Ethology Ecology & Evolution 11: 197-201, 1999

Induced homosexual behaviour in male house finches (*Carpodacus mexicanus*): the "Prisoner Effect"

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Received 30 September 1998, accepted 20 March 1999

We observed homosexual behaviour within a captive flock of male house finches (*Carpodacus mexicanus*) that was physically isolated from females for the duration of a breeding season. Male-male begging, allofeeding and copulation attempts were linked to social dominance rank within the group, as subordinate males begged from, were fed by, and attempted to copulate with dominant males. Levels of circulating testosterone were not significantly related to inter-male behaviour. Along with the assertion of dominance, we presume that the regulation of sociosexual tension is another potential function of the male homosexual behaviour observed in this study.

KEY WORDS: homosexuality, house finch, *Carpodacus mexicanus*, social dominance, aggression, testosterone, allofeeding, copulatory behaviour.

Recent work on avian species has generated considerable interest both within and beyond the scientific community in the homosexual behaviour of birds (Angier 1998, Heg & Van Treuren 1998, Lanctot et al. 1998). In these observational field studies, homosexuality has been found to be an inherent component of the mating systems and apparently exists as the result of natural or sexual selection. Of equal interest to biologists trying to understand the function of homosexual behaviour are cases in which homosexuality is induced in a species in which the behaviour is otherwise rare or unknown. Here we report several incidents of homosexual behaviour within a captive group of male house finches (*Carpodacus mexicanus*). These males were kept in physical isolation from female finches throughout the breeding season, and we observed begging, allofeeding, and copulatory behaviour among these individuals.

In February of 1998, ten adult male house finches were captured at feeders from the Auburn University campus in Lee County, AL, USA as part of a separate

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Winners

Losers	1	2	3	4	5	6	7	8	9	10
1	X	4	4						1	
2	5	X	5	1	2	4	2			1
3	24	9	X	5	4	2	3	2	3	
4	20	2	13	X	4	2	4	4	3	
5	12	2	20	5	X	3	2	1	2	1
6	9	4	5	3	5	X	1	2	1	
7	14	7	17	8	5	5	X	1	3	
8	6	1	8	5	1	4	2	X		1
9	8	2	14	5	5	3	5	1	X	
10	8	3	6	1	1	2	5	1	1	X

Fig. 1. — Dominance relationships among the ten males used in this study. The value in each cell indicates the number of aggressive interactions either won or lost by the two participating males. Individual birds are represented by their dominance ranks (in bold) along the top and side, and males are arranged in rank order from top to bottom and left to right.

study on male dominance during the breeding season (McGraw & Hill unpub. data). Males were fitted with a US Fish and Wildlife metal band and a unique combination of coloured leg bands for individual identification. We housed males in a large outdoor cage at a site where few free-flying house finches reside, allowing the males virtually no access to females. As part of a separate study, a cage of females was located nearby, and these females were visually, but not vocally, isolated from the study males. We accumulated 6 hr of morning observations on the flock of males to determine the dominance status of individuals from all aggressive and submissive interactions. Observations were conducted from 4-16 May 1998 in 1-hr intervals during the first 3 hr of sunlight. A total of 370 interactions were observed, and for each interaction a winner and loser was determined based on the success of males in supplanting other males on perches and at food sources. We summed all wins and losses for each bird and those birds having more wins over others were assigned higher dominance ranks. The resulting hierarchy was linear with no reversals and this allowed us to assign each bird an absolute position in the flock (Fig. 1).

During these observations, we incidentally recorded a variety of types of male homosexual behaviour involving six of the males. We considered both male-male courtship, including both begging and allofeeding, and copulation attempts to be homosexual behaviours because they are sexual activities that are normally directed towards members of the opposite sex in the wild (Hill 1993). Two males were repeatedly seen attempting to solicit food from other males and two males were regularly observed feeding the begging individuals; two additional males both solicited feedings and fed (Table 1). A total of 24 feeding events were recorded. Additionally, we observed two copulation attempts.

Previous studies have shown that homosexuality can be a function of dominance behaviour in certain primates (De Waal 1989, Mazur & Booth 1998) and birds (Sauer 1972, Fujioka & Yamagishi 1981). In our flock of male house finches, despite

Table 1.

Dominance ranks, homosexual behaviour and testosterone levels of ten caged male house finches. The four males that were fed by other males in the cage were also the only birds that we observed begging for food. Males ranked 1, 5, 7 and 8 were never observed feeding, begging, or attempting copulations and these males did not have significantly different dominance ranks (Mann-Whitney U = 13, P = 0.83) or testosterone levels (U = 15, P = 0.52) than did homosexual males.

Dominance rank	Type of behaviour	Testosterone (ng/mL)
1	None	0.73
2	Feeding, was mounted	0.90
3	Feeding	0.00
4	Feeding, begging, was fed	0.58
5	None	0.21
6	Feeding, Begging, was fed	0.20
7	None	0.82
8	None	0.82
9	Begging, was fed	0.74
10	Begging, was fed, attempted copulation	0.80

very small sample sizes, feeding males (n = 4) occupied significantly higher positions in the dominance hierarchy than those being fed (n = 4) (one-tailed Mann-Whitney U-test, U = 14, P = 0.04). Males that performed both types of behaviour had intermediate dominance ranks (4th and 6th) in the flock. In every feeding event except one, a dominant male fed a subordinate male (χ^2-test, χ^2 = 20.2, df = 1, $P < 0.001$) and this is largely because the most dominant male among the six homosexuals in the flock was the feeding male in 19 of the 24 allofeeding events observed (Fig. 2). The two observed copulations were the result of the lowest ranked male attempting to mount the most dominant homosexual male on separate occasions.

Gonadal hormones have been shown to play a role in both the aggressive interactions (WINGFIELD et al. 1987) and the sexual orientation (ADKINS-REGAN 1998) of birds. We considered the possibility that these male-male behav-iours may have been hormone-mediated and measured levels of testosterone in 25-75 µl of blood plasma that was drawn from each bird after the last behavioural observation period had been completed. Extraction and radioimmunoassay procedures follow those outlined in MENDONÇA et al. (1996), but note the following additional details. Plasma samples were incubated with both tritiated testosterone and a testosterone antibody that cross-reacts 49% with dihydrotestosterone, and thus we present results as total androgens measured. Percent extraction efficiency averaged 85% and intraassay variation averaged 14%. Sensitivity of the assay was 10 pg/mL.

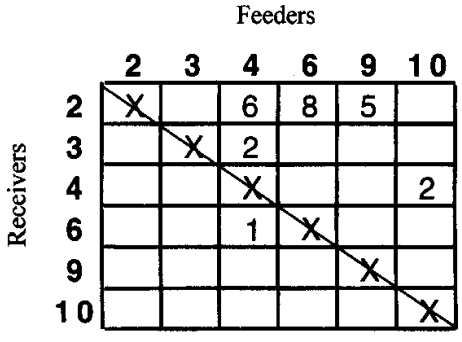

Fig. 2. — Matrix for 24 allofeeding events observed during this study. Only males that exhibited some form of homosexual behaviour are included here. Again males are identified by their dominance ranks and are arranged in rank order. Note that in all but one case a dominant male fed a subordinate male, and that males did not seem to restrict their behaviour to one mate or to a specific sex role (male or female).

We felt that our sampling technique would allow us to assess the role that testosterone played in the regulation of the social behaviours we had just observed. However, we found no significant relationship between circulating testosterone and dominance rank for the entire flock (Spearman's rank-order correlation, $r_s = 0.24$, $n = 10$, $P = 0.47$), nor were there differences in testosterone levels between allofeeding and begging birds ($U = 10$, $P = 0.28$) (Table 1). It is important to point out that testosterone may play a limited role in regulating aggression in breeding male house finches because their natural levels of circulating testosterone are uncharacteristically low for songbirds (A. STOEHR unpub. data). Additionally, testosterone may have had little to do with the proximate mediation of male behaviour in this particular study (conducted in May) because testosterone levels exhibit a seasonal decline after pair bonds are established in February and March (A. STOEHR unpub. data). Lastly, our sampling method prevented us from determining the significance of testosterone levels in the initial organization of the social hierarchy as well as the influence of other hormones on social behaviour in this flock.

In addition to reconciliation through the assertion of dominance, a number of alternative explanations have been proposed for the existence of homosexuality in birds (LOMBARDO et al. 1994). Mistaken identity has been cited as the reason for male-male copulations in common murres (*Uria aalge*) (BIRKHEAD et al. 1985, HATCHWELL 1988), but this is an unlikely cause of male behaviour in our finch flock, as sexual dichromatism easily separates the sexes (HILL 1993) and as males were familiar with one another having spent the entire breeding season in captivity together. Sexual play may also incorporate homosexual activity, typically among juveniles (FORD & BEACH 1980). However, the behaviours we observed occurred among adults, and most of the interactions were somewhat aggressive and not playful. We believe that because males were unable to pair with females and care for offspring throughout the course of a breeding season, they may have re-directed traditional pairing and parental activities toward other males. However, it does not appear that males formed stable intrasexual pair bonds, with one of the males assuming the female role (hypothesis of "feminization") (HUNT et al. 1984), because individual males did not limit their homosexual behaviour to a single "mate", nor did they confine themselves to either male or female roles (Fig. 2). Instead, male aggression appeared to mediate the sociosexual tension that contributed to the promiscuous homosexual behaviours observed in this study (SAUER 1972, HANBY 1974, DE WAAL 1989, MOYNIHAN 1998).

Male-male allofeeding (SENAR 1984) and copulations (LOMBARDO et al. 1994, LANCTOT et al. 1998) have previously been described in avian species, but not together in a captive setting such as the one we report here. Furthermore, this behaviour has never been documented in wild house finches; only male/female copulations and begging by females and chicks have been noted (HILL 1993). In this study, male house finches that were removed from a natural reproductive context and isolated with members of the same sex for the duration of a breeding season exhibited homosexual behaviour that was directly tied to aggression and tension within the group (the "Prisoner Effect"). This example highlights the potential for proximate control of sexual orientation in birds in direct response to stressful social and environmental conditions.

ACKNOWLEDGEMENTS

We thank L.A. Phillips and S. Ducharme for their assistance with aviary work, A. Stoehr for collecting blood samples, J. Ott for running hormone assays, M. Mendonça for use of lab

resources, and P. Nolan for commenting on early versions of the manuscript. Support for this work was provided by the National Science Foundation (Grant #IBN9722171 to G.E. Hill) and by the College of Science and Mathematics, the Alabama Agricultural Experiment Station, and the Department of Zoology and Wildlife Science at Auburn University. Birds were obtained under a State of Alabama permit (no. 12) and federal permit (no. 784373) and the treatment of captive birds was approved by the Institutional Animal Care and Use Committee at Auburn University (PRN #0004-R-2011).

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