

## Mate Choice in Experimentally Parasitized Rock Doves: Lousy Males Lose<sup>1</sup>

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**SYNOPSIS.** A recent model by Hamilton and Zuk (1982) suggests that exaggerated secondary sexual traits facilitate mate choice for genetic resistance to parasites. The model predicts that individuals discriminate against parasitized mates by scrutinizing traits indicative of parasite load. In the case of birds and their feather-feeding lice, for example, individuals might avoid parasitized mates by detecting reduced plumage brightness, reduced courtship display, or increased grooming. I conducted a series of mate choice trials in which female Rock Doves (*Columba livia*) were allowed to choose between "clean" males without lice and "lousy" males with experimentally increased loads. Clean males displayed significantly more often than lousy males and females demonstrated a significant preference for clean males. Lousy males were subject to plumage damage; however, none of the damage was externally visible, and the time spent grooming by clean and lousy males did not differ significantly. Female louse loads, which were also manipulated, were not significantly related to female mating preferences. These results are consistent with the Hamilton-Zuk model. They are also consistent with a model of sexual selection for the avoidance of parasite transmission, which is discussed. The general relevance of lice and other ectoparasites to models of parasite-mediated sexual selection is reviewed.

### INTRODUCTION

The proposal by Hamilton and Zuk (1982) that parasites influence the evolution of secondary sexual traits in their hosts has stimulated widespread research and numerous recent papers (reviewed by Read, 1988, 1990). Hamilton and Zuk's proposal is a "good genes" model of sexual selection in which individuals increase their net fitness by choosing mates with high genetic parasite resistance. The model, based on the assumption that heritable variation in fitness is maintained by host-parasite coevolution, predicts that hosts will select mates on the basis of condition-dependent traits that are indicative of parasite levels.

The genetic assumption is that coadaptation cycles between parasite virulence and host defense result in the maintenance of additive genetic variance in fitness of both the parasite and host. This mechanism is the striking feature of the Hamilton-Zuk model. If correct, it avoids the theoretical paradox of most good genes models that selection on a fitness-enhancing trait will exhaust the heritable variation in that

trait (assuming negligible mutation or migration), thus neutralizing its relative fitness benefit and potential evolutionary response (Fisher, 1930; Maynard Smith, 1978; Kirkpatrick, 1987). The model's prediction regarding mate choice assumes that high parasite loads negatively influence the expression of sexually selected traits. For example, high parasite levels in brightly colored birds might cause fading of the plumage or an inability to perform courtship displays, such as strutting or singing.

In this paper I focus on the mate choice prediction of the Hamilton-Zuk model in reference to a host-ectoparasite system. I conducted a series of mate choice trials to determine 1) whether or not birds discriminate among potential mates on the basis of ectoparasite load, and 2) the cue(s) facilitating such discrimination. Parasite "load" is defined herein as the number of parasites on a host (= "intensity," Margolis *et al.*, 1982). The system studied was the Rock Dove (*Columba livia*), or feral pigeon, and its North American species of Ischnoceran (Insecta: Mallophaga) chewing lice, *Columbicola columbae* and *Campanulotes bidentatus*. Feral pigeons are a monogamous species in which both males and females actively choose mates (Burley, 1977, 1981; Burley

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FIG. 1. Dorsal view of an Ischnoceran louse (*Philopterus* sp.), *in situ*, on a host's feather. Scale bar = 500  $\mu$ m. SEM by K. Hamann.

and Moran, 1979). Chewing lice are obligate ectoparasites that complete their entire life cycle on the host. Members of the suborder Ischnocera (Fig. 1) feed on feathers, which they metabolize with the aid of symbiotic bacteria (Marshall, 1981). *Columbicola columbae* and *Campanulotes bidentatus* feed exclusively on the barbules of the host's abdominal contour feathers (Fig. 2).

To test whether or not pigeons discriminate against lousy mates, I allowed females to choose between "clean" males without lice and "lousy" males with experimentally increased loads. To test possible cues facilitating discrimination, I tested 3 hypothesized effects of lice on pigeons:

1. Lice reduce plumage brightness. Although Rock Doves are not brightly colored, *per se*, their neck and upper breast feathers are strikingly iridescent due to the prismatic effect of feather microstructure

(Simon, 1971). Structural damage to feathers by feeding lice could reduce the iridescence of pigeons by a detectable margin.

2. Lice reduce male display. The display rates of male guppies (*Poecilia reticulata*) are inversely correlated with ectoparasite load (Kennedy *et al.*, 1987). The display of male Rock Doves, which is vigorous during courtship (Goodwin, 1983), could likewise be related to louse load.

3. Lice increase male grooming. Generally, individuals with large ectoparasite loads groom more than individuals with small loads (Nelson *et al.*, 1975, 1977; Hart, 1990). The grooming of Rock Doves could be proportional to louse load.

## METHODS

### *Manipulation of parasite loads*

Preening is the primary defense of Rock Doves and other birds against ectoparasites (Clayton, 1990; Nelson and Murray, 1971). To manipulate louse loads I impaired preening with metal "bits," small C-shaped pieces of plated steel inserted between the mandibles. The bits were crimped slightly in the nostrils to prevent dislodging, but not so far as to pierce any tissue. Bits create a 1.0–3.0 mm gap between the mandibles that prevents the full occlusion of the bill necessary for efficient preening. Birds typically shake their heads for several minutes immediately after receiving bits, but ignore them thereafter. Bits have no effect on a pigeon's ability to feed itself or its young. During the aviary project described below, there was no significant difference in the weight or reproductive success of louse-free birds with bits, compared to louse-free birds without bits (Clayton, 1989).

Louse loads were quantified using a regression models ( $r^2 = 0.81$ ,  $P < 0.001$ ) derived from an independent sample of parasitized Rock Doves that predict total load from timed visual censuses of lice on specific body regions. Feather damage was quantified by weighing 10 abdominal contour feathers selected at random from each of 8 regions on the host. See Clayton (1990) for a complete description of both techniques.

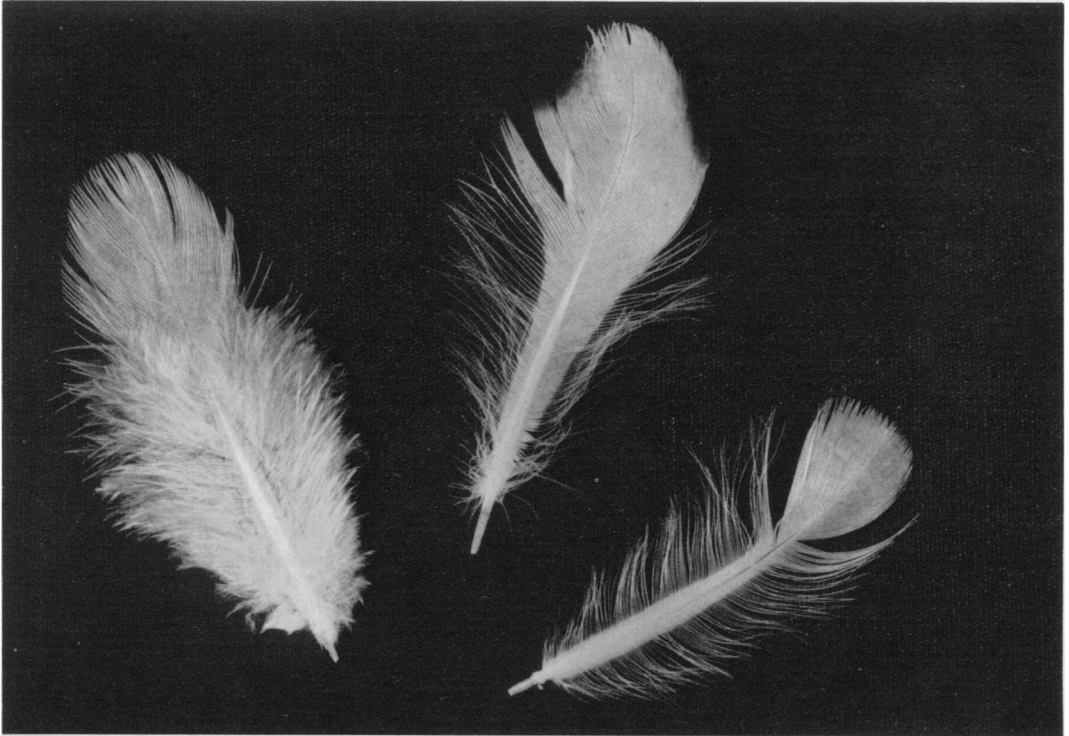


FIG. 2. Damage to abdominal contour feathers by feeding lice: (left to right) no damage, average damage and severe damage. Only the basal downy region and the barbules of the basal and medial regions of a feather are consumed, never the distal region. The barbs and shaft are not damaged, apparently because they are too large to ingest (Clay, 1950).

#### *Mate choice trials*

The birds used in mate choice trials were selected from an aviary flock of 46 breeding pairs of pigeons located near the University of Illinois, Urbana-Champaign. The  $9.2 \times 3.7 \times 2.5$  m aviary was constructed by another worker in 1982 in the loft of a university-owned barn and was originally stocked with 72 feral pigeons captured on local rooftops and under bridges (Droge, 1986). The wire mesh aviary exposed birds to fresh air and sunlight (ambient temperature and photoperiod), while protecting them from wind and precipitation. Pigeons were fed a commercial grain mixture (Kay-tee Breeder and Conditioner Pigeon Feed #6®) and were provided with grit, water, and nesting material. Birds in the aviary bred all year, with greatest success during months of relatively moderate temperature (March–July and October–December). Wild birds in Illinois attempt to breed

year-round if the winter is mild, but normally breed from March–November (Clayton, 1989).

In July 1987, in conjunction with a study of the influence of lice on host reproduction, I fitted both sexes of 46 breeding pairs in the aviary with bits. One month later, after ranking the pairs on the basis of age and reproductive history, I randomly fumigated one of every two pairs with a 1% aqueous solution of pyrethrum (“clean” pair), and sham fumigated the other pair with water (“lousy” pair). These treatments were repeated monthly on the same selected pairs. Dilute aqueous pyrethrum has no effect on birds or mammals and leaves no residue. There was no difference in the growth rates or survival of squabs in the aviary sprayed at hatching and periodically thereafter with pyrethrum *versus* water (Clayton, 1989).

For the mate choice trials, I designated

12 "stimulus pairs" of males, each consisting of a clean male and a lousy male (both wearing bits). From the 46 males in the aviary, a maximum of 12 stimulus pairs could be created after matching for plumage color and pattern, age, weight (within 10%), and reproductive experience, all of which influence mate choice in Rock Doves (Burley, 1981). In late October I removed the 24 males comprising the 12 stimulus pairs from the aviary and isolated them in individual cages. I also removed the 24 mates of these males and six additional females for a total of 30 "choosers," which were isolated in individual cages visually removed from the cages of the males. Fourteen choosers were clean and 16 were lousy and all wore bits. The colored leg bands of all birds were removed for the duration of the study. Each bird retained a single numbered aluminum band.

Trials were performed in 3 arenas constructed by subdividing an 11 m long, frontless, roofless, cement-block shed into  $3.6 \times 4 \times 2.4$  m sections. The open ceiling and front of each arena was covered with chicken wire for good lighting and visibility. Each arena had a wooden perch along its back wall and a parallel "front" perch. The perches, which were 1.8 m apart, were 1.5 m above the cement floor. The back perch had a  $30 \times 30 \times 30$  cm wooden nest box at each end. Because pigeons prefer semi-darkened nest sites (Goodwin, 1983), the insides of nest boxes were painted black. During the trials the males of the stimulus pairs were tethered to opposite sides of the arena to prevent intrasexual interference competition (Burley and Moran, 1979). During the week prior to the initiation of the trials each stimulus pair was "practice tethered." Once tethered, males were capable of walking or flying distances of several feet, giving them access to the back perch, their nest box, and the floor of the arena. A supply of food and water was available on the floor under the nest box of each male. In all cases males quickly became accustomed to tethers.

The trials began 1 week after isolation of the aviary birds. Temperature during the trials averaged  $8^{\circ}\text{C}$  (range =  $-3^{\circ}$  to  $19^{\circ}$ ), similar to that of the previous March

(mean =  $10^{\circ}\text{C}$ , range =  $-1^{\circ}$  to  $24^{\circ}$ ), during which most birds in the aviary raised their first young of the year. I usually ran 3 trials simultaneously, and varied the duration from 5 hr to 2 days (most trials lasted 9–10 hr). The long trials were conducted to determine whether females would reverse their choice of mates (see below) on subsequent days, but this never occurred. Burley and Moran (1979) noted one such reversal over the course of 29 trials of 4–6 days each.

The use of male stimulus pairs followed a predetermined schedule. The assignment of female choosers to trials was random, except that females were temporarily skipped if assigned to a trial occurring the same day as a trial involving their former aviary mate, or a former nearest-neighbor male. The birds in each arena were visually, but not auditorily, isolated from the birds in adjacent arenas. For this reason the assignment of birds to arenas was randomized, as well as the assignment of males to nest boxes within arenas. For the most part, vocalizations or other sounds from adjacent arenas did not appear to influence the behavior of birds during trials.

At the start of a trial I placed the female chooser in a cage in the center of the arena for 15 min to ensure that she observed the males and that they observed her. I then released the female remotely and allowed her free rein of the arena for the duration of the trial. Throughout the trial, I periodically quantified the location and behavior of the female and males with 15 or 30 min sessions of scan sampling (Altmann, 1974). Scan sampling consisted of repeated "instantaneous" (2–5 sec) observations of each bird every 90 sec throughout the sampling session. The observations were made from behind a waist-high fence 6 m from the arenas. Birds largely ignored my presence during the trials. During approximately one-half of the trials I was blind to the identity of the clean and lousy males.

Female choice was scored by comparing the percent time spent by a female in proximity to each male (within 40 cm = length of arena wall's cement-blocks), including physical contact such as allopreening, billing, copulation and nesting activity.

“Choice” trials were those that met the following criteria: 1) A minimum of 70% of the time spent in proximity to males was spent with the chosen male. 2) A minimum of 95% of the time spent in proximity during the final observation session was spent with the chosen male (females associated with the chosen male 100% of the final session in 20 of 21 cases). 3) In trials terminated after sunset ( $n = 14$ ), the female roosted with the chosen male. Trials in which females did not meet these criteria were designated “no choice” trials ( $n = 9$ ), as per Burley and Moran (1979).

For 27 trials (first 3 trials excluded) I also calculated the relative time males displayed to females. Display behavior included bowing, circling, cooing, nodding, and tail dragging, all of which are ritualized behaviors used by males to attract females (Goodwin, 1983).

#### Grooming trials

After the first 12 mate-choice trials I conducted 12 “grooming trials” with just the male stimulus pairs. Excluding females allowed me to quantify male preening in the absence of displacement preening due to courtship (Goodwin, 1983). Courtship behavior did not occur during the grooming trials. I operationally defined preening as manipulation of the plumage with the bill. I also quantified scratching, an unambiguous grooming behavior always performed with the foot.

### RESULTS

#### Manipulation of parasite loads

The louse loads of sham-fumigated (lousy) males increased dramatically (mean = 1923, SD = 849, range = 387 to 2,960), whereas the loads of fumigated (clean) males were completely eliminated. The weights of lousy males did not change significantly relative to the weights of clean males ( $P > 0.10$ ; Paired *t*-test, one-tailed), diminishing the possibility of reduced general condition as a confounding variable in mate choice.

Lousy males experienced considerable plumage damage. The mean feather weight of lousy males was significantly lower than that of clean males for all 8 regions sam-

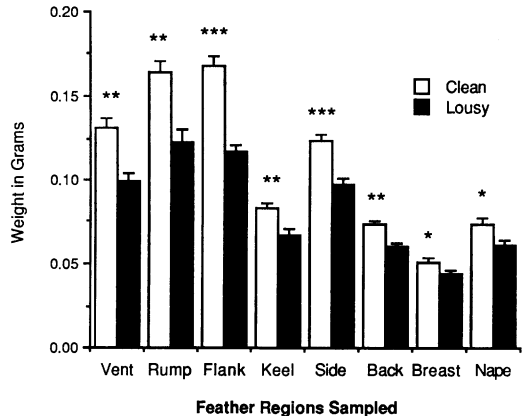


FIG. 3. Comparison of mean (+1 SE) feather weights for clean ( $n = 12$ ) and lousy ( $n = 12$ ) male pigeons. Each bar represents the average combined weight of 10 feathers selected at random from each of 12 birds. The mean feather weight of lousy birds was significantly lower for all 8 regions sampled ( $P < 0.05^*$ ,  $0.001^{**}$ ,  $0.0001^{***}$ ; Paired *t*-test, one-tailed).

pled (Fig. 3). The mean overall feather weight of lousy males was 23% less than that of clean males, a remarkable reduction given that lice consumed only the downy regions and barbules of feathers, never the much larger barbs or shafts. The comparison is conservative because both lousy and clean males were host to moderate louse loads in the aviary for several months prior to the mate choice trials. Thus, clean males were not completely free of damage when feather samples were weighed at the conclusion of the experiment.

Although extensive, none of the feather damage was outwardly visible because lice consumed only the basal-medial portions of feathers, never the distal portions (Fig. 2; Nelson and Murray, 1971). Iridescence, which is strictly limited to the distal regions of pigeon feathers, was unaffected by lice. I asked four observers, who did not know the identity of birds, to choose the male with the poorest quality plumage after 1–3 min of close-up observation of tethered stimulus pairs selected at random. Observers were wrong slightly more often than right, selecting lousy birds in only 14 of 31 cases (45%). Despite extensive handling of clean and lousy birds, I was never able to distinguish them, even in the hand, without subsurface examination of their plumage.

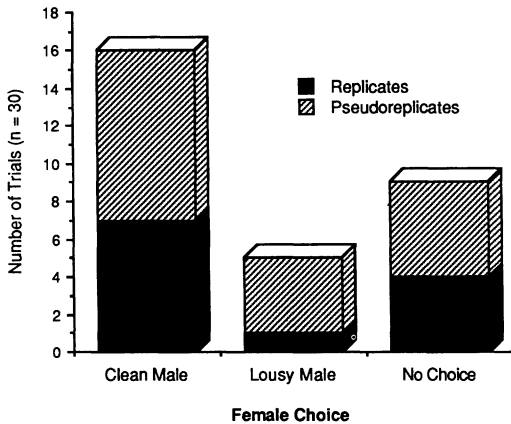


FIG. 4. Female choice of clean and lousy males. Replicate trials (#1–12) were conducted with a novel female chooser and novel male stimulus pair. Pseudoreplicate trials (#13–30) employed a novel female chooser and veteran stimulus pair.

#### Mate choice trials

Females chose males in 21 trials, but did not choose males in 9 trials (Fig. 4). Four of the 9 cases of no choice occurred during the first 6 trials, presumably because these were conducted only 1 wk after the birds were separated from their former mates. Most pigeons will remate following a 2 week separation (Levi, 1957). Females chose clean males in 16 of the 21 trials in which choice occurred, demonstrating a significant preference for clean mates ( $P = 0.013$ , Binomial test, one-tailed). Although a novel female chooser was used in each of the 30 trials, the availability of only 12 male stimulus pairs necessitated using some pairs in as many as 3 trials. The repeated use of pairs reduced the statistical independence of 18 of the 30 trials, *i.e.*, 18 trials were pseudoreplications of the 12 trials in which novel pairs were used (Fig. 4) (Hurlbert, 1984). Of the 12 trials with novel pairs, females chose clean males in 7 out of 8 cases in which choice occurred, again demonstrating a significant preference for clean mates ( $P = 0.035$ ).

Female choice was not significantly related to female louse load. Clean males were preferred by 8 of the 16 lousy females and 8 of the 14 clean females ( $G = 0.15$ ,  $P = 0.70$ ). The use of repeated male pairs should have had little effect on this analysis

because the distribution of pseudoreplications did not covary significantly with female choice ( $G = 1.36$ ,  $P = 0.25$ ; in this case the null hypothesis was not rejected despite the increased probability of a Type I error due to expected frequencies  $< 5$  (Zar, 1984)). Five lousy females and 4 clean females exerted no choice during the trials.

Although male display behavior was extremely variable during the trials (Fig. 5), clean males displayed significantly more often than lousy males. For the 27 trials in which display behavior was measured, the mean percent display time of clean males was 15%, compared to 8% for lousy males (Wilcoxon  $T = 79$ ,  $P < 0.05$ , one-tailed,  $n = 23$  trials in which display actually occurred). Fifty percent of the display time by clean males was performed by only 2 individuals (Fig. 5: G, G', H & H'). The disproportionate influence of these individuals on the data can be reduced by a categorical comparison of the number of trials in which clean *versus* lousy males were the predominant displayers ( $> 50\%$  of total display time). Clean males predominated significantly more often than lousy males (16 of 23 trials;  $P = 0.047$ , Sign test, one-tailed). Clean males also predominated in the 12 trials with novel stimulus pairs (7 of 9 trials in which display occurred;  $P = 0.09$ ).

#### Grooming trials

During the grooming trials, the time spent preening by clean males did not differ significantly from that of lousy males (Fig. 6): the mean percent preening time for clean males was 11%, compared to 12% for lousy males (Wilcoxon  $T = 30$ ,  $P > 0.5$ , one-tailed). The time spent preening by clean and lousy males within stimulus pairs was significantly correlated ( $r_s = 0.75$ ,  $P < 0.01$ ) (Fig. 7), probably due to social facilitation and/or covariation with relative humidity (Brown, 1974). Scratching, the other component of grooming behavior, was rarely observed and did not differ between clean males and lousy males.

#### DISCUSSION

Lousy males experienced a dramatic increase in louse load and a significant reduction in plumage density. Although

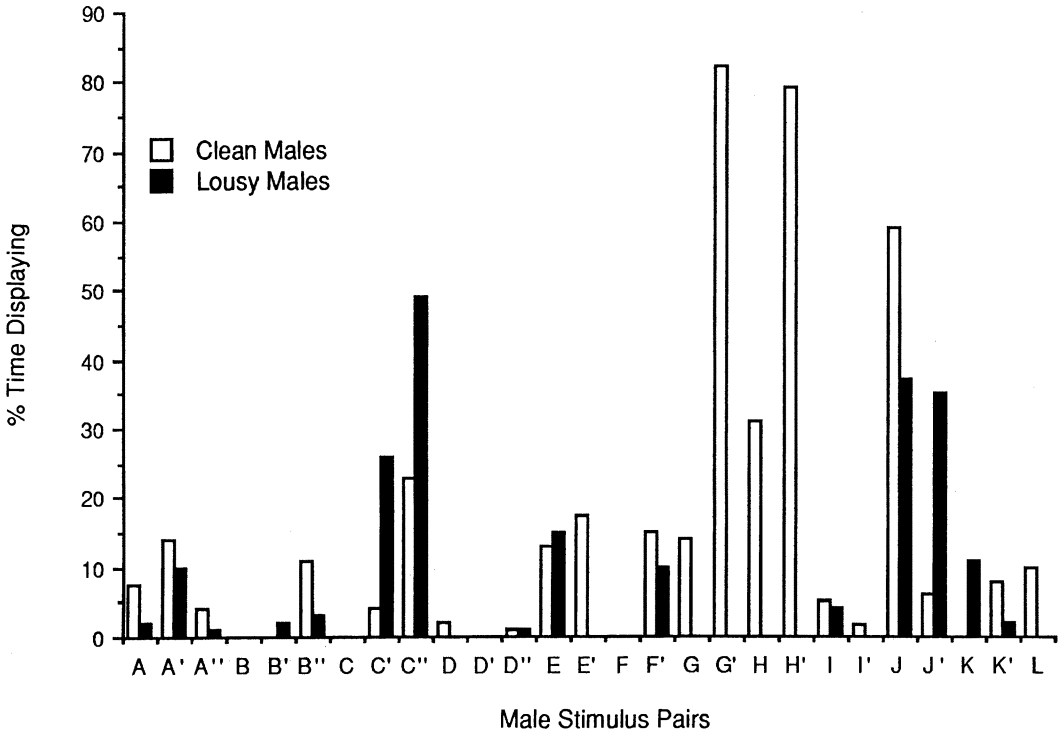


FIG. 5. The percent of time males spent displaying in 27 mate choice trials (A = Pair A, Trial 1; A' = Pair A, Trial 2; etc.).

high, the loads of lousy males did not exceed the maximum loads of wild Rock Doves in a field study of the effects of lice on host reproduction and survival (Clayton, 1989). Of 190 wild pigeons (without bits) censused in rural Illinois, 6 individuals (3.2%) supported loads as high or higher than those on the lousy birds in this study. The upper mandibles of 4 of the 6 birds were overgrown by 5–10 mm, and a fifth bird was missing the tip of its lower mandible. The remaining bird had no obvious deformities. Thus, bit-induced increases in lice mimic naturally occurring increases, which are not uncommon (Rothschild and Clay, 1952; Ash, 1960; Pomeroy, 1962; Ledger, 1969). Increases of lice and other ectoparasites may select against bill deformities in natural populations. Because louse-free Rock Doves also occur in the field (Clayton, 1989), the experimentally-induced range of variation in this study did not exceed the range of natural variation in louse load.

The results of the mate choice trials show

that females prefer to mate with parasite-free males, as predicted by the Hamilton-Zuk model. These results also suggest that the cue used by females to detect heavily parasitized males is altered courtship display. This study does not, however, con-

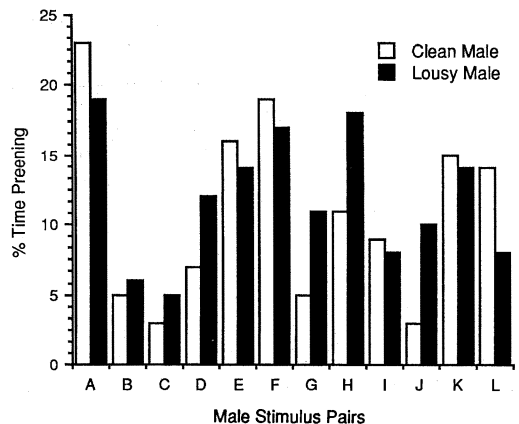


FIG. 6. The percent of time males spent preening in 12 grooming trials.

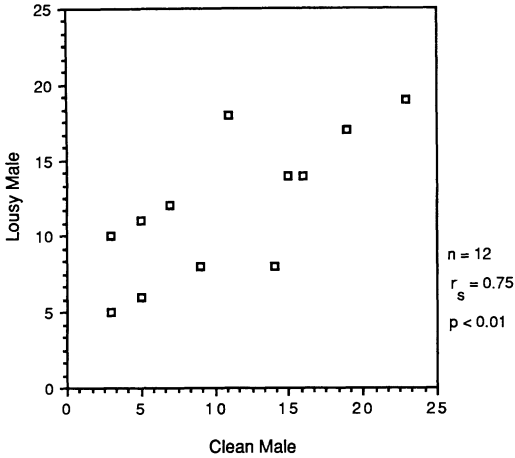


FIG. 7. Relation between the percent of time spent preening by the members of male stimulus pairs in grooming trials.

clusively demonstrate that this is the cue used. The results bearing on each of the 3 hypothetical cues presented in the Introduction are considered below.

#### *Reduced plumage brightness*

Although the lousy males were subject to plumage damage, none of this damage was outwardly visible. It is possible that the females detected damage not perceived by humans, but this seems unlikely, given that lice did not damage the surface plumage. It is more likely that the females detected subsurface louse damage—or even lice themselves—while in close proximity to males. For example, lice or louse damage might have been noticed during the common bowing display in which males approach the female with “. . . marked inflation of the neck . . . and feathers of neck, rump, lower back and belly erected.” (Goodwin, 1983).

The possibility that birds see lice directly is suggested by the circumstantial evidence for cryptic coloration in some species of Mallophaga, which may be an adaptation for avoiding host preening (Rothschild and Clay, 1952; Clay, 1957; Blagoveshchenskii, 1959; Marshall, 1981). Borgia and Collis (1990) suggest that the display and plumage patterns of Satin Bowerbirds (*Ptilonorhynchus violaceus*) enhance the ability of

females to see lice, but data to test this hypothesis are lacking. Boyce (1990) presents experimental evidence in support of the related hypothesis that female Sage Grouse (*Centrocercus urophasianus*) perceive louse-inflicted lesions on the air sacs of displaying males.

Females might also notice lice or louse damage during allopreening, a social behavior that probably helps to control inaccessible ectoparasites on the head (Hart, 1990). During the mate choice trials 6 clean males and 5 lousy males were observed allopreening with females. Five of the clean males and only 1 lousy male were chosen as mates, but these data are inconclusive due to the small sample size.

#### *Reduced display*

The display times of the clean males were greater than those of the lousy males, and may have been a cue influencing female choice. The limited displays of lousy males may have resulted from energetic constraints due to impaired thermoregulation, given their extensive feather damage. Such constraints probably would be greater under natural conditions, where courtship includes an advertisement flight in which “The bird flies outwards from the cliff or building with clapping wings, then glides with tail somewhat spread and wings lifted above the horizontal plane . . . some individuals tend to have rather more exuberant and emphasized forms of display flight . . .” (Goodwin, 1983). Although lice might affect the display flight for energetic reasons, lice probably do not affect the aerodynamics of flight because their damage is restricted to the subsurface abdominal plumage.

Despite their limited displays, the lousy males were not “sick” (*i.e.*, both clean and lousy males were generally active during the mate choice trials and the grooming trials). This is an important point in light of the Hamilton-Zuk model because sexual selection should exaggerate parasite-indicative traits only if parasites are otherwise hidden. If females can detect and avoid lousy males due to malaise or other general effects, then selection will not favor the exaggeration of secondary sexual cues.



Additional study is required to determine the extent to which lice affect the behavior of Rock Doves.

That female behavior was independent of louse load further suggests that lice had no effect on general behavior. This also illustrates the importance of considering both host sexes during studies of parasite-mediated sexual selection. To date, most researchers have ignored the direct effect of parasites on females, despite the fact that both sexes usually are parasitized in nature.

#### *Increased grooming*

The prediction that lousy males groom more than clean males was not supported; the grooming times of the clean and lousy males did not differ significantly. Brown (1974) reported a significant positive correlation between the grooming and louse loads of domestic chickens (*Gallus domesticus*). The species of louse was *Menacanthus stramineus*, a blood feeder of the suborder Amblycera, whose members promote dermatitis and itching of the host's skin (Nelson *et al.*, 1977; Marshall, 1981). The species in my study, *Columbicola columbae* and *Campanulotes bidentatus*, are both members of the suborder Ischnocera, with appendages so highly specialized for locomotion on feathers that they never venture onto the skin of the host (Stenram, 1956; Marshall, 1981). During many hours of censusing lice, I have never observed an individual of either species on a pigeon's skin. Apparently, lousy birds in my study did not groom more than clean birds because they did not perceive their high loads. In other words, the Ischnocera-control function of grooming appears to be density independent.

Because grooming was unaltered by higher louse loads, it could not have facilitated the detection of lousy males by females in my study. This counter-intuitive result emphasizes the need for accurate data regarding the natural history of parasites during studies of parasite-mediated sexual selection.

#### *Ectoparasites and sexual selection*

This study extends the application of the Hamilton-Zuk model to a *monogamous* host-

ectoparasite system. Andersson (1986) suggested that sexual selection can drive the evolution of condition-dependent traits in monogamous mating systems; a Fisherian mating advantage is not required. Of more immediate concern is whether the application of the Hamilton-Zuk model to ectoparasite systems is realistic, *e.g.*, do ectoparasites satisfy the genetic assumptions of the model? The few available data addressing this question are reviewed below and an alternative model of parasite-mediated sexual selection is proposed.

The likelihood of host-parasite coadaptive cycles is greatest when parasites are acute at one stage of the host's life history, but chronic during other stages (Hamilton and Zuk, 1982; Read, 1988, 1990). Ectoparasites are commonly acute on young hosts, but chronic on mature hosts (Rothschild and Clay, 1952; Eveleigh and Threlfall, 1976; Marshall, 1981). For example, the Mesostigmatid mite, *Dermanyssus gallinae*, which feeds on the blood of young and adult Rock Doves in central Illinois, causes extensive nestling mortality but little or no adult mortality (Clayton, 1989). Rock Dove lice are also both chronic and acute; they have virtually no effect on host survival or reproductive success during most of the year, but a significant negative impact on winter survival, presumably due to the thermoregulatory cost of feather damage (Clayton, 1989).

Although ectoparasites may be good candidates for the Hamilton-Zuk scenario, it is not known whether they (or endoparasites for that matter) undergo coevolutionary cycles with their hosts. Ectoparasites elicit antibody- and cell-mediated immune responses (Wikel, 1982) that are possibly under quantitative genetic control (Wakelin and Blackwell, 1988), and heritable resistance to ectoparasites has been documented in a few domestic hosts (Seifert, 1971; Hewetson, 1972; Nelson *et al.*, 1977). However, these data do not address the plausibility of the coadaptational cycles of parasite virulence and host defense assumed by the Hamilton-Zuk model.

Ectoparasites may also relate to the Hamilton-Zuk model indirectly. In addition to causing direct pathology, many

ectoparasites serve as vectors or developmental intermediate hosts for a wide variety of endoparasites and pathogens (Nelson *et al.*, 1977; Harwood and James, 1979). "Even at low levels ectoparasites may be a serious hazard to health as vectors of disease" (Marshall, 1981). For example, despite the fact that relatively little is known about chewing lice, they are established cyclodevelopmental hosts for a cestode and 4 filarial nematodes, including a common heartworm of swans and geese (Bartlett and Anderson, 1987; Dutton, 1905; Pennington and Phelps, 1969; Seegar *et al.*, 1976). Viruses and bacteria have also been isolated from chewing lice, but whether they are true intermediate hosts remains undetermined (Eddie *et al.*, 1962; Hewitt *et al.*, 1948; Seegar *et al.*, 1976). This indirect threat of ectoparasites to their hosts suggests that mate choice might occur on the basis of traits altered by the ectoparasitic vectors of endoparasitic pathogens. A related, less specific scenario is the "correlated infection" model of Borgia and Collis (1990).

The results of this study are consistent with an alternative model of parasite-mediated sexual selection. Rather than choosing parasite-free mates to acquire genetic resistance, choosers may select them simply to avoid the direct transmission of parasites to themselves or their offspring. Many ectoparasites, and some endoparasites, rely on direct contact between hosts for transmission (Harwood and James, 1979; Marshall, 1981). For example, Rock Dove lice are transferred in large numbers from parent to offspring in the nest (Clayton, 1989), and Ring-necked Pheasant (*Phasianus colchicus*) lice are transferred between the male and female during copulation (Hillgarth, personal communication). This ecological scenario is equivalent to the "parasite-avoidance" model of Borgia and Collis (1990), but it could more precisely be called a model of "transmission-avoidance," since both it and the Hamilton-Zuk model address parasite avoidance *sensu lato*.

Although the Hamilton-Zuk and transmission-avoidance models both predict choice for parasite-free mates, the latter

does not assume heritable parasite resistance. While the Hamilton-Zuk model postulates that additive genetic variance in fitness is maintained by host-parasite coevolution, the transmission-avoidance model makes no assumptions regarding the genetics of host-parasite interactions. Research on the quantitative genetics of parasite virulence and host resistance will help to distinguish between these alternative models of sexual selection for particular host-ectoparasite systems.

In conclusion, female Rock Doves choose louse-free males, possibly on the basis of an altered secondary sexual trait, male display. Further data regarding the specific effects of lice on host behavior are needed to positively identify the cue used in female choice. The results of this study are consistent with both the Hamilton-Zuk and transmission-avoidance models. Combined studies of the behavior and genetics (*e.g.*, Hillgarth, 1990) of host-ectoparasite interactions are needed to compare the feasibility of these models.

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