The hypothesis of reproductive compensation and its assumptions about mate preferences and offspring viability

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The Compensation Hypothesis says that parents and prospective parents attempt to make up for lowered offspring viability by increasing reproductive effort to produce healthy, competitive offspring and by increasing investment in less viable, but still-living progeny (parental effects). The hypothesis assumes that offspring viability is lower when individuals are constrained (often through sexual conflict) to breed with individuals they do not prefer. We review results of experimental tests of the offspring-viability assumption in Tanzanian cockroaches, fruit flies, pipefish, wild mallards, and feral house mice. Experimental constraints on mating preferences lowered offspring viability in each of the studies. Females breeding under constraints laid more eggs or gave birth to more young than females breeding without or with fewer constraints on their mating preferences, and males mating under constraints on their mate preferences ejaculated more sperm than males mating without constraints. The number of eggs laid or offspring born was higher when female choosers were experimentally constrained to reproduce with males they did not prefer. Constrained females may increase fecundity to enhance the probability that they produce adult offspring with rarer phenotypes with survival benefits against offspring generation pathogens. Similarly, ejaculation of more sperm when males are paired with females they do not prefer may be a mechanism that provides more variable sperm haplotypes for prospective mothers or that may provide nutritional benefits to mothers and zygotes.

differential allocation | fecundity | sexual conflict | constraints hypothesis

The Compensation Hypothesis (CH) (1, 2) says that parents and prospective parents increase reproductive effort and investments in offspring to make up for lowered offspring viability resulting from reproduction under constraints. It predicts what individuals do when they are unable to mate with preferred partners as often happens under sexual conflict, i.e., when individuals are constrained to reproduce with partners they do not prefer. The hypothesis assumes that (*i*) when constrained individuals have other options, they resist reproduction with partners they do not prefer, but sometimes resistance is unsuccessful and individuals then attempt to make the best of a bad job; and (*ii*) constraints on the free expression of mate preferences negatively affect offspring viability. In this work, we introduce the assumptions and predictions of the CH; in *Results and Discussion* we describe combined analyses over independent studies designed to test the assumptions and predictions of the CH, and we contrast our results with predictions from classical sexual selection.

Assumptions. Many examples of mating under constraints support the first assumption of the CH. For example, male coercion manipulates female mating options (1, 3–5). Forced copulations obviate female choice (6). Dispersal limitation and intrasexual competitive interactions (7, 8) reduce the exposure of individuals to all potential breeding partners. Arranged marriages often coerce women and men (9). Individuals in some mating systems sometimes must trade copulations for access to essential resources controlled by the opposite sex (10, 11). Predation risk (12) can also constrain mate choice, as can ecological and life-history limitations affecting the time left for reproduction (13). Constraints on the free expression of mate preferences may sometimes occur in almost all species (14), thus, the first assumption of the CH may be met in most species. Individuals of each of our study species sometimes reproduce under constraints in nature: Female mallards (*Anas platyrhynchos*) (15–17) and flies (*Drosophila pseudoobscura*) (6) are sometimes force-copulated. Male and female flies, pipefish (*Syngnathus typhle*), and mice (*Mus musculus*) sometimes court under predation risk and experience limits to dispersal that constrain their mate preferences. Intrasexual competitive interactions also may constrain individuals in all of the study species.

The second assumption, that constrained parents produce offspring with lower viability than those not under constraints, has partial theoretical support from Hamilton and Zuk (55), who hypothesized that heritable showy traits in male birds signaled the bearers' possession of good genes that protected against pathogens common in the parental generation. When this hypothesis is true, females will prefer males with the most extreme expression of showy traits. Their idea assumed that the pathogens in the offspring generation were similar or identical to the pathogens in the parental generation. If pathogens evolve quickly so that pathogens that the parents experience are different from the pathogens that the offspring experience (18), showy male traits are unlikely to be reliable signals of offspring health, as Hamilton and Zuk (55) also originally pointed out. In this case, female choice for showy traits would be unlikely to evolve through offspring-viability variation. Nevertheless, some data do support a link between offspring health and mating preferences for showy traits in males (19–21).

If pathogen evolution is rapid, heterozygosity (22) or complementary (dissimilar) immune alleles (23, 24) may mediate mate preferences, not just in females but also in males. When pathogen evolution is rapid, there is unlikely to be a single "best male" or a few best males that all females prefer, or a single "best female" that all males prefer. Rather, mate preferences are more likely to be "self-referential" (25) in that the best partner for one individual is unlikely to be the best partner for another because

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Table 1. Offspring viability for C (experimentally paired with their NP partners) and UC (experimentally paired with their P partners) individuals

| Species | Chooser | Offspring viability as % eggs or pups at reproductive age, mean $\pm$ SE (n) | | Probability | C or UC absolutely larger |
		Constrained	Unconstrained		
D. pseudooscura (28)	Female	65.4 $\pm$ 2.19 (60)	69.13 $\pm$ 1.4 (60)	<0.04	UC
D. pseudooscura (28)	Male	60.6 $\pm$ 2.6 (65)	65.5 $\pm$ 2.2 (62)	<0.04	UC
N. cinerea (34)	Female	77.5 $\pm$ 12.3 (55)	80.0 $\pm$ 10.2 (55)	0.246	UC
*S. typhle** (35)	Female	17 (32)	55 (35)	<0.01	UC
*S. typhle** (35)	Male	27 (33)	65 (32)	<0.01	UC
A. platyrhynchos (29)	Female	51 $\pm$ 5.4 (23)	69 $\pm$ 5.2 (26)	<0.022	UC
M. musculus (30)	Female	35 $\pm$ 4.6 (32)	52 $\pm$ 4.1 (42)	<0.04	UC
M. musculus (32)	Male	35.6 $\pm$ 4.72 (37)	50.8 $\pm$ 4.1 (44)	<0.019	UC
M. musculus (31)	Mutual	76.1 $\pm$ 6.9 (28)	91.9 $\pm$ 6.9 (26)	0.176	UC

The experimental protocols assessed mate preferences using discriminatees at random with respect to their phenotypes.
*Percentage of fry surviving a predation experiment.

choosers also vary and contribute to offspring genotypes that influence the offspring phenotypes that work against pathogens. If this hypothesis is so, mate preferences in potential fathers (26, 27) as well as mothers will evolve.

Against this backdrop, we tested the effects of constrained mate preferences on offspring viability in a phylogenetically diverse group of species (2, 28–35). Here we report the collective results of these explicit tests of the offspring-viability assumption. We tested preferences of focal individuals for opposite-sex individuals, which we included in the tests at random with respect to their phenotypes that may or may not have mediated choosers' preferences. We then put choosers in enforced pairs with their preferred (P) or nonpreferred (NP) partners and compared the fitness of breeders and their offspring when individuals were constrained to breed with individuals they did not prefer compared with those with individuals they did prefer. Thus, unlike most mate preference tests, ours were for the most part silent about the cues mediating preferences. Our focus was on the fitness consequences for individuals when the expression of their individual mating preferences was constrained.

Predictions. Given that the assumptions fit, the CH predicts adaptively flexible, induced parental physiology and behavior of constrained individuals (1, 21, 36; and P.A.G. and S. P. Hubbell, unpublished data) that increase the probability that their current reproductive bout is as successful or nearly as successful as reproduction of unconstrained competitors or constrained competitors unable to compensate. Among its predictions is that constrained females increase the numbers of oocytes and thus the number of offspring born or eggs laid (fecundity), an induced response that increases the variation expressed among progeny (37) and thereby increases the likelihood of survival to reproductive age of some of them. A male mechanism that might achieve a similar result would be to increase the numbers of sperm and the resulting haplotypes available to females in an ejaculate (38).

Because the species we studied fit the assumptions of the CH, we report the results of tests of its predictions and contrast these predictions with those of sexual selection (39). Under sexual conflict in some species, males manipulate fecundity of their mates (40). Whereas constraints suggest that sexual conflict often operates, once individuals have committed to reproduction together, synergistic interactions that positively influence offspring health may be as likely or more likely than continued conflict. Thus, the CH does not predict "manipulation" of females by males to increase fecundity but rather predicts that when males are constrained to reproduction with females that they do not prefer or that do not prefer them, synergistic

interactions of the sexes enhance offspring health and survivorship. Flexibly contributed nutrition to females or zygotes, perhaps delivered in ejaculates (41–43), is one way that males can collaborate with females to increase the likelihood that less-competitive offspring survive to reproductive age.

In four of the studies, in which we tested the offspring-viability assumption (28–32, 34), we had data that allowed evaluation of the CH prediction about fecundity variation, which we report here. We also review tests of additional predictions of the CH. (*i*) There is no best male that all females prefer (29). (*ii*) Compensation by maternal effects on egg size occurs (2). (*iii*) Compensation is costly, decreasing the survival probabilities of compensating females (33). (*iv*) The costs of compensation interact with its benefits to affect net reproductive success of breeding pairs (28).

Results and Discussion

Offspring-Viability Assumption. In all of the studies (2, 28–35), constrained (C) individuals had offspring of absolutely lower viability or quality than unconstrained (UC) individuals (Table 1). Seven of the nine comparisons were statistically significantly lower in C than UC pairings. The binomial probability that nine of nine tests would have a larger value for UC matings is <0.002. Fisher's test of combined probabilities of these independent tests also indicated a significant effect ($\chi^2 = 59.6$, 18 df, $P < 0.001$). We thus conclude that the second assumption of the CH is met in a wide variety of species, including insects, fish, birds, and mammals.

Because we included discriminatees in preference trials at random with respect to phenotypes, we are unable to comment on potential cues that may have mediated individual preferences, except in *Nauphoeta cinerea*. In this species, we picked male discriminatees at random, but the olfactory arena we used constrained female choosers to discriminate among them by using only olfactory cues (Table 1). Although we found consistent results in *N. cinerea*, this species also showed the weakest pattern. The pheromone used by females to discriminate among male *N. cinerea* also manipulates female reproduction (34). Do showy and elaborate traits in males of other species constrain or manipulate preferences of choosers, as they do in *N. cinerea*? Could the previous paucity of studies showing offspring-viability benefits of mate choice (44) be because showy traits manipulate choosers?

Offspring-Viability Variation and Best Males. If best males (or females) exist, mate preferences for particular discriminatees should be obvious in repeat tests with the same discriminatees. Only in mallards (29) did we perform trials with the same male

Table 2. Fecundity (no. of eggs laid or pups or nymphs born) for C (experimentally paired with their NP partners) and unconstrained (experimentally paired with their P partners) individuals

Species	Chooser	Fecundity, mean ± SE (n)		Probability	C or UC absolutely larger
		C	UC		
D. pseudoobscura (28)	Female	561.13 ± 27.5 (60)	529.4 ± 23.8 (60)	<0.39	C
N. cinerea (34)	Female	31.8 ± 3.6 (55)	31.1 ± 3.6 (55)	<0.27	C
A. platyrhynchos (29)	Female	19.8 ± 2.2 (31)	17.9 ± 1.6 (41)	<0.56	C
M. musculus (30)	Female	6.2 ± 0.2 (32)	5.7 ± 0.2 (42)	<0.1	C
M. musculus (31)	Female	6.5 ± 0.2 (28)	6.3 ± 0.3 (26)	<0.81	C

For *D. pseudoobscura*, we conservatively used the results of mean fecundity for probability values in this table. Note that a test (28) of by-day difference scores in UC–C was significantly different favoring C ($P < 0.013$).

discriminatees with different female choosers. Three males displayed to one female in three consecutive tests with a different female each time. The probability that a given male would be preferred was almost exactly one-third. Thus, for wild mallards under the conditions of our tests, there was no evidence for a best-male effect. Additional studies should include similar evaluations of best males and females in which investigators place discriminatees in trials at random with respect to phenotype.

Female Compensation by Fecundity Enhancement. Fecundity variation (Table 2) over the studies with female choosers provides a test of one of the main predictions of the CH. If females control fecundity variation through the number of oocytes they produce, the CH predicts that female choosers flexibly enhance fecundity to be larger when in C mateships. A combined analysis of fecundity over all of the studies revealed that fecundity was higher in C than UC pairings. In every study with female choosers (Table 2), fecundity was absolutely higher for females experimentally constrained to reproduce with their NP than with their P partners. Although Fisher's test of combined probabilities indicated that our combined result was not significant ($\chi^2 = 10.7$, df = 10, $P > 0.05$), it is a statistically significant difference when these studies are tested against the null expectation that half of the time they would show greater fecundity in UC and half the time greater fecundity in C ($P < 0.032$). We conclude that female choosers constrained to breeding with their NP partners enhance fecundity to compensate for lower offspring viability.

These results do not match the prediction from classical sexual selection that when individuals breed with P partners, they give

birth to more offspring or lay more eggs (39). Our combined analysis (Table 2) supports the idea that enhanced fecundity may be compensatory for lower offspring viability. The fact that none of the tabled differences was statistically significant when considered alone but that all were in the same direction compels us to wonder whether in other tests between NP (i.e., C) and P (i.e., UC) there was similar variation.

Constraints on Males Matter. Table 1 shows that in three species males enhance the fitness of their offspring although free expression of mate preferences. For male choosers in flies and mice, productivity (the number of offspring surviving to reproductive age) was lower when they were constrained to reproduce with their NP rather than their P partners (Table 3). Even for males, experimental constraints on the expression of mate preferences reduce male fitness. Flies and mice show little or no paternal care, so fitness effects from male mate choice may be more surprising in these two species than in male pipefish, whose elaborate male parental care predicts male mate preferences (45, 46). Yet, if females contribute to immune competence in offspring as males do, mate preferences in males, and not just in females in species with female-biased parental investment, would make adaptive sense (47, 48) and be far more common (49) than traditionally expected (44).

Increased Sperm Number. Using *D. pseudoobscura*, we tested the idea that males may compensate by increasing the number of sperm in an ejaculate (50). The mean number of sperm over 80 trials was 2,321 ± 1,095 (SD). The number of sperm in ejaculates

Table 3. No. of offspring surviving to independence or reproductive age for C (experimentally paired with their NP partners) and UC (experimentally paired with their P partners) individuals in species tested using similar protocols

Species	Chooser	No. of offspring at reproductive age/pair, mean ± SE (n)		Probability as reported	C or UC absolutely larger
		C	UC		
D. pseudoobscura (28)	Female	350.3 ± 17.3 (60)	360.4 ± 17.3 (60)	0.6803	UC
D. pseudoobscura (28)	Male	319.9 ± 17.8 (65)	382.5 ± 17.9 (62)	0.0148	UC
N. cinerea (34)	Female	24.6 ± 0.6 (55)	24.9 ± 0.6 (55)	0.728	UC
*S. typhle** (35)	Female	1.4	4	Not tested	UC
*S. typhle** (35)	Male	2.3	5.3	Not tested	UC
A. platyrhynchos (29)	Female	8.5 ± 1.2 (23)	12.3 ± 1.2 (26)	0.0025	UC
M. musculus[†] (30)	Female	2.2 (32)	3.0 (42)	0.0022	UC
M. musculus[‡] (32)	Male	2.6 (37)	3.09 (44)	0.19	UC
M. musculus[§] (31)	Mutual	4.9 ± 0.52 (28)	5.8 ± 0.37 (26)	0.1471	UC

*Estimated from number that survived 0–7 days; proportion that survived a predation experiment in shown in parentheses [female choice, NP 8.4 (0.17); P 7.2 (0.55); male choice NP 8.7 (0.27); P 8.1 (0.65)].
[†]No. weaned (proportion surviving to 60 days after release).
[‡]No. weaned (proportion surviving to 30 days after release).
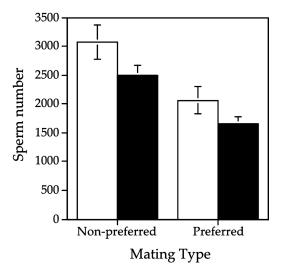[§]No. weaned.

Fig. 1. No. of sperm in a 1-μl sample of a ejaculate in 20 μl of 1$\times$ PBS solution, when males were mated to females that did and did not prefer them (female choice tests, open bars) and to females they did and did not prefer (male choice tests, filled bars).

was significantly different for male- and female-choice trials (Fig. 1; $P < 0.043$). Chooser males constrained to reproduce with females they did not prefer ejaculated significantly more sperm than did males with females they did prefer (Fig. 1). Similarly, males mated to female choosers constrained to mate with them also ejaculated more sperm than males mated to females that did prefer them (Fig. 1).

D. pseudoobscura is a species with sperm of at least two lengths (51). Unfortunately, in this experiment we were unable to count numbers of sperm of different lengths. It is possible, however, that the excess sperm in the constrained matings were not fertilizing sperm, but those that function in delivering nutrients to females (52, 53) or in sperm competition (54). Ejaculating more sperm when males are with females they do not prefer or when males are with females that do not prefer them might be a flexible response to anticipated sperm competition (all individuals in these experiments were virgins). If so, one would not expect sperm haplotypes to be more variable when males are in NP (C) pairings. However, if ejaculating more sperm is a compensatory mechanism for lower offspring viability, one would expect that larger ejaculates contain more variable haplotypes that females might discriminate before fertilization to enhance the probability that offspring have phenotypes competitive in the pathogen environments experienced by offspring. We have not yet tested this prediction.

Female Compensation by Increased Egg Size. We tested the prediction that parents attempt to make up for lowered offspring viability by increasing investment in less viable, but still-living progeny in mallards (2, 29). Although first- and second-year virgin females suffered significantly lower offspring viability when constrained to reproduction with their NP partners (2, 29), second-year virgins, but not first-year virgins, laid larger eggs (2), a compensatory effect that enhanced the quality of their living offspring up to fledging. We suspect that first-year virgins could not compensate because of trade-offs with their own growth.

Evidence of Successful Compensation. The CH says that individuals attempt to increase productivity during the compensated bout of reproduction so that productivity of C matings is similar to UC matings. Therefore, we also examined data over all of our studies for evidence of successful compensation. We asked whether

overall fitness [the number of offspring that survived to reproductive age (Table 3)] varied when individuals were constrained to mate with individuals they did not prefer compared with individuals that were unconstrained.

Three of nine studies were statistically significantly different (28–30), four were not (28, 31, 32, 34), and two (35) were not tested for statistical significance (Table 3). Because the absolute differences between C and UC in Table 3 are all in the same direction, we tested the significance of the tabled results with Fisher's test, which indicated that overall productivity from UC matings was higher than C ($\chi^2 = 41.2$, 18 df, $P < 0.005$). The binomial probability that all nine tests would show a larger effect for UC is <0.002. Despite the fact that productivity is higher when individuals are unconstrained, the four in which C and UC had equal productivity suggest that compensation sometimes may be effective in overcoming lower offspring viability, at least during a single bout of reproduction, i.e., sometimes it may pay to increase fecundity because sometimes compensating parents can be successful enough to have some of their offspring reproducing in the offspring generation.

Costs of Compensation. Not only is compensation not always successful, compensation is costly (ref. 2 and P.A.G. and S. P. Hubbell, unpublished data), yet compensation can evolve so that variation in mating circumstances may induce flexible compensation in all individuals (P.A.G. and S. P. Hubbell, unpublished data). Theoretically, individuals that compensate have lower survival probabilities from the end of one bout of reproduction and the next, thus only individuals with a strong probability of having less competitive offspring, such as C individuals, should compensate. We had life span data on only one of our study species, *N. cinerea*. In this species, C females died before UC (33). Further needed studies of the costs of compensation are those that specifically evaluate costs under different levels of environmental resource variation, intrinsic metabolic efficiency of breeders, and different levels of pathogen pressure, as well as in species with showy male traits.

Net Reproductive Success and Compensation. The theoretical trade-off between the costs and benefits of compensation should have effects on net reproductive success, an idea we tested in *D. pseudoobscura*. Net reproductive success takes into account not only the number of eggs laid or individuals born, egg-to-adult survival, other measures of offspring quality, and the number of offspring that survive to reproductive age, but also the probability of survival for breeders for each day of the experiment. Although we did not study the life span of our *D. pseudoobscura* subjects, we did note their survival probabilities over the days of the experiment, so we were able to compute reproductive success, expressed as $\sum l_x m_x v_x$, where x is the day of female life; l_x is the probability of survival to day x; m_x is the number of eggs laid on day x; and v_x is the offspring viability on day x. The reproductive success of female *D. pseudoobscura* was significantly lower for C choosers than for UC (28).

Additional life course experiments should include those that also manipulate resource availability and intrinsic metabolic efficiency of females to study their effects on the ability of constrained individuals to successfully compensate and simultaneously avoid the survival costs of compensation.

Effect of Compensation on Fecundity Is Alternative to Prediction of Classical Sexual Selection. We emphasize that tests of the CH should be on species in which the assumption of offspring viability has been tested and shown to be significantly lower when individuals breed under constraints than when they do not. Fair tests must eliminate opportunities for individuals of one sex to manipulate the decisions of another, as, for example, happens in open-field tests when intrasexual combat or sexual coercion can

manipulate or constrain individual reproductive decisions in ways opaque to investigators. Otherwise, investigators run the risk of competing two C choosers against each other.

Methods

Individual Experiments. Experimental details for individual studies by species are in the published reports on each species (2, 28–35). Briefly, the experiments consisted of mate preference trials followed by breeding trials. Mate preference trials evaluated whether choosers preferred one opposite-sex discriminatee to another based on time near one or the other. We placed discriminatees in trials at random with respect to their phenotypes. Only choosers that repeated the same preference in two consecutive tests advanced to breeding trials. Repeatability in these experiments was important because it increased the likelihood that experimenters would identify choosers that did not prefer one of the discriminatees and also the reliability of experimental comparisons meant to simulate breeding under constraints and the absence of constraints. In breeding trials, choosers experimentally paired with the partner they did not prefer represented C individuals. We measured components of fitness of breeding pairs and their offspring.

In mice, we completed female (30), male (32), and mutual choice (31) studies in 3 separate years. In mallards (2, 29) and cockroaches (33, 34), we completed only female-choice experiments in a single year. In *D. pseudoobscura*, we completed the single experiment (28) testing simultaneously the outcomes of male and female choice trials in 2 years. Sandvick *et al.* (35) completed their observations over two seasons.

We tested predictions about sperm numbers in *D. pseudoobscura* by using methods (50) for evaluating preference status as in our earlier experiments (28). We randomly placed choosers to breed with individuals they preferred or did not prefer. We then estimated the number of sperm in the reproductive tracts of just-mated females by examining a random volume-controlled subsample with vision software (National Institutes of Heath, Bethesda, MD) (50).

Combining Results of Independent Statistical Tests. We used the binomial test and Fisher's test of combined probabilities from independent experiments to test for significance across studies. In Table 3, two of the listed comparisons were not tested for statistical significance in the original report; so we used only the seven available probabilities that were reported to compute χ^2 under Fisher's combined probability of independent tests. Nevertheless, we took a conservative approach and used the entire list to compute degrees of freedom for this test, which is $2 \times k$ (the number of probabilities). We set statistical significance at <0.05.

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