Relative Importance of Vision and Olfaction for Detection of Estrus by Bulls

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ABSTRACT: The objective of this experiment was to determine the relative importance of olfaction and visual observation of heifer mounting behavior to the detection of estrus by bulls. An observation pen was designed to allow the evaluation of the preference of five sexually experienced bulls under three sets of stimuli. The observation pen was 4 m x 17 m with a smaller enclosure (2 m x 4 m) at each end that housed either a pair of heifers in diestrus (D), a pair of heifers in estrus that were allowed to mount one another (EM), or a pair of heifers in estrus that were separated by an aluminum panel to prevent mounting behavior (E). The preference of bulls was determined between EM heifers compared to D heifers, EM heifers compared to E heifers, and E heifers compared to D heifers. Each bull was individually allowed 5 min inside the observation pen to demonstrate its preference. Preference was defined as the total time that bulls spent within 2.5 m of either pair of heifers. Each bull was subjected to 10 observation periods of each set of stimuli during a 4-mo period. Bulls preferred to be near EM heifers compared with either E or D heifers (P < .05). However, the bulls demonstrated no preference (P > .05) for E heifers compared with D heifers. These data indicate that when physical contact is denied, bulls use visual observation of female homosexual behavior as the primary indicator of estrus and that olfaction alone provides insufficient stimuli for bulls to indicate preference toward heifers in estrus compared with heifers in diestrus.

Key Words: Bulls, Estrus Detection, Flehmen, Olfactory Stimulation, Pheromones, Vision

Introduction

In cattle, it has been generally accepted that bulls search for estrual heifers and cows; however, the relative importance of the sensory systems that are used by bulls to locate these animals is unclear. The relationship between the auditory communication of cattle and their estrous states has not been carefully examined. However, Alexander et al. (1980) reported that during estrus there was an increased frequency of nonspecific bellowing in cows. Tactile stimuli have been proven to be important to the bull, which will mount and serve heifers that are held immobile in stanchions with no preference for estrous animals (Chenoweth et al., 1979; Blockey, 1981). Most researchers would agree that immobilization of the heifer or cow is the final indicator of estrus to the bull. Observations by Williamson et al. (1972) and Blockey (1978) revealed that estrous heifers formed a sexually active group. Within the group, heifers were active in chin resting, chin rubbing, mounting, and being mounted. To detect estrus, bulls merely had to locate the sexually active group, which they seemed to do by visual rather than by olfactory cues (Blockey, 1978).

The importance of olfactory stimuli to bulls has recently been challenged by Geary et al. (1991), who revealed that when physical contact was denied, bulls demonstrated no preference to be near a heifer in estrus compared with a heifer in diestrus. Geary et al. (1991) further reported that the number of flehmen reactions by bulls in the vicinity of heifers in estrus and heifers in diestrus was not different. Other researchers have reported that olfaction is important to bulls and that bulls are attracted to heifers and cows as early as 4 d

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before estrus based on olfaction (Albone et al., 1986; Blazquez et al., 1988). The objective of this experiment was to determine the relative importance of visual observation of heifer homosexual behavior and olfaction for the detection of estrus by bulls when tactile stimuli were denied. The ideal experimental design for testing the importance of vision for estrus detection by bulls would include two treatments: 1) testing bulls with normal vision and 2) blindfolding the same bulls and evaluating their ability to identify an estrual heifer. However, because blindfolding bulls would require extensive training to accustom the bulls to a blindfold, we elected to provide mounting heifers as the visual cue. Similarly, the ideal experimental design for testing the importance of olfaction for estrus detection by bulls would include testing bulls before and after olfactory bulbectomy. However, because of the surgical difficulties of olfactory bulbectomy and the questionable necessity of this procedure under animal care considerations, we elected to test for olfaction indirectly by eliminating visual observation of heifer mounting behavior among pairs of heifers in estrus.

Materials and Methods

Observation Pen. Our hypothesis was that bulls use visual observation of heifer homosexual behavior rather than olfaction as the primary indicator of a heifer in estrus when physical contact is denied. We expected the bull to indicate preference by occupying for a longer time the area adjacent to two heifers in estrus that were mounting one another, compared with either two heifers in estrus that were denied mounting activity or two heifers in diestrus. The method of Geary et al. (1991), with slight modifications, was used to study this hypothesis. A 4-m x 17-m outdoor pen was designed with a 2.5-m x 4-m enclosure at each end, which contained two heifers that served as one of three possible stimuli (Figure 1): 1) estrus with mounting activity (two heifers in estrus that were allowed to mount one another, EM); 2) estrus without mounting activity (two heifers in estrus that were separated by an aluminum panel to prevent any heifer homosexual behaviors, E); or 3) diestrus (two heifers that were in the luteal phase of their estrous cycle, D). During an observation period, a bull was individually placed into the middle area of the observation pen and allowed 5 min to display a preference between the two sets of heifers. A gate covered with 15-cm² wire paneling prevented bulls from resting their chins on heifers' tailheads but did not prevent bulls from extending their noses sufficiently to ingest genital secretions. Thus, olfactory investigation by the bull was not impaired, although intense genital examination was not always possible and was dependent on the exact positioning of the heifers. Five 16- to 24-mo-old crossbred beef bulls with prior natural service experience were used. Four of the five bulls had been exposed to heifers for at least one breeding season. The fifth bull (No. 1; Table 1) had been with 20 cycling heifers for 2 mo before initiation of this project. The preference of each bull was determined toward 1) EM vs D heifers, 2) EM vs E heifers, and 3) E vs D heifers. The preference of bulls during each of these three comparisons was used to identify the stimuli that were used by the bull to identify a heifer in estrus. During observation periods that compared mounting activity with either estrous or diestrous heifers, bulls were held in a pretest area until heifers displayed mounting activity (Figure 1). Bulls were held in the pretest area for two reasons. First, because we wanted to compare mounting behav-

![Figure 1](image_url). Observation pen that was used to evaluate the preference of five bulls toward one of three sets of stimuli. As an example, this illustration represents heifers in estrus with mounting (EM) compared with heifers in estrus without mounting (E).

<table>
<thead>
<tr>
<th>Bull</th>
<th>EM-D*</th>
<th>EM-E</th>
<th>E-Db</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>233^d</td>
<td>51^d</td>
<td>182^d</td>
</tr>
<tr>
<td>2</td>
<td>150^ef</td>
<td>21^d</td>
<td>-19^d</td>
</tr>
<tr>
<td>3</td>
<td>43^d</td>
<td>47^d</td>
<td>11^d</td>
</tr>
<tr>
<td>4</td>
<td>166^de</td>
<td>7^d</td>
<td>-16^d</td>
</tr>
<tr>
<td>5</td>
<td>97^ef</td>
<td>76^d</td>
<td>9^d</td>
</tr>
<tr>
<td>Mean</td>
<td>138</td>
<td>41</td>
<td>8</td>
</tr>
</tbody>
</table>

*As an example, EM - D represents the mean time near heifers in estrus that displayed mounting activity minus the mean time near heifers in diestrus. The mean time near the heifers in estrus that were denied mounting activity is designated E.

bNegative values indicate that the bull spent more time near the heifers in diestrus rather than the heifers in estrus.

cMeans within columns that do not share a common superscript differ (P < .05).
ior, we had to be sure that the stimulus heifers were still sexually active in mounting. Second, we assumed (perhaps incorrectly) that if we were trying to compare vision with olfaction, that any volatile signal from heifers in estrus was already available to bulls and therefore an opportunity for visual stimuli should be presented to bulls before they entered the observation pen. Bulls were released into the observation pen immediately after heifers displayed mounting activity for the first time regardless of whether the bull seemed to notice this stimulus. The total time that a bull spent within 2.5 m of either pair of heifers (timed zone; Figure 1) was used to evaluate his preference. Bulls were considered to be within the timed zones by subjective observation when 75% of their body was within 2.5 m of either pair of heifers. Each bull was individually exposed to 10 observation periods of each set of stimuli (5 min each) during the 4-mo treatment period. Bulls were subjected to no more than two observation periods per day. The number of flehmen reactions and pre-ejaculatory emissions exhibited by bulls while adjacent to each pair of heifers was also recorded. Pre-ejaculatory emissions were quantified as the number of times that seminal plasma began to drip from the bulls' prepuce and not as individual drops. Bulls were housed in an area where visual contact with the heifers was not possible until they were subjected to a preference test.

Heifers. Crossbred beef heifers (350 to 450 kg) were chosen from a herd of 50 cyclic heifers by visual observation of estrus at 12-h intervals. Estrual heifers that were used in this study stood to be mounted by herdmates immediately before each observation period. Diestrual heifers that were used in this experiment were considered to be in the luteal phase of their estrous cycle based on twice-daily heat check records. The heifers were used to represent three comparisons of stimuli to bulls: estrus with mounting vs estrus without mounting, estrus with mounting vs diestrus, and estrus without mounting vs diestrus. Pairs of heifers were positioned in the respective ends of the observation pen at random. Ideally, each treatment would have been completely balanced with each heifer pair used for each bull and each observation day. However, because of the difficulties inherent to induction of estrus in a group of heifers to completely balance this experiment, we elected to assign heifers at random to each treatment group and replicate each treatment within each bull 10 times. Such an approach would tend to minimize heifer effects that may affect bull behavior.

Statistical Analysis. Because these data do not meet the criteria of independence required for parametric analysis, nonparametric methods were used in the analysis. The mean difference in time that bulls occupied the timed zone adjacent to the different sets of heifers was analyzed by Wilcoxon signed-rank test. Variations in total time between bulls and observation periods for each set of stimuli was determined by analysis of variance using a randomized complete block model with bull as the block and observation period as the class variable. Pairwise comparisons between bulls were determined by a lsd test. The mean number of flehmen reactions and pre-ejaculatory emissions exhibited by bulls while adjacent to heifers in each set of stimuli was also analyzed by Wilcoxon signed-rank test. Variations in the number of flehmen reactions and pre-ejaculatory emissions between bulls and observation periods were determined by analysis of variance using a randomized complete block model with bull as the block and observation period as the class variable.

In the preference tests comparing E heifers with D heifers, EM heifers with E heifers, and EM heifers with D heifers, the bulls entered both ends of the observation pen in 25/50, 33/50, and 23/50 observation periods, respectively. Analysis of the data excluding those observation periods when the bull did not enter both timed zones did not alter the results. The results that are reported include all the data collected to simplify statistical analysis.

Results

The preference of five bulls was observed toward pairs of heifers that served as one of three possible stimuli: estrus with mounting, estrus
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Figure 3. Comparison of the mean (+ SE) number of flehmen reactions by bulls per observation period toward heifers in estrus that were allowed mounting behavior, heifers in estrus that were denied mounting behavior, or heifers in diestrus. The mean time that bulls occupied the timed zone adjacent to EM heifers was greater \((P < .05)\) than the total time that bulls occupied the timed zone adjacent to either E or D heifers (Figure 2). However, the total time that bulls occupied the timed zone adjacent to E heifers was not different \((P > .05)\) from the total time that bulls occupied the timed zone adjacent to D heifers.

The total number of flehmen reactions by bulls throughout this experiment was surprisingly low (86 flehmen reactions per 150 observation periods). The number of flehmen reactions by bulls was greater \((P < .05)\) when they were adjacent to EM heifers than when they were adjacent to D heifers (Figure 3). However, the number of flehmen reactions performed by bulls while adjacent to E heifers was not different \((P > .05)\) from the number of flehmen reactions performed by bulls while adjacent to either EM or D heifers (Figure 3). Bulls had pre-ejaculatory emissions more frequently \((P < .05)\) when adjacent to EM heifers than when adjacent to D heifers (Figure 4). The frequency of pre-ejaculatory emissions by bulls was not different \((P > .05)\) among E heifers compared with either EM or D heifers. Differences between bulls \((P < .05)\) were observed in mean time (Table 1), number of flehmen reactions (data not shown), and number of pre-ejaculatory emissions (data not shown) in the comparison of EM vs D heifers. Similarly, a difference between observation periods \((P < .05)\) in mean time and number of pre-ejaculatory emissions was observed in the comparison of EM vs D heifers (data not shown). No other differences \((P > .05)\) were observed between bulls or observation periods.

Discussion

Our original hypothesis was that bulls use visual observation of heifer homosexual behavior rather than olfaction as the primary indicator of estrus in heifers when physical contact is denied. We expected the bull to demonstrate this preference by occupying the area adjacent to estrual heifers that were displaying mounting activity (EM) for a longer period of time than it would occupy the area adjacent to heifers at the other end of the observation pen, regardless of whether they were in estrus (E) or diestrus (D). The results of this study agree with our hypothesis and showed that when physical contact was denied, bulls preferred to be nearer to heifers that were displaying mounting behavior and thus the bulls seemed to use visual observation of heifer mounting behavior rather than olfaction as the primary indicator of estrus in heifers. These results are supported by the observations of Blockey (1978) and Williamson et al. (1972), who reported that in mating pastures, bulls located heifers in estrus by visual observation of heifer homosexual behavior rather than olfaction. In addition, Hale (1966) reported that both bulls that were blind since birth and blindfolded bulls were deficient in their ability to locate a teaser cow, whereas normal bulls mounted and served the teaser cow immediately upon entering the test area. Hale (1966) concluded that the olfactory system of bulls was ineffective because blind and blindfolded bulls often came close to the teaser cow without detecting its presence. When bulls did come in contact with the teaser cow, the bulls mounted whatever portion of
bulls with natural service experience were able to achieve adequate orientation. Our results are also supported by work previously done in this laboratory in which bulls failed to demonstrate olfactory preference toward a heifer in estrus compared with a heifer in diestrus (Geary et al., 1991).

Our data do not agree with the finding of Sambraus and Waring (1975), who reported that bulls with natural service experience were able to differentiate between estrus and nonestrous odors, whereas bulls that were trained to mount nonestrous cows showed no preference. The bulls used in our study had previous natural service experience and had never been trained to mount nonestrous cows. Sambraus and Waring (1975) did not mention the use of the accessory olfactory system (vomeronasal organ) by bulls in locating estrus odors, therefore it is assumed that bulls were able to recognize estrus odors through the use of the main olfactory system. Donovan (1967) and Paleologou (1977) have also reported that bulls were attracted to estrus odors, presumably through the use of the main olfactory system. Although it may seem that holding the bull in the pretest area of the observation pen until mounting activity began represents a bias in our study, the results of the above researchers led us to believe that estrus odors were already available to bulls held in the pretest area. Therefore, we judged that if estrus odors were available to bulls before entering the observation pen, we would create a greater bias by not allowing bulls an opportunity to use visual cues to indicate preference.

Flehmen reactions are performed by most ungulates. In the goat, flehmen reactions transfer nonvolatile substances from the mouth to the vomeronasal organ (Ladewig and Hart, 1980). This mechanism is also believed to occur in the bull, although it has not been proven. Flehmen reactions are believed to transfer nonvolatile or lowly volatile compounds in the urine and/or vaginal secretions from females to receptors of the vomeronasal organ of the male to determine whether the female is receptive. The number of flehmen reactions by the male goat was greater toward urine from does in diestrus than toward urine from does in estrus (Ladewig et al., 1980). Ladewig et al. (1980) concluded that the goats had already distinguished between the urine samples of estrous and nonestrous does by regular olfactory perception before flehmen, and that the flehmen reactions served to confirm information already received. In cattle there are reports of an increased number of flehmen reactions by bulls toward females or urine samples from females in estrus (Hradecky et al., 1983; Houpt et al., 1989). However, McGrath (cited by Hradecky et al., 1983) and Geary et al. (1991) found no difference in the number of flehmen reactions by bulls toward estrous and diestrous cows. In the present study, bulls demonstrated more ($P < .05$) flehmen reactions while adjacent to EM heifers than when adjacent to D heifers. However, the number of flehmen reactions performed by bulls while adjacent to EM heifers was not different ($P > .05$) from the number of flehmen reactions performed by bulls while adjacent to E heifers. In addition, the number of flehmen reactions performed by bulls while adjacent to E heifers was not different ($P > .05$) from the number of flehmen reactions performed by bulls while adjacent to D heifers (Figure 3). From our data, the flehmen responses did not seem to change the bulls' behavior toward the stimulus heifers. The increased number of flehmen reactions toward EM heifers was probably a function of the amount of time that bulls spent adjacent to that group of heifers. The total number of flehmen reactions that were performed by bulls throughout this experiment as quite low. Bulls performed flehmen reactions at both ends of the observation pen in only 6 out of 150 observation periods. Although the observation pen was designed so that the aluminum panels that separated the bull from the heifers would not prevent intense anogenital examination by the bulls, it may have been sufficient to discourage such examinations.

The pairs of heifers that were used as stimuli in this study seem to have provided varied degrees of sexual stimulation to bulls. When bulls were exposed to EM heifers compared with D heifers, they exhibited more ($P < .05$) pre-ejaculatory emissions while adjacent to the EM heifers. However, when bulls were exposed to both EM and E heifers, the number of pre-ejaculatory emissions exhibited while adjacent to the EM heifers was not as great ($P > .05$).

Individual differences between bulls were observed in each trait measured (mean time, number of flehmen reactions, and number of pre-ejaculatory emissions), but only in the comparison of EM heifers vs D heifers. These differences probably reflect differences in libido between bulls. Additionally, one bull (No. 3; Table 1) seemed to be somewhat afraid of the mounting behavior displayed by the heifers, even though it seemed to associate their mounting behavior with being in estrus. It is unclear, however, why these differences were only observed in one of the treatments. There were also differences in mean time and number of pre-ejaculatory emissions by bulls due to the observation period, but again, only in the comparison of EM vs D heifers. Differences due to
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the observation period probably reflect variations among the heifers that were used and/or variations due to the day of the observation period.

In this model system, heifer mounting activity stimulated more interest in bulls than did odors from estrous or diestrous heifers (Figures 2, 3, and 4). Mader and Price (1984) have demonstrated that bulls are sexually stimulated by watching other bulls breed restrained cows. This fact alone may explain the greater amount of time that bulls spent adjacent to mounting heifers. However, the reverse may be true. The bulls that were used by Mader and Price (1984) may have become sexually excited by watching bulls breed because visual stimuli provide a primary indication that a cow is in estrus to the bull. Bulls showed no preference toward E heifers compared with D heifers as indicated by the three traits measured (time, flehmen responses, and pre-ejaculatory emissions). We conclude that when physical contact is denied, bulls use visual observation of heifer homosexual behavior as the primary indicator of estrus and that olfaction alone provides insufficient stimulus for bulls to indicate preference toward heifers in estrus compared with heifers in diestrus.

Implications

These results indicate that bulls use their sense of vision rather than olfaction as a long-distance detector of estrus in heifers. These data also lead one to question the ability of bulls to locate and identify a heifer in estrus by olfaction when contact is limited, especially because this model system has been proven valid for evaluating a bull's visual preference.

Literature Cited


