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Adaptive female choice for middle-aged mates in a lekking sandfly

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Most theoretical models of age-related mate choice predict that females should prefer older males because they have proven survival ability. An alternative view is that older males represent inferior mates because of negative genetic correlations between early and late fitness components, or because older males have traded off longevity against other fitness components, have accumulated deleterious germ-line mutations, or are less well adapted to current conditions than more recently born individuals. While numerous studies have reported female choice for older males, few have explicitly examined the fitness consequences of such a preference. We present evidence from a lekking sandfly, *Lutzomyia longipalpis*, showing that choosy females discriminate against older males and gain a fitness benefit from their choice. When permitted free choice from an aggregation consisting of males aged zero to two days (young), four to six days (middle-aged) and eight to ten days (old), females preferentially mated with middle-aged males, but all measures of female reproductive success were independent of male age. In contrast, when a second set of females was randomly assigned single virgin males of known age, the eggs of those paired to old mates exhibited lower hatching success than the eggs of females mated to young or middle-aged males. These results suggest that females avoid mating with older males because they represent poorer quality mates. Age-related differences in male quality may have a genetic basis, but could equally well arise through a phenotypic decline in sperm quality or sperm transfer ability with male age. The lack of evidence of female discrimination against older males from other studies may be because these did not explore the reproductive success of the full age range of males.

Keywords: female choice; lekking; male age; *Lutzomyia longipalpis*; male mating success

1. INTRODUCTION

A series of verbal models (Trivers 1972; Halliday 1978, 1983; Manning 1985), confirmed by a recent simulation (Kokko & Lindström 1996), predict that, given a choice, females should prefer older mates. As old males have proven survival ability, choosy females may gain indirect benefits from their choice of an old mate through the production of higher-quality offspring. Hence these 'viability indicator' models of age-related mate choice argue that females can use age as a reliable signal of heritable variation in male quality. This view has been challenged in a quantitative genetic model (Hansen & Price 1995), which emphasizes possible negative genetic correlations between early and late fitness components, or direct trade-offs between different fitness components (for examples, see Partridge & Farquhar 1981; Cordts & Partridge 1996). Consequently, long-lived individuals do not necessarily have higher overall fitness: a pattern which may be reinforced through the accumulation of germ-line mutations with age, or via ongoing selection on parents, which will result in young animals being born to parents whose current fitness is higher than that of the parents of earlier-born individuals. Any of these factors may make older males genetically inferior to younger mates.

Theoretical considerations aside, there is much empirical evidence of female preference for older males both in the presence and absence of resources offered in exchange for mating access (for examples of the former, see Burley 1981; Zuk 1987, 1988; Partridge 1988; Simmons 1988, 1995; Conner 1989; Komers & Dhindsa 1989; Simmons & Zuk 1992; Côté & Hunte 1993; Sætre *et al.* 1995; Wagner *et al.* 1996; for the latter, see Weatherhead 1984; Sundberg & Dixon 1996; Widemo 1996). Far fewer studies have found evidence of female discrimination against older males (Burley & Moran 1979; Ritchie *et al.* 1995), or no effect of age on mating success (Alatalo *et al.* 1986; Hill 1990; Petrie 1993; Olsson & Madsen 1995; Savalli & Fox 1999). Moreover, very few studies have directly investigated the relationship between offspring quality and male age, and their findings have often been contradictory (Howard *et al.* 1994; Tatar *et al.* 1996; Rogers & Marti 1997; Price & Hansen 1998).

What is needed is a study which explicitly tests competing predictions about both female preferences and reproductive success. Viability indicator models predict that females should prefer older males and that the offspring sired by those males should exhibit higher viability than those of young or middle-aged mates. In contrast, the model by Hansen & Price (1995) predicts that females should actively discriminate against older males, and if mated by them, should experience a reduction in fitness as a result of these males' low fertility and/or genetic quality. In order to eliminate the potentially confounding effects of variation in resources offered to

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females, these tests are best conducted on a species with a non-resource-based mating system.

We tested these predictions in a lek-breeding insect, *Lutzomyia longipalpis*. Phlebotomine sandflies of the *L. longipalpis* species complex form leks on or near their vertebrate hosts (Jones 1997). In the laboratory males will readily establish leks in small net cages, with or without a host (Jarvis & Rutledge 1992; Jones 1997). Visiting females typically sample several males prior to mating only once, and can readily terminate an unwanted mating attempt by depressing their abdomens or moving away (Jones 1997). Previous laboratory experiments on *L. longipalpis* leks made up of middle-aged males found that male mating success is highly skewed (Jones *et al.* 1998), largely determined by female choice (Jones 1997), and correlated with pheromone production and dispersal via a wing-fanning display (Jones & Hamilton 1998). Moreover, discriminating females benefit because their sons inherit their father's attractiveness and in turn enjoy disproportionately high reproductive success (Jones *et al.* 1998). In the field, males return to leks on successive nights (Kelly & Dye 1996), so that females presumably also have an opportunity to select between males differing in age (although we have no direct evidence for this).

Here we present the results of two experiments. In the first we assessed whether, when presented with a choice of young, middle-aged and old males, female choice was age dependent. We then explored whether the behaviour and reproductive output of our experimental females varied depending on the age class of the male they chose. However, because all females in this first trial chose their mates freely, the results of these analyses could be confounded by age-independent variation in male quality. This could mean that successful males from generally unpopular age classes were of above-average quality, masking any link between female reproductive success and mate age. Hence we performed a second experiment in which virgin females were randomly allocated single virgin males from known age classes. Again, we compared the behaviour and reproductive output of females mating with males from each category, but this time in the absence of female choice.

2. METHODS

Experimental flies were obtained from a 24-generation captive colony originating from the Salvaterra district of Marajó, Brazil (48°31′S, 0°46′W), 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 (10 cm diameter, 1.5 cm height) on a diet of dried liver powder. The population was maintained at approximately 500 adults by regulating the numbers of females breeding in each generation. Virgin flies were obtained by releasing adults into single-sex cages less than 12 h after emergence, which was prior to male sexual maturity (Chaniotis 1967). To eliminate potential cage effects, cages contributed to more than one age group on different days. All females used in the trials were four to six days old and were blood-fed on an anaesthetized hamster (*Cricetus cricetus*) 24 h prior to experimental use (after Flecknell 1987). As the numbers of eggs laid by females are dependent on the size of blood meal (Ready 1979), and females are reluctant to feed individually (T. M. Jones, personal observations), only those females with fully extended abdomens were selected for use in experiments.

(a) *Male age and female choice*

To assess whether a male's mating success was age related, females were permitted a choice of six males, consisting of two drawn from each of three age classes: young (zero to two days), middle-aged (four to six days) and old (eight to ten days). In the absence of data on the age structure of free-ranging populations, these categories were selected such that the age of the oldest males was comparable to the average age at death of males in the laboratory population used in this study (10.8 ± 0.15 days; Jones 1997). In total, 16 sextets of males were set up. In each one, both males of a given age class were marked with the same colour fluorescent dye; this was rotated between trials, and has no detectable impact on male mating success (Jones 1997; also see § 3(a)). Each marked set of six males was placed in a net cage and permitted a 10-min acclimatization period, after which, ten four-to-six-day-old virgin females were sequentially added. For each female, we noted the age class of the male she mated with and the length of copulation. After copulation, the female was removed and the males were left for 10 min prior to the introduction of the next female.

To investigate subsequent female reproductive success, mated females were individually placed in small glass tubes for egg laying and monitored daily until death. All eggs laid were then counted and transferred to a Petri dish lined with moistened filter paper. Petri dishes were checked daily and the number and proportion of broken eggshells were counted as measures of hatching success. To avoid pseudoreplication (by treating females who may have mated with the same males independently of one another), for each measure of female reproductive success we calculated an average score across all females mating with a given age of male in a particular trial. These averages, rather than individual female scores, were used in all statistical analyses, reducing sample sizes to a maximum of 16 trials per male age class (if every age class was preferred at least once in each trial; in practice, young, middle-aged and old males were preferred in only 15, 16 and 15 trials, respectively). Averaging all scores for females mating with a particular male age class within a trial was unlikely to obscure differences in fertilization success across females as males may mate sequentially with six females without reducing the proportion of fertile eggs produced (Jones 1997).

(b) *Male age and female reproductive success*

To explore how the quality of males as mates varied with age, 225 females were allocated a single male from one of the three age classes defined above. A total of 75 virgin males were selected from each age class and randomly paired to four-to-six-day-old virgin females drawn from a single-sex stock cage. Each pair was introduced into a net cage, left until they copulated, and the length of copulation noted. The numbers of eggs laid and hatched and the proportion of eggs hatched was monitored as above.

(c) *Statistics*

The proportion of matings obtained by males from different age classes were compared using a logistic regression in GLIM, v. 4.0, specifying a binomial error distribution. Male age class,

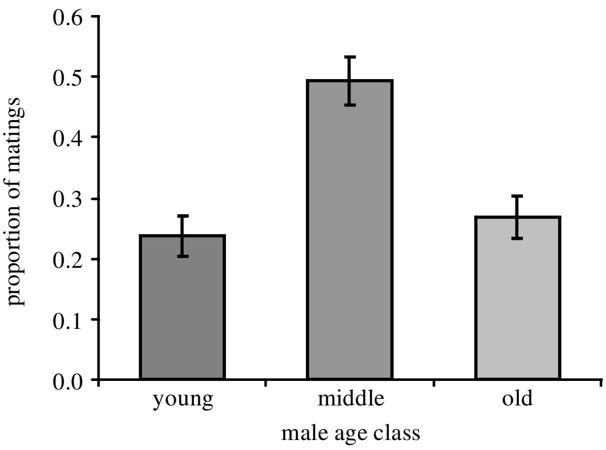

Figure 1. Proportion of matings obtained by young, middle-aged and old males when females were permitted a free choice of mate. The figure depicts the median value, 25th and 75th percentiles for each age class.

trial and dye were added as factors with three, 16 and three levels, respectively. The minimal adequate model was scaled to correct for overdispersion and the significance of each parameter was determined after Crawley (1993). In both experiments, all measures of female reproductive success (numbers of eggs laid, and the number and proportion of eggs hatched) and the length of copulation were compared using non-parametric statistics, as transformation of the data did not sufficiently improve normality. Sequential Bonferroni correction was applied at a table-wide level to correct for multiple comparisons (Rice 1989), although in practice this did not alter the interpretation of the results.

3. RESULTS

(a) *Male age and female choice*

When presented with a choice between young, middle-aged and old males, females consistently preferred to mate with middle-aged males: they obtained 50% of all matings ($\chi_2^2 = 13.80$, $p < 0.001$, figure 1). Male mating success was independent of trial and colour of fluorescent dye ($p < 0.05$). Males of all ages approached and fanned their wings towards females, although this was not quantified. The length of time spent *in copula* was similar across age classes (table 1).

There was no evidence that female reproductive fitness was related to the age of the chosen male (table 1). The number of eggs produced by females, and the proportion and number of eggs hatching were independent of male age class.

In five trials more than six females mated with the same male age class, however female mating order had no detectable impact on the length of copulation, the number of eggs laid, or the number and proportion of eggs hatching (Kruskal–Wallis tests, all n.s.).

(b) *Male age and female reproductive success*

In the second experiment, all females mated with the assigned male irrespective of his age, and the length of time spent *in copula* was again independent of male age class (table 2). The number of eggs laid did not vary with male age class. However, a significantly lower proportion of eggs hatched from females mated to old males than from females mating with young or middle-aged males (table 2, figure 2; Kruskal–Wallis comparisons between groups, young versus old, $p < 0.001$; middle-aged versus old, $p < 0.001$). The proportion of eggs hatching was similar for females mated to middle-aged or young males ($p > 0.05$). These differences in the proportion of eggs hatching were not reflected in significant differences in overall fitness between groups: the number of eggs hatching from all mated females was unaffected by male age (table 2).

4. DISCUSSION

(a) *Overview of results*

The experiments outlined here yield two clear findings. First, given a free choice of mate, female *L. longipalpis* prefer middle-aged rather than younger or older males. Second, the observed avoidance of older mates appears to be adaptive (while the avoidance of younger mates may be due to a constraint in signal production—see §4(d)). When potential differences in fertility across male age groups were explored in the absence of choice, a significantly higher proportion of offspring emerged from eggs sired by young and middle-aged males. The observed differences did not reflect variation in the proportion of males siring no offspring at all: in experiment 2, out of 225 males, only four young, one middle-aged and one old male sired no offspring. These benefits did not translate into detectable differences across sire groups in the overall number of eggs hatched per female, which may reflect the high variance in several components of fitness. Our inability to detect any mate-choice benefits in the first experiment, where females were allowed to choose their own partners, is a little more surprising. However, it might well arise (as suggested in §1) because males vary in quality independently of their age, and females choose older mates only when they are of above-average quality for their age class; if females are less discriminating of other males, it would be difficult to detect any underlying link between age and male quality in a situation where females choose their mates freely.

(b) *Relevance to models*

Our results seem at first to provide clear insights into the relative merits of the viability indicator and Hansen & Price (1995) models. The observation that females prefer middle-aged males over older and younger mates runs directly counter to the predictions of the early verbal models and the simulation model of Kokko & Lindström (1996), but is in line with Hansen & Price's (1995) prediction that older males should be less attractive. Likewise, the lower hatching success of females mating with old males is hard to explain with viability indicator models, but matches suggestions that older males are less well adapted, have accumulated germ-line mutations, or have traded off late reproduction against early survival (Hansen & Price 1995).

However, our findings are also consistent with the predictions of recent, more sophisticated viability indicator models (Kokko 1997, 1998). Rather than implicitly assuming that differences between individuals are entirely due either to heritable variation in quality (as in previous

Table 1. *Median length of copulations, number of eggs laid, and the proportion and number of eggs hatched by females permitted a free choice between young, middle-aged and old males*

(Values in parentheses give the interquartile range and those in square brackets give the sample size, which is lower in the fourth line because some females died before oviposition. Analyses were performed using a Kruskal–Wallis test (test statistic H) on the calculated average value for each age class in each trial (see §2(a) for details).)

	young	middle-aged	old	H [n]	p
length of copulation(s)	55.1 (38.3–76.0) [15]	55.2 (41.3–77.1) [16]	47.0(41.0–59.0) [15]	1.25 [46]	0.53
no. of eggs laid	44.4 (34.5–59.7) [15]	44.8 (31.6–52.9) [16]	53.0 (33.5–59) [15]	1.56 [46]	0.46
no. of eggs hatched	36.0 (26.5–39.0) [15]	28.6 (22.3–39.8) [16]	37.0 (18.5–48.6) [15]	2.11 [46]	0.35
proportion hatched	0.76 (0.70–0.90) [14]	0.71 (0.64–0.81) [15]	0.73 (0.57–0.85) [15]	3.42 [44]	0.18

Table 2. *Median length of copulations, number of eggs laid, and the proportion and number of eggs hatched by females randomly mated to young, middle-aged and old males*

(Values in parentheses give the interquartile range and those in square brackets give the sample size, which is lower in the first and fourth lines because some copulations were not observed in their entirety, and some females died before oviposition.)

	young	middle-aged	old	H [n]	p
length of copulation(s)	35.0 (30.0–45.0) [71]	37.5 (31.0–49.0) [74]	38.0 (31.0–48.0) [74]	2.13 [219]	0.34
no. of eggs laid	54.0 (10–61) [75]	49.0 (34.0–60.0) [75]	52.0 (0.0–68.0) [75]	0.55 [225]	0.76
no. of eggs hatched	41.0 (0.0–56.0) [75]	43.0 (28.0–54.0) [75]	40.0 (0.0–57.0) [75]	2.05 [225]	0.36
proportion hatched	0.91 (0.81–0.97) [59]	0.93 (0.83–0.96) [67]	0.82 (0.73–0.88) [54]	20.8 [180]	0.00001 (***)

$^{***}p < 0.001$, after sequential Bonferroni correction (Rice 1989).

viability indicator models) or to life-history trade-offs (as in Hansen & Price 1995), these models explore evolutionarily stable, age-dependent strategies of investment in reproduction given both life-history trade-offs and underlying variation in quality. They conclude that, in general, an increase in the expression of a sexually selected trait with age is evolutionarily stable, but that nevertheless, under certain conditions one might expect trait expression (and male attractiveness) to peak at intermediate ages (see Kokko 1997, fig. 1*c*). Hence our results are in principle compatible with these modified viability indicator models, though a better understanding of why male attractiveness peaks at intermediate ages requires more extensive information on the ontogeny and costs of male investment in pheromone production and wing-fanning behaviour.

(c) *Benefits of age-based mate choice*

So why exactly do females paired to middle-aged males produce eggs with higher hatching success? One essentially trivial explanation, that females paired to more attractive partners invest more heavily in their offspring, seems unlikely on several counts. First, all experimental females were virgins, and hence had no prior experience with which to judge male quality. Second, and more importantly, because sandflies are highly fecund we might expect increased maternal effort to be manifested via an increase in egg quantity rather than quality (Simmons 1987; Petrie 1994). However, we found no evidence that females mating with middle-aged males laid more eggs (tables 1 and 2). We did observe a difference in the proportion of eggs hatching between the two experiments: females permitted a choice of mate consistently produced a higher proportion of offspring than those females randomly allocated a mate (comparison of tables 1 and 2). These differences are however within the normal variation in hatching success observed in this colony in the laboratory (median, 0.77; range, 0.51–0.91; Jones 1997; T. M. Jones, unpublished data) and are likely to have arisen through random environmental effects as a result of a two-month gap between the experiments. (It should be noted however that, within an experiment, treatment groups were maintained under identical conditions.)

How differently aged males vary in quality remains unclear. One possibility is that sperm quality or the ability to transfer sperm declines with male age (as a consequence of general senescence or the accumulation of germ-line mutations; Woodhead 1986; Conner 1989). Our data do not allow us to test this possibility in *L. longipalpis* (indeed, there is little information generally on the effects of old age on sperm storage in male insects; Birkhead & Møller 1998; M. Siva-Jothy, personal communication). However, if age-related differences in male quality are essentially phenotypic they should not be detected in the offspring of choosy females after hatching. On the other hand, an alternative (non-exclusive) possibility is that while males of all ages transfer equal amounts of viable sperm, the observed differences arose through variation in ejaculate donation (Markow 1988; Markow *et al.* 1990). Data showing that older males have indeed been subjected to viability selection would provide convincing evidence that age-related choice was linked to genetic rather than phenotypic benefits.

(d) *Cues used*

Given the design of our experiments, at present we can only speculate about how females assess male age. Based on other studies, it seems likely that male production and

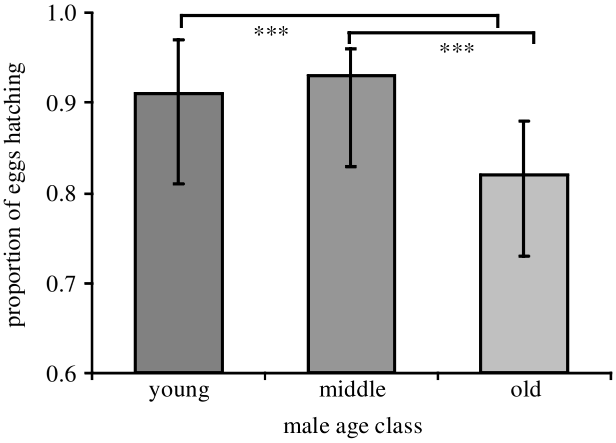

Figure 2. Proportion of eggs hatching from females randomly mated to young, middle-aged and old males. The figure depicts the median value, 25th and 75th percentiles for each age class; levels of significance derived from post-hoc comparisons between treatment groups are given by ***, $p < 0.001$.

dispersal of pheromones plays an important role. When presented with a choice of middle-aged males, female sandflies prefer males that contain large amounts of pheromone in their abdominal glands, and that invest most time in fanning their wings (dispersing this pheromone) during courtship (Jones & Hamilton 1998). Significantly, males less than four days old are incapable of pheromone production (Boufana *et al.* 1986; J. G. C. Hamilton, personal communication); hence, assessment based on pheromones may well explain why females do not choose young mates, despite the fact that they mate readily, and their eggs (like those of middle-aged males) have relatively high hatching success (this study; Chaniotis 1967). If pheromone production is also used to distinguish middle-aged and old males, then one would predict that male pheromone production and wing-fanning behaviour should decline with age. This is certainly plausible: several quantitative models predict a decrease in sexual advertisement in old age (Hansen & Price 1995; Kokko 1997, 1998), and the phenomenon has been recorded in bush crickets (Ritchie *et al.* 1995). These ideas now need testing through quantitative assessments of investment in pheromone production and dispersal across age classes.

(e) *Other issues*

Our findings raise two other issues. First, although we based the age classes used in the experiments around the life span of captive males, it is possible that our old males were unnaturally old and would in fact never be encountered by females in the field. However, it is known that female *L. longipalpis* can survive for at least nine days in the field (Dye *et al.* 1991) and, while there is no successful method of ageing wild male sandflies, ovipositing females survive less well than males in the laboratory environment (Jones 1997). Also, the fact that egg to adult survival in our colony averages 23% (Jones 1997) suggests that laboratory conditions are not especially benign. Consideration of all these points suggests that females probably do encounter eight-to-ten-day-old males in the field, although further data on natural survival and lek attendance is required to confirm this.

Second, why did we find that females prefer middle-aged males, when most studies to date have instead reported a preference for older mates? This may be a consequence of differences in experimental design rather than biology. Hansen & Price (1995) argue that the age categories used in many studies are such that males labelled 'old' are in fact of intermediate age (but see Woodhead 1986; Conner 1989). If this suggestion is true, then current evidence that females generally prefer 'old' males may in fact mask a general preference for mates of intermediate age. We suggest that future studies investigating age-related mating success should wherever possible include the entire life span of their study species in the design of experiments.

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