

## Variable female preferences drive complex male displays

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**Complexity in male sexual displays is widely appreciated<sup>1</sup> but diversity in female mate choice has received little attention. Males of many species have sexual displays composed of multiple display traits, and females are thought to use these different traits in mate choice<sup>1</sup>. Models of multiple display trait evolution suggest that these traits provide females with different kinds of information in different stages of the mate choice process<sup>2</sup>, or function as redundant signals to improve the accuracy of mate assessment<sup>3,4</sup>. We suggest that complex male displays might also arise because of variation in female preferences for particular male display traits. The causes of female preference variation have received little attention<sup>5–7</sup>, and the role of preference variation in shaping complex male displays is unclear. Here we show that in satin bowerbirds (*Ptilonorhynchus violaceus*) female mate choice is a multistage process, where females of different ages use different male display traits in successive stages. Age- and stage-specific female preferences may contribute to explaining the widespread occurrence of multifaceted male displays.**

Male satin bowerbirds build specialized stick structures, called bowers, where courtship and copulation take place<sup>8</sup>. Males have multiple display elements combining intense behavioural displays with bower decoration displays<sup>8,9</sup>. Intense behavioural displays can be both attractive and threatening to females; however, this threat is reduced when males adjust their display in response to female signals that indicate the level of intensity the female will tolerate<sup>9</sup>. Females differ in their tolerance of intense display, with age/experience as a likely cause<sup>10</sup>. If young, inexperienced females have a lower tolerance for intense display, then we expect them to emphasize non-threatening display elements, such as bower decorations, in their mate choice decisions. If older, more experienced females are both more tolerant of intense display and are better able to assess males using intense display, then we expect them to emphasize male display intensity in their mate choice decisions. Here we consider two questions: (1) do females show age-related differences in how they use male display traits to choose mates, and (2) are those differences related to female tolerance of male display intensity? To test these hypotheses, we augmented the blue decorations (Fig. 1; see also Supplementary Fig. S1) at a subset of bowers in a natural population of satin bowerbirds, separated females into age classes (first-year females, second-year females, three-plus females (females with two or more years of mating experience)), and then monitored individual female's mating-related decisions throughout the mate choice process.

In satin bowerbirds, female mate choice occurs in three stages: 'visits', 'pre-nest-building courtships' (pre-NB) and 'post-nest-building courtships' (post-NB)<sup>11–13</sup>. Before pre-NB courtships, most females (year 1999, 80%; year 2000, 77%) engage in a stage of visits to males' bowers while the bower owners are absent—visits allowed us to evaluate the effect of blue bower decorations on female mate choice decisions independent of a male's intense courtship display. After visits, each female engages in pre-NB courtships at the bowers of several males. During courtship, the female stands inside the bower while the male displays intensely on the platform in front of the bower<sup>9</sup>. After pre-NB courtships, each female spends approximately 1 week building her nest before returning for several

post-NB courtships with a subset of the males previously sampled<sup>11</sup>. From this subset, each female typically chooses a single male as a mate. After each visit to a bower, a female has two options: reject the male, or return for pre-NB courtship. After each courtship a female has three options: reject the male, return for another courtship, or copulate. Detailed information on individual female's mate-searching patterns allowed us to evaluate which of these options was chosen at each stage of mate choice and whether female age affected the use of blue bower decorations and male display intensity in these decisions.

In the first stage of the mate choice process, females visit males' bowers while the bower-owning males are absent. After each visit, a female must decide whether to reject the bower-owning male from her pool of potential mates or return to him for pre-NB courtship. By evaluating the mean proportion of females that returned to 'experimental' or 'control' males (Fig. 1) for pre-NB courtships after visits, we tested the hypothesis that females use blue decorations in the first stage of mate choice. In both 1999 and 2000, all age classes of females preferentially returned for pre-NB courtships with experimental males over control males (Fig. 2a, b; see also Supplementary Tables S1 and S2). These results show that females of all age classes assess blue bower decorations during visits and use the information in decisions related to returning for pre-NB courtships.

In the second stage of the mate choice process, females engage in pre-NB courtships with multiple males. During these courtships, the bower-owning male is present and all elements of male display, including courtship display intensity, are available for assessment. We tested the hypothesis that blue decorations affect females' decisions to return for post-NB courtships. After pre-NB courtships, we found age-related differences in the proportion of females returning to experimental and control males. First- and second-year females returned preferentially to experimental males for post-NB courtships in both years, whereas there was no effect on the post-NB return rates of three-plus females in either year (Fig. 3a, b; see also Supplementary Tables S1 and S2). In both years, larger proportions of first- and second-year females compared with three-plus females returned to experimental males for post-NB courtships (Fig. 3a, b).

After building their nests, females initiate the third stage of the mate choice process by engaging in post-NB courtships with a subset of the males sampled in pre-NB courtships<sup>11,12</sup>. From this subset, a female typically chooses a single male as a mate, and we tested the hypothesis that females prefer males with augmented blue decorations as mates. In 1999, second-year and three-plus females did not prefer experimental males as mates, whereas first-year

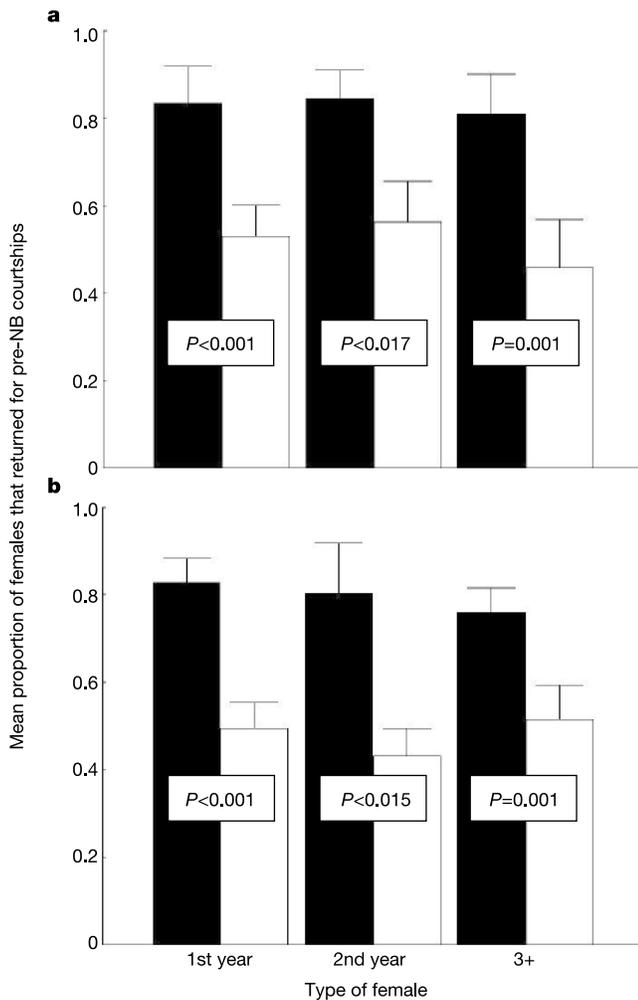


**Figure 1** Photograph of a bower with experimentally augmented blue decorations in 2000. Experimental males placed 20 blue tiles and 50 blue plastic strands on their bower platforms; bower decorations of control males remained unaugmented.

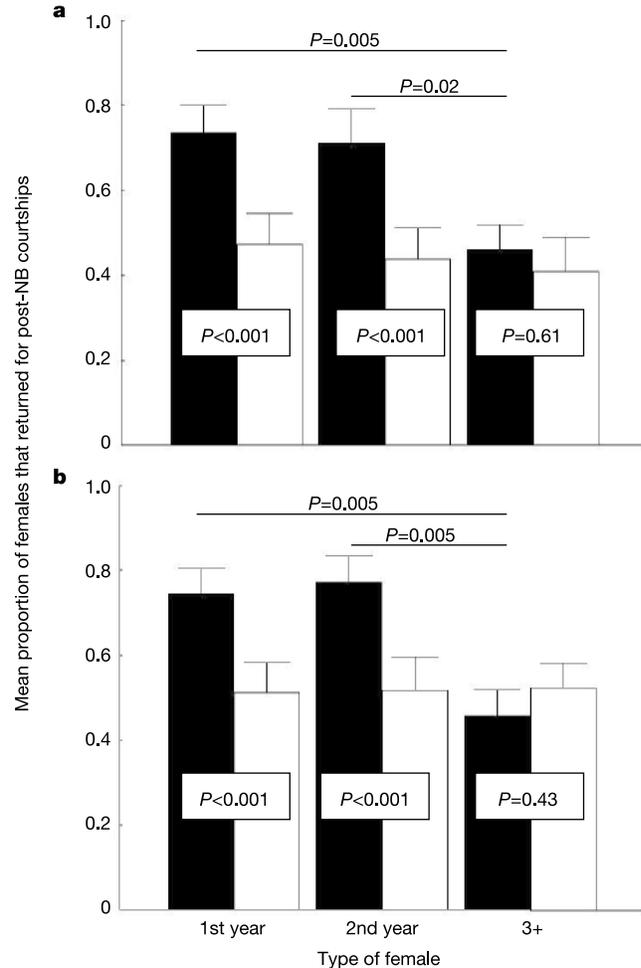
females tended to prefer experimental males as mates (Fig. 4a; see also Supplementary Table S1). In 2000, we increased the number of males in the experiment and increased the number of decorations used to augment bowers (Fig. 1). Again, the mate choices of three-plus females were not affected by the augmentation (Fig. 4b); however, first- and second-year females showed significant mating preferences for experimental males (Fig. 4b; see also Supplementary Table S2). Among age classes in 1999, there were no differences in the proportion of females that chose experimental males as mates, whereas in 2000, larger proportions of first- and second-year females compared with three-plus females chose experimental males as mates (Supplementary Table S7).

Our study shows that young females place an emphasis on blue decorations in decisions made throughout the mate choice process, whereas older females use blue decorations in decisions only when a male's behavioural displays are unavailable for assessment. A previous study suggested that young females are more threatened and less tolerant of intense male displays than older females<sup>10</sup>, and therefore may be averse to using intense male displays in mate choice. In 2000, we tested the hypothesis that the mate choice

decisions of older females are affected by male display intensity, whereas the decisions of younger females are not. There was no difference in mean display intensity between experimental and control males (experimental males =  $3,130.25 \pm 189.21$ ; control males =  $2,949.33 \pm 210.04$ ;  $t_{26} = 0.64$ ,  $P = 0.53$ ), therefore, we considered all males as a single group for regression analyses. As predicted, display intensity did not explain a significant amount of the variation in the proportion of first-year females ( $r^2 = 0.07$ ,  $F_{1,20} = 1.67$ ,  $P = 0.21$ ) or second-year females ( $r^2 = 0.003$ ,  $F_{1,12} = 0.04$ ,  $P = 0.83$ ) that returned for post-NB courtships. In contrast, male display intensity explained a significant amount of the variation in the proportion of three-plus females that returned for post-NB courtships ( $r^2 = 0.38$ ,  $F_{1,26} = 15.67$ ,  $P < 0.01$ ). Comparisons of regression coefficients among age classes showed that male display intensity had a larger effect on the decisions of three-plus females than younger females ( $F_{2,58} = 29.30$ ,  $P < 0.001$ ). These results are consistent with those from the decoration augmentation experiment: young females place an emphasis on blue decorations throughout the mate choice process, whereas older females use blue decorations only when a



**Figure 2** Mean proportion of females that returned to experimental (filled bars) or control (open bars) males for pre-NB courtships in 1999 (a) and 2000 (b). In both years, after visits all females preferentially returned to experimental males for pre-NB courtships. Bars and error bars represent mean + standard error. *P* values for within-age class comparisons are inset. Among age classes, there were no differences in the mean proportion of females that returned to experimental males for pre-NB courtships. For complete *t* values, degrees of freedom and *P* values, see Supplementary Table S4.



**Figure 3** Mean proportion of females that returned to experimental (filled bars) or control (open bars) males for post-NB courtships in 1999 (a) and 2000 (b). In both years, after pre-NB courtships first- and second-year females preferentially returned to experimental males for post-NB courtships; three-plus females did not. Bars and error bars represent mean + standard error. *P* values for within-age class comparisons are inset. *P* values at the top of each panel indicate significant differences among age classes in the mean proportion of females that returned to experimental males for post-NB courtship. For complete *t* values, degrees of freedom and *P* values, see Supplementary Table S5.

male's behavioural display elements, such as display intensity, are unavailable for assessment. Age-related differences in females' tolerance of intense male displays<sup>10</sup> may explain the age-related reliance on different display elements in mate choice. An alternative explanation is that the differences in old and young females' use of blue decorations could result because of age-related differences in female fidelity<sup>11,12</sup> but we found no support for this hypothesis (Supplementary Table S3).

We show that mate choice in satin bowerbirds is a complex process made up of multiple stages, where females make sequential stage-specific decisions based on the assessment of male display traits, and there are age-specific differences among females in the male traits used in assessment. The differences in females' use of blue decorations versus display intensity may be related to the threatening nature of male displays. Display intensity may be a better indicator of male quality than are blue decorations<sup>1,9,10</sup>, but because young females are more easily threatened by intense displays than are older females<sup>11</sup>, young females may be unable to assess display intensity during mate choice. Similar age- and stage-specific female preferences may occur in the numerous other species where males have multifaceted displays, where females sample multiple

males before choosing mates, and where females choose mates based on the assessment of multiple display traits<sup>1,14-17</sup>. The variation in female preferences may not have been detected previously because detection requires experimental manipulation of male traits combined with intensive monitoring of individual females throughout the mate choice process. We suggest that as more intensive studies of mate choice are done in which intrinsic female factors (that is age/experience) and the stages of mate choice are considered, variable female preferences will be discovered and may help explain the widespread occurrence of multifaceted male displays. □

Methods

Marking and monitoring

This work was conducted in 1999 and 2000 at Wallaby Creek, New South Wales, Australia. Before the mating season, birds were captured using traps and mist nets. Each individual was fitted with three plastic leg bands arranged in a unique colour combination. In our study population, all adult males and most (1999, 87%; 2000, 91%) of the females were uniquely marked for identification. From 1 November to 20 December, automatic Hi-8 video cameras recorded behaviours at 24 (1999) and 28 (2000) adjacent bowers. This monitoring provided a complete record of all courtships and copulations. Individuals were only classified as female if they were observed copulating with a male on videotape. Detailed mate-sampling patterns and mate choice for 52 (1999) and 64 (2000) females were reconstructed from video footage.

Decoration augmentation experiment

Using information from 1998 (refs 12,13), bower-owning males were paired to maximize similarity in mating success (number of different mates). In 1999, the bower of one male in each dyad was randomly selected for augmentation with blue bower decorations (experimental males), while the other male's decorations remained unaugmented (control males). In 1999, 20 blue plastic tiles (2.54 cm<sup>2</sup>) were placed in two arcs of 10 tiles on the bower platform of each experimental male. In 2000, we used the same males in the experimental and control groups in addition to two new experimental males, paired with two new control males. In this second year, 20 blue tiles and 50 strands of blue plastic (25 x ~0.20 cm) (Fig. S1) were placed in caches 1 m from the bower platform. Within 2 h, each experimental male placed all of the tiles and plastic strands on his bower platform (Fig. 1). Blue plastic strands are frequently used as bower decorations in the Wallaby Creek population, and the number of strands used in the augmentation was within the range of plastic strands displayed by bower-owning males before the augmentation (mean number ± standard error of plastic strands on bowers before the experiment, 45 ± 7.73) (S.W.C. and G.B., manuscript in preparation). To prevent decoration stealing<sup>18</sup>, after experimental males placed their tiles each tile was glued to the head of a long screw then secured into the ground. Plastic strands were frequently woven into the bower platform by bower owners, probably reducing the frequency of stealing (S.W.C. and G.B., personal observations). Twice a day at each bower, the number of tiles and plastic strands were counted and replaced to original levels if necessary. Tiles and plastic strands found on the bowers of control males as a result of decoration stealing<sup>18</sup> were removed. All other bower decorations<sup>8</sup> remained unmanipulated.

Female age classes

Females were grouped based on their years of mating experience. Three-plus females had at least 2 yr of previous mating experience. Second-year females had 1 yr of previous mating experience. First-year females were not previously observed mating. All first-year females in 1999 (n = 12) and 2000 (n = 16) were captured and marked for the first time in those years. Further suggesting that these were first-year females, we found that they weighed significantly less than three-plus females (t<sub>65</sub> = 2.11, P < 0.01). All females used in our analyses were courted by at least one experimental male and one control male.

Male display intensity

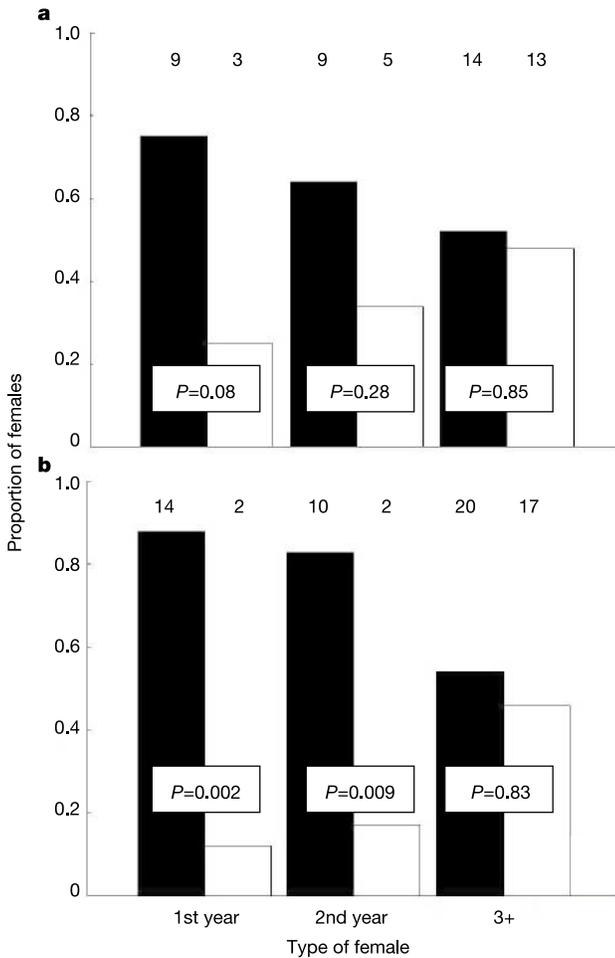
Intense male displays involve loud buzzing vocalizations, piloerection and vigorous running across the bower platform with wings extended, all performed in close proximity to the female<sup>9</sup>. For each male, we calculated display intensity in the first pre-NB courtship with each courted female in 2000. We calculated display intensity based on four variables: (1) the distance run by the male during his display; (2) the degree of male piloerection, appearing larger; (3) the location of the male on the bower platform; and (4) the degree of the male's wing extension, appearing larger<sup>9,10</sup>. For each male we calculated mean display intensity, and used these means in regression analyses to evaluate the relative contribution of display intensity to the proportion of females returning for post-NB courtships.

Statistical analyses

To account for the unequal numbers of females sampling each male in visits and pre-NB courtships (Supplementary Tables S1 and S2), we treated each male as a replicate and weighted the proportion of returning females by the inverse of the variances in the proportion of females observed in visits and pre-NB courtships.

Received 21 November 2003; accepted 11 February 2004; doi:10.1038/nature02419.

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**Figure 4** Proportion of females that mated with experimental males (filled bars) or control males (open bars) in 1999 (a) and 2000 (b). In 1999, first-year females tended to prefer experimental males as mates; second-year and three-plus females did not. In 2000, first- and second-year females preferred experimental males; three-plus females did not. P-values for within-age class comparisons are inset. For  $\chi^2$  values and degrees of freedom, see Supplementary Table S6. For comparisons among age classes in the proportion of females that chose experimental males as mates, see Supplementary Table S7. Sample sizes are indicated above the bars.

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Supplementary Information accompanies the paper on [www.nature.com/nature](http://www.nature.com/nature).

**Acknowledgements** We thank G. S. Wilkinson, K. L. Shaw, J. A. C. Uy and T. C. Mendelson for comments on the manuscript, and M. C. Christman for statistical advice. We also thank the Australian Bird and Bat Banding Scheme, New South Wales National Parks and Wildlife Service, the landowners at Wallaby Creek, and the 1998–2000 field assistants. This research was funded by the National Science Foundation, Animal Behavior Program (USA) to G.B., and by fellowships from the Behavior, Ecology, Evolution and Systematics Program of the University of Maryland, and the N.S.F. Research Training Grant to S.W.C. and G.L.P.

**Competing interests statement** The authors declare that they have no competing financial interests.

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## Variation in behaviour promotes cooperation in the Prisoner's Dilemma game

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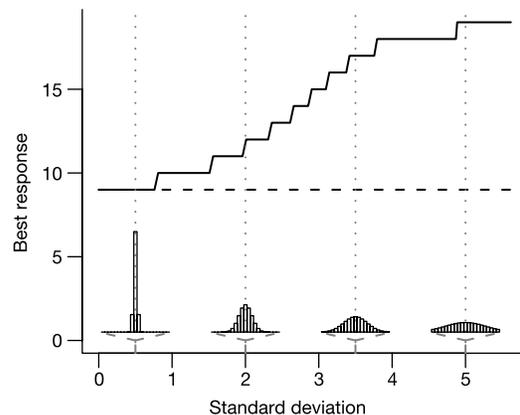
The Prisoner's Dilemma game<sup>1–4</sup> is widely used to investigate how cooperation between unrelated individuals can evolve by natural selection. In this game, each player can either 'cooperate' (invest in a common good) or 'defect' (exploit the other's investment). If the opponent cooperates, you get  $R$  if you cooperate and  $T$  if you defect. If the opponent defects, you get  $S$  if you cooperate and  $P$  if you defect. Here  $T > R > 0$  and  $P > S$ , so that 'defect' is the best response to any action by the opponent. Thus in a single play of the game, each player should defect. In our game, a fixed maximum number of rounds of the Prisoner's Dilemma game is played against the same opponent. A standard argument based on working backwards from the last round<sup>1,5</sup> shows that

defection on all rounds is the only stable outcome. In contrast, we show that if extrinsic factors maintain variation in behaviour, high levels of co-operation are stable. Our results highlight the importance of extrinsic variability in determining the outcome of evolutionary games.

In our version of the Prisoner's Dilemma game, the fixed maximum number of possible rounds,  $N$ , is known to both players. On each round before the last one, if either player defects then the game ends; only if both cooperate do they proceed to the next round. (This approach reflects the ability of mobile organisms to terminate an unfavourable interaction by leaving<sup>6,7</sup>.) After  $N$  rounds, the interaction ends whatever decisions are made. The total payoff is the sum of the payoff from each round.

We assume that  $T > (P + R)$ . The standard arguments based on working backwards then lead to the conclusion that defection on all rounds is the only evolutionarily stable outcome in our game (see Supplementary Information). At evolutionary stability all population members behave in this way, so that there is no variation in the population, and unlike some iterated Prisoner's Dilemma games, variation cannot be maintained by frequency dependence. We believe, however, that in real populations there are always factors other than frequency dependence—such as mutation, immigration, recombination and epistasis—that maintain genetic variation. We show that maintaining variation fundamentally changes the nature of the game. The intuition behind this is as follows. In a population at the defect evolutionarily stable strategy, a player should defect on the first round. But if variability is maintained, and hence there is a chance that an opponent will cooperate, then there is the potential for a substantial gain, and it may be worth cooperating initially in the hope that the opponent is cooperative (compare ref. 1). Whether for this or for other reasons, humans do not defect as much as expected in the Prisoner's Dilemma and related games<sup>5,8</sup>.

In our model, a strategy specifies the number of rounds  $n$  to cooperate before defecting. (The game may not last for  $n + 1$  rounds because the opponent may terminate the game by defecting beforehand.) We consider the evolution of an infinite population with discrete generations. The number of offspring left by an individual in the next generation is the individual's total payoff plus a positive constant,  $K$ , which represents the contributions to fitness that come from outside the game. If a parent adopts strategy  $n$  then each offspring is also  $n$  with probability  $1 - 2\varepsilon$ . Genetic variability is maintained by mutation; with probability  $\varepsilon$  offspring are  $n - 1$  and with probability  $\varepsilon$  they are  $n + 1$ . We use the standard



**Figure 1** The best response (continuous line) as a function of the variation in the degree of cooperation in the population. In all cases, the mean number of rounds of cooperation before defection is  $E(n) = 10$ . The distribution of  $n$  about this mean is pseudo-normal with the standard deviation indicated. Four actual distributions are illustrated. The dashed line gives the best response when each round is chosen against a new opponent, randomly selected from the population. In these calculations,  $N = 20$ .