractiveness of their fathers (significance of paternal group as a non-directional variable in general linear model: $F_{2,113}=6.55$, $p<0.02$; ordered heterogeneity test (Rice & Gaines 1994): $r_sP_c=0.96$, $p<0.01$; figure 1*b*). Specifically, sons of more attractive fathers obtained far more than one-third of all the matings in their trial (one-sample *t*-test on logistically transformed data: $t=2.93$, d.f. $=37$, $p<0.01$). Although these results provide important support for a Fisherian interpretation of female

Table 2. *Relationships between measures of female fitness and the attractiveness of chosen mates*

| fitness measure | mean[a] | statistic | $N$ | $p$ |
|---|---|---|---|---|
| total maternal survival (days)[b] | 9.7 | $\chi^2_1 = 3.82$ | 186 | n.s. |
| time between mating and oviposition (days) | 2.9 | $r = 0.12$ | 186 | n.s. |
| survival from start of oviposition (days) | 2.5 | $r = 0.22$ | 186 | 0.003[c] |
| eggs laid | 57.3 | $r = 0.10$ | 186 | n.s. |

[a] All means calculated from untransformed data.

[b] Total survival modelled by fitting a Weibull distribution (Pinder *et al.* 1978), after Crawley (1993).

[c] After correcting for multiple tests of the same hypothesis (Rice 1989), this value remained significant at $p < 0.05$.

preferences, they could conceivably have a good-genes explanation (with inherited high viability enabling sons of attractive males to invest heavily in preferred traits).

In an attempt to distinguish between these alternatives, we compared offspring survival to paternal attractiveness. We found no evidence that a female's mate choice influenced the viability of her offspring when sibs were reared in family groups (for a detailed breakdown, see table 3). Survival of offspring from egg hatch to adulthood (table 3 and figure 1*c*), survival across each developmental stage, and the number of adult offspring each female produced were all independent of paternal mating success. Likewise, the survival as adults of sons and both reproducing and non-reproducing daughters did not increase with sire attractiveness (table 3 and figure 1*d*). There was a weak trend for survival to decrease with sire mating success in the group of daughters that was allowed to reproduce, but after correction for multiple comparisons (Rice 1989) this pattern was non-significant. Finally, the fecundity of reproducing daughters was again unrelated to their mothers' choice of mate. These results appear to contradict key predictions of good-genes models.

## 4. DISCUSSION

In 1994, Malte Andersson wrote that 'no critical test has been performed that supports Fisherian sexual selection and excludes the alternatives, or estimates their relative importance' (Andersson 1994, p.52). Here, we have attempted to assess the relative importance of the three main models proposed for the maintenance of female choice at leks. We found that females mating with generally attractive males did not obtain any clear-cut direct benefits from their choice of mate. Similarly, we found no evidence to suggest that families of offspring sired by more attractive males exhibit higher viability, at any stage of development. However, we did find that sons of attractive fathers themselves obtained disproportionately more matings. The evidence presented thus shows that females gain indirect benefits from mating with particularly attractive males, and highlights a Fisherian mechanism as being at least in part responsible for the current maintenance of female mate choice in *L. longipalpis*.

Differential maternal investment (a potential problem elsewhere (Partridge 1980; Simmons 1987)) is unlikely to confound the observed correlation between the attractiveness of fathers and sons. Sandflies are highly fecund, so we would expect differences in reproductive effort to be mediated via variation in egg number rather than quality (Simmons 1987; Petrie 1994), yet we found no evidence that females laid more eggs for attractive mates. A more subtle maternal effect might arise because, although we allocated some females to groups of generally unattractive males, all our females chose their mates themselves (cf. Moore 1994; Petrie 1994). Fisherian models rely on linkage disequilibrium between genes coding for female preferences and for preferred traits. Thus maternally rather than (or as well as) paternally inherited genes might be responsible for the attractiveness of those sons whose mothers chose generally attractive mates. Nevertheless, it is hard to explain such a pattern of inheritance without invoking an underlying Fisherian mechanism. It would be worthwhile replicating this study using first-generation captive stock to rule out the possibility that the observed heritability of male attractiveness might be the result of the rapid evolution of trait and preference in the laboratory (Shelly *et al.* 1994).

A common criticism of laboratory-based studies of evolutionary questions is that an inability to detect variations in fitness may be a result of experimental conditions. Our tests of putative direct and good-genes benefits are potentially vulnerable to the same criticism. For example, most direct benefits accrued by choosy females should be reflected in increased survival or immediate fecundity. We found no evidence of this, but it is conceivable that the enhanced post-oviposition survival detected here might translate into a direct benefit if it appreciably increases the probability of free-ranging females entering a second gonotrophic cycle. Likewise, certain postulated direct benefits of mate choice (such as avoidance of predators or sexually transmitted diseases) could not be detected in our system. However, there is little empirical support for the predator- or disease-avoidance hypotheses in the current lekking literature (Höglund & Alatalo 1995).

Moving on to good-genes benefits, it could be argued that these do accrue to choosy female sandflies but were masked here by the 'welfare state' conditions of our experiment. However, genetic differences in offspring survival are frequently detected in laboratory experiments (Simmons 1987; Taylor *et al.* 1987; Reynolds & Gross 1992; Moore 1994), and importantly in this particular case, conditions were clearly not favourable enough to mask genetic differences in the attractiveness of sons. In addition, we are confident that, despite a large amount of within-group variation, our methodology was capable of detecting meaningful differences in offspring survival across treatment groups if these existed. Power analysis (Cohen 1988) shows that with our sample size and variation in survival, we had a 95% chance of detecting a correlation coefficient between offspring survival and mating success of as little as 0.26. To put this in context, the median $r$-value between measures of offspring survival and sire attractiveness reported by field studies claiming good-genes effects is 0.47 (von Schantz *et al.* 1989; Norris 1993; Petrie 1994; Hasselquist *et al.* 1996; Sheldon *et al.* 1997); the equivalent figure from the laboratory is 0.65 (Taylor *et al.* 1987; Reynolds & Gross

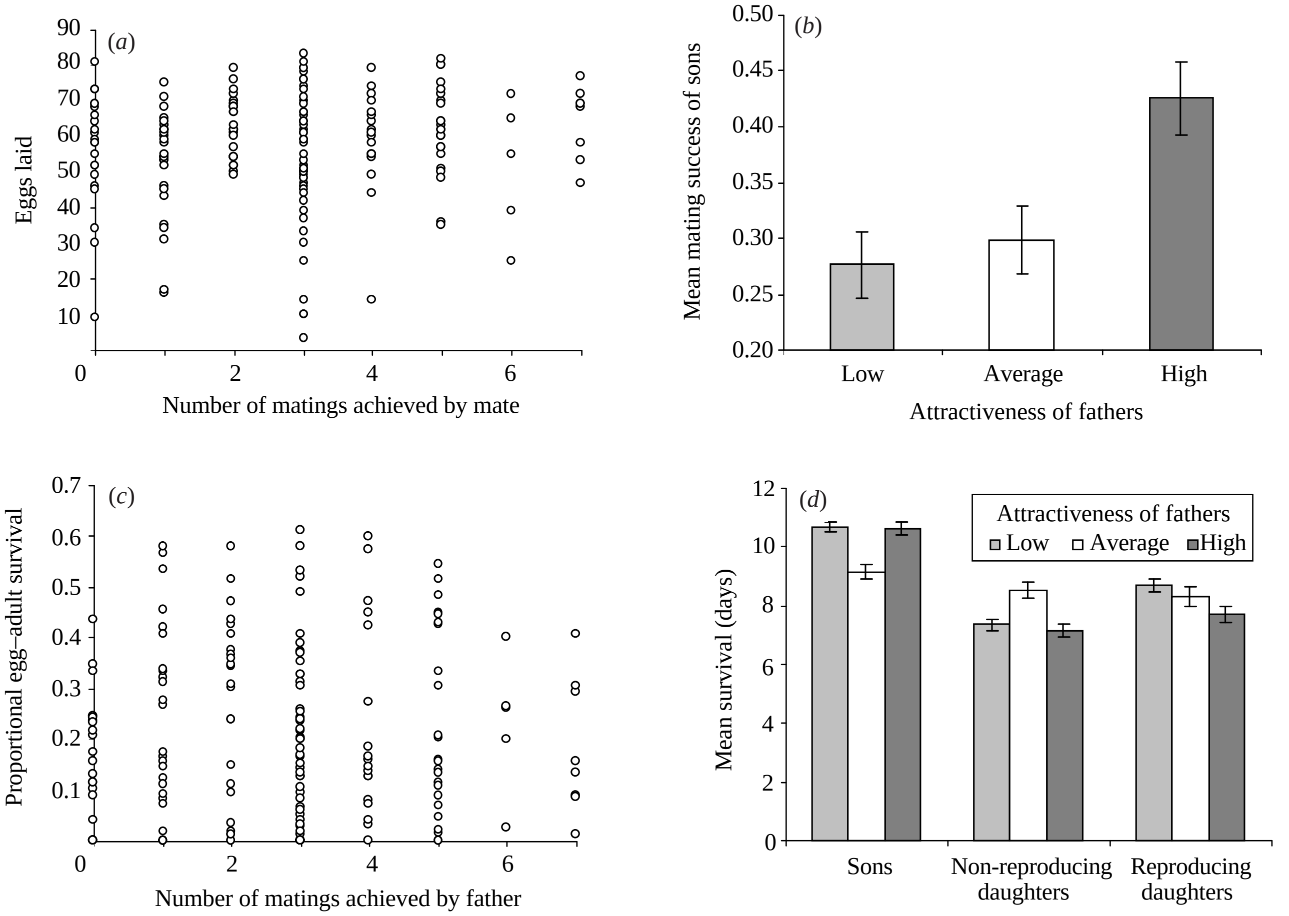

Figure 1. Tests of proposed benefits of mate choice at sandfly leks. (*a*) Number of eggs laid by females in relation to the attractiveness of the males they chose. (*b*) Proportion of matings (mean ±s.e., calculated using logistically transformed data) achieved by sons of males of low, average and high attractiveness, competing in three-male leks. (*c*) Proportional survival of offspring of females in relation to the mating success of their mates. (*d*) Survival as adults (mean ±s.e.) of non-reproducing sons and daughters and reproducing daughters sired by males of low, average and high attractiveness. Detailed statistical breakdowns are given in tables 2 and 3.

Table 3. *Relationships between measures of offspring fitness and the attractiveness of their fathers*

| fitness measure | mean[a] | statistic | *N*[c] | *P*[d] |
|---|---|---|---|---|
| proportional egg-to-adult survival | 0.22 | $r=0.02$ | 173 | n.s. |
| proportional survival as eggs | 0.69 | $r=0.10$ | 185 | n.s. |
| proportional survival as first-instar larvae | 0.66 | $r=-0.09$ | 173 | n.s. |
| proportional survival as second-instar larvae | 0.89 | $r=-0.06$ | 168 | n.s. |
| proportional survival as third-instar larvae | 0.89 | $r_s=-0.02$ | 167 | n.s. |
| proportional survival as fourth-instar larvae | 0.82 | $r_s=0.08$ | 165 | n.s. |
| proportional survival as pupae | 0.73 | $r_s=0.07$ | 161 | n.s. |
| number of adult offspring | 13.1 | $r_s=0.001$ | 173 | n.s. |
| survival of non-reproducing sons (days)[b] | 10.2 | $\chi^2_2=1.64$, $r_sP_c=-0.35$[e] | 114 | n.s. |
| survival of non-reproducing daughters (days)[b] | 7.7 | $\chi^2_2=2.74$, $r_sP_c=-0.37$[e] | 116 | n.s. |
| survival of reproducing daughters (days)[b] | 8.2 | $\chi^2_2=3.93$, $r_sP_c=-0.86$[e] | 68 | 0.047[d] |
| eggs laid by reproducing daughters | 46.1 | $F_{2,65}=0.65$ | 68 | n.s. |

[a] All means calculated from untransformed data.

[b] Survival modelled by fitting a Weibull distribution.

[c] Decreasing sample sizes are due to the death of all of a female's relevant offspring.

[d] After correcting for multiple tests of the same hypothesis (Rice 1989), no value remained significant at $p < 0.05$.

[e] Ordered heterogeneity test (Rice & Gaines 1994) after a non-directional $\chi^2$-test.

1992; Moore 1994). Thus good-genes effects in lekking *L. longipalpis* would have to be considerably weaker than those found in other species to have been missed by our experimental protocol.

A final consideration is that larvae in this study only had the opportunity to compete with full sibs. It is possible that competition within a family of low-quality individuals and within a family of high-quality individuals may yield similar mean survival rates, thereby obscuring true fitness differences: low-quality individuals may only survive when they have low-quality competition. However, several studies of other species have shown good-genes effects despite rearing young alongside their sibs (Simmons 1987; Norris 1993; Moore 1994). Moreover, laboratory studies of *L. longipalpis* suggest that eggs and larvae are likely to be aggregated in family groups in the field (Elnaiem & Ward 1992; Dougherty *et al*. 1993, 1994). Thus, even if rearing in family groups did mask some underlying differences in offspring competitive ability in our experiment, such differences might be equally masked (and unavailable to choosy females) in free-ranging populations.

In conclusion, we found evidence for Fisherian but no other detectable mate-choice benefits in *L. longipalpis*. We therefore suggest that heritability of male attractiveness is an important factor maintaining female mating preferences in this species (although this does not of course preclude the possibility that other adaptive or non-adaptive mechanisms were responsible for the origin of these preferences (Balmford & Read 1991)). Other studies, particularly those claiming good-genes effects, have often not even looked for Fisherian benefits, and we suggest that indirect fitness gains via increased attractiveness of sons may turn out to be more widespread than generally thought. We believe that future studies should no longer argue for the importance of particular mate-choice benefits unless they also test for alternatives. The approach adopted here, with concurrent tests of all the main postulated benefits (and with further modification of the protocol for assessing offspring viability, if possible using genetic markers) provides a robust way forward for studies into the maintenance of female mating preferences.

T.M.J. was funded by NERC (GT4/93/24/L) and the Central Research Fund (AR/CRF) of the University of London. We thank the Director, Jorge Travassos da Rosa, Jeffery Shaw and the Wellcome Trust for facilities at the Instituto Evandro Chagas, and José Itamar for technical support. We thank Steve Albon, Andrew Bourke, Tim Coulson, Chris Dye, Kevin Fowler, R. Killick-Kendrick, Richard Lane and Andrew Pomiankowski for advice, and Tim Birkhead, Nick Colegrave, Ben Hatchwell, Geoff Parker, Ben Sheldon and two anonymous referees for constructive comments on the manuscript.

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As this paper exceeds the maximum length normally permitted, the authors have agreed to contribute to production costs.