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Dominance and Display Impresses the Males:

Female Bobwhite Quail Are Attracted

To Other Qualities in a Mate.

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SIGNATURE PAGE

This thesis for honors recognition has been approved for the Department of Psychology.

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Abstract

A study of Bobwhite Quail *Colinus virginianus virginianus* (Linnaeus) was conducted to determine the relationship between male-male dominance, male display ritual, and the attraction of the female to a particular male. After quantification of male dominance and display ritual, the female quail's level of attraction to a particular male was assessed. Resulting data showed a wide variation in the relationships among dominance, display, and attraction. Findings suggest that morphological traits such as eye shape and the amount of white markings on the face rather than dominance and display are what female quail seek in a mate.

Dominance and Display Impresses the Males:

Female Bobwhite Quail Are Attracted

To Other Qualities in a Mate.

Historically, mate attraction has been attributed to dominance and display. The male fights, struts, and attracts the female. The female, apparently incapable of resisting, mates with the alpha and/or the properly displaying males. The female's contribution to the reproductive process consisted of being a repository for the male's genetic material, incubator of his developing young, and caretaker of the resulting offspring. I felt this line of thought ignored the probability that the female is an active participant in choosing a mate. Females are more than pawns in the males mating strategy. Incubation and rearing are enormous reproductive investments for a female. In light of her investment, a female must be making some decisions in the mating game.

In recent years, the role females play in mate choice has been questioned and subsequently observed more closely. Findings vary among species, but it has become apparent that females are more involved in mate choice than once thought. My observations of Bobwhite quail showed that females exercised choice beyond dominance and display. The question was what attributes do male quail possess besides dominance and display? Certainly not ornamentation, as that is absent in the Bobwhite quail. The key must be in the sexually dimorphic plumage. Male quail show no sexual dimorphism other than striking facial markings and a slight difference in breast plumage. Due to a lack, or subtlety, of other cues, I hypothesized that the male's bold facial markings are either a primary attractant, or a secondary attractant that acts to focus the female's attention on a phenotypically significant characteristic.

Other research has been done in the area of female choice and mate attraction. Most is based on the fact that a female's prime directive is to choose the most suitable mate to ensure the most viable offspring (Godin & Dugatkin, 1998), and that ornamentation in the way of combs or exaggerated plumage is a good indicator of viability (Sargent, Rush, Wisenden, Hong & Yan, 1998). Ornamentation may involve some or all of the following: plumage coloration, dimorphism of color and shape of crests, ruffs or tails, weaponry, and size. In domestic fowl, Leonard and Zann found that tarsus length had the highest correlation with female attraction (1998) while in a study of Red Jungle fowl it was the male's comb size that was the main attractor (Zuk et al., 1990a). Leonard and Zuk reiterated the findings of other researchers: "Female galliforms of many species prefer males with well developed ornaments or weapons, presumably because they are reliable indicators of viability" (1998 p 1099). Zahavi's handicap principle states that if a male can sport gaudy coloration, extreme feathering, and ornamentation and still manage to survive he must possess viable genes.

Interestingly, plumage color was shown not to affect mate choice in Red Jungle fowl (Ligon & Zwartjes, 1995). Non-galliforms apparently have slightly different agendas. Hill's previous work stated that among finches plumage coloration is an indicator of mate quality (1991). This preference for certain coloration could be due to the differences in locomotion, mating habits, and the amount of cover present in each species habitat.

Veiga, in a study on sparrows, found that badges were a form of intrasexual, rather than intersexual, communication (1993). This finding indicates that many markings presumed to be enticers for females may be deterrents for opposing males.

Many species of birds, especially galliforms, rely on methods such as display. Display can be used in conjunction with, or in place of, ornamentation. Other than a platform to show off ornamentation (if present), display adequately advertises strengths such as food gathering ability, limb strength, and physical fitness (Kotiaho, Simmons & Tomkins, 2001) but there are other requirements to ensure survival. Sensory acuity is an extremely important feature for both predator and prey animals. Females are likely seeking clues about the male's sensory abilities when choosing a mate. If sensory acuity is an important cue, what criteria are the females using? Are the size, shape and location of sensory organs important? What of the bold markings about the face; are these markings intended to draw the female's attention to a particular feature? It is possible that markings may merely be aesthetically pleasing as Symanski and Burley found to be true with a species of finch (1998). Another attractor of females, discovered by Waas and Wordsworth, was symmetry (1999). It was found that female finches preferred males that were well balanced. A balanced body is a good indicator of health and vigor while inequalities of the body may signify disease or congenital deformity.

To accurately test my hypothesis a series of morphological measurements would be taken to determine what physical traits in the male are most highly correlated with female attraction. Correlations would be made between the measurements, and then be compared to the degree of successful dominance competition, display ability, and the female's attraction to each male. All sampling would occur in the same sample population.

Methods

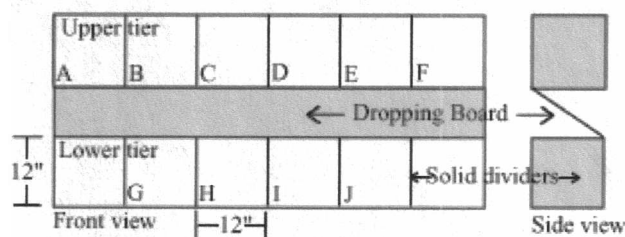
Subjects

There were 10 male subjects used in the trials, and a population of 13 females that were used as observers. The subjects in the study were Bobwhite quail *Colinus virginianus virginianus* (Linnaeus) purchased from the BlueSky Hatchery in Winston, MT. Permit #H-01-07 was procured from the Department of Fish, Wildlife and Parks in order to hold wild game. The quail were chosen because of the tendencies of galliforms to utilize dominance battles and ritual display during mating season (lekking), small size, and availability. They were reared using universally accepted methods. The chicks originated from the same hatch and varied by no more than 1 day in age. The subjects shared the same environment throughout their lives. The day length was manipulated throughout the process of raising the birds in order to simulate spring time at 17-18 weeks, the approximate age of adulthood (See Appendix A). At 7 weeks of age the birds were banded on one leg with size 5 numbered bands—recommended for quail. The bands were plastic spiral and numbered for identification purposes. The quail were able to remove their bands due to the bands large size. The rapid movement of the quail also made positive ID difficult. It became apparent an alternative method of ID would be necessary. A more efficient system was set up to prevent further ID failure. The birds were allowed to grow for another 5 weeks, and at 12 weeks were rebanded. Size 4 bands were purchased to better fit the slender legs of the nearly full grown quail. Birds would be coded using color combinations instead of numbers; therefore bands were purchased in 3 different colors: white, blue, and yellow. These bands were split in half longitudinally to allow three of each to be placed on both legs of each bird. The bands were placed on

both legs. Splitting the bands increased their flexibility, allowing for growth of the birds without inhibiting circulation. Different combinations of the three colors were placed on each bird; identical combinations of bands were applied to each leg as a precaution against accidental loss, thus eliminating the chances that a bird, or birds, would become unidentifiable. The colors were read from top to bottom and data recorded using the color order as each bird's respective ID.

At the age of 15 weeks, the birds began to show signs of having reached adulthood. Secondary sex characteristics such as plumage coloration were evident. The males were making copulation attempts at an increasing rate. Egg laying had not begun at this point, reflecting the immaturity of the females. At 17 weeks it was determined, by the advent of egg laying and successful copulations, that the birds had completed puberty. At this point the sexes were segregated. The males were housed in individual wire cages, each 12" x 12" x 12" in size. There were two tiers, 6 units per tier (see Figure 1) that were suspended from the ceiling. The partitions of the cages were of solid construction, and a dropping board placed between the two tiers to prevent the upper birds from soiling the lower birds and to keep the male birds from viewing one another. The male birds, though visually isolated from each other, were able to hear one another.

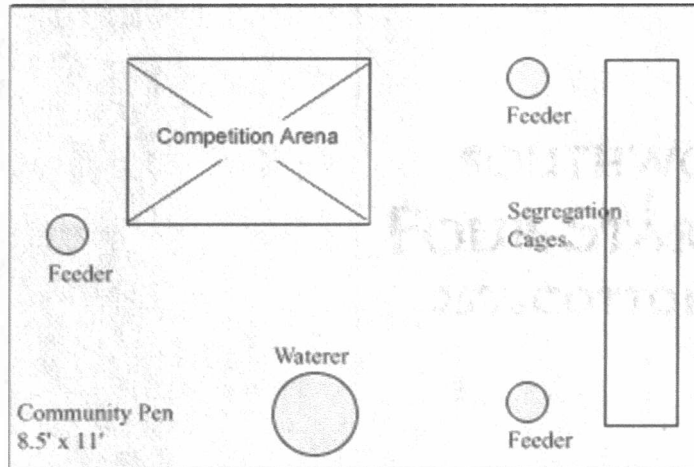
Figure 1: Segregation cages, front view and side view



Apparatus

The apparatus used for the competitions consisted of a competition arena 40" x 48" in size. It was located within the confines of the community pen (see Figure 2).

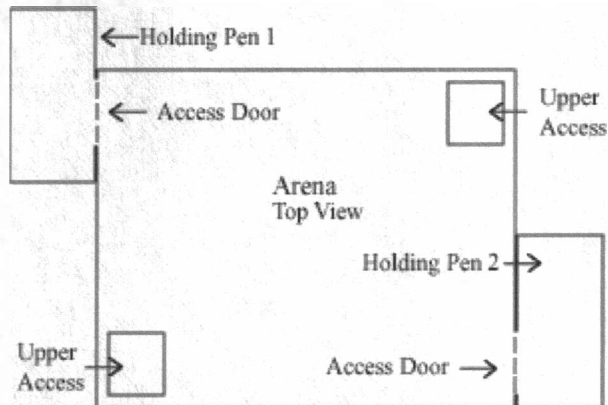
Figure 2: Location of competition arena within community pen, top view



The competition arena walls (see Figure 3) were 30" high, and the entire unit was covered with a section of $\frac{1}{2}$ " mesh hardware cloth to prevent escape. The mesh covering of the competition arena had openings at either end for simultaneous release of the males into the pen. At floor level were two entrance doors. The first door allowed a randomly chosen female, waiting in holding pen 1, to enter the competition arena and observe a competition. A second door was located at the opposite end of the pen for the exit of the competing males and observing female from the competition arena into holding pen 2. From the second holding pen, the males were immediately transferred to their respective cages and the female released into the main area to prevent being selected for another observation in the same day. Each of the before-mentioned doors was equipped with vertically sliding access doors to prevent unplanned entrance or exit from the competition

arena. The holding pens were constructed of $\frac{1}{2}$ " wire mesh and arranged so the openings matched those of the competition arena.

Figure 3: Competition arena, top view



A timer was used to ensure that no match went over 30 minutes. Tally sheets were employed to record behaviors. Other apparatus used in the study were metric rulers for the measurements of birds. A Canon 115Z 35 mm camera using Kodak B/W film was used to photograph the male birds for later analysis of features. Other equipment used in the measurement and processing of photographs included *Adobe Photoshop 6.01*, HP 3500C flatbed scanner, and an HP 960C printer. Pelouze postal scales and a black cloth bag were used to weigh the male birds. A standard, short-handled fishing net was employed to recapture any escapees. *Statistix* statistics software was used to determine correlations.

Procedure

The 10 males were each assigned an identifying letter that was recorded with their leg band code. For example D-WWW represented the male with three white bands and designated as D for the competition trials. A marker was placed on each cage with the appropriate letter and band color sequences for that cage's occupant. Six letters, from A

through J, were chosen at random and paired with each male. If a letter was chosen that matched the letter of the male in question, the matching letter was discarded and a new letter drawn. This drawing process was repeated 6 times per male, for all 10 males, totaling 60 pairings. These pairings were then scheduled so that no male would compete more than one time per day. The competitions followed the schedule laid out, with 30 minutes allotted for each pairing. At the beginning of the daily competitions, the female quail were rounded up and placed in holding pen 1 to await possible selection as observers. One female was allowed to enter the competition arena via the sliding access door. Once the female was in place, the researcher and assistant would remove the scheduled pair of males from their respective cages and simultaneously drop them through the upper access openings in the mesh top. Trials were 30 minutes each and the subject's behaviors were recorded on tally sheets.

- Male dominance—determined by the cumulative tally of the following behaviors:
 - Attack and chase—male bites opponent about head and neck and/or pursues the other male. Mueller stated that adapted aggressiveness is an important aspect in establishing dominance (1998).
 - Use of physical pushing of, or head pecks to, another male.
 - Mating—the male mounts the female and achieves cloacal contact, incomplete attempts are included.
 - Crowing (male vocalization) —two calls were counted, the “bob-white” call and a harsher “whoo-whaank” call. Crowing is status related (Leonard & Horn, 1995; Vines, 1992) as well as being “indicative of

the resource-holding potential of the rooster” (Furlow, Kimball & Marshall, 1998).

- Mate guarding—one male drives between another male and female and prevents her return by pushing her with his flank. This behavior may be due to higher levels of testosterone (T) (Saino & Moller, 1995).
- Male display—determined by the cumulative tally of the following behaviors:
 - Wing drop—male’s wings are held extended downward and the female approached laterally.
 - Feather puffing and/or shaking—when in proximity of a female the male loosens his feathers, making himself appear larger than he actually is.
- Female attraction
 - Female allows male to mate.
 - Female approaches male—the male was followed or approached by female.
 - Female makes body contact with male—female pushes into a male with her shoulder and then presses her side to his.
 - Female grooms the male—female uses her beak to smooth the male’s feathers.

These behaviors were given a hash mark for every occurrence in the 30-minute period. When the allotted time was over, the three participants in the competition were herded out of the arena into holding pen 2. The researcher and assistant would take each male bird back to his respective cage, and the female was turned out into the community pen.

This process was repeated until the matches for the day were complete and continued each day until the last match was finished. All of the matches were held as close to 12 am as possible to prevent any effect that the quail's ultradian cycles such as sleeping, eating, and grooming might have on behaviors and measurements.

Morphological Measurements

Morphological measurements were made of the birds; several different measures were taken. The initial measurement of the wing was made from the spine, between the shoulders, to the tip of the longest primary feather. The second wing measurement was made from the wrist joint to the most medial primary feather. The birds were weighed by placing them in a dark cloth bag that was suspended from Pelouze scales. The weight of the bag was subtracted from the total to find the birds weight. Measurements of the head were done using profile photographs of the birds. All photography was done using Kodak 35mm B/W film in a Cannon 115Z camera and developed pictures were scanned into *Adobe Photoshop 6.01* using a HP 3500C scanner. It is important to note that all measurements were compared as percentages and proportions to correct for any differences in image size associated with photography of live subjects. Due to the effect that neck stretch or contraction had on the area of white, only those portions of the head where the skin was immobile were considered. See Appendix B for an illustration of the measuring procedures used in determining the position and sizes of eye and head. On each bird's photograph (profile) an outline, using colored pen, of the skull was made. The bird's jaw line, occipital bump, and forehead were used as landmarks. Once the outline (A) was established, the widest points between the upper and lower portions of the head were established; this measurement is head height. Head length was measured

from the corner of the mouth to the back of the head. A bisection point was established, and a line (BC) was drawn from the corner of the mouth through this bisection point, dividing the head into upper and lower halves. A perpendicular line (DD') was drawn from BC dividing the eye in half. Drawing a perpendicular (EE') line through DD' divided the eye into quarters. The eye's distance from the corner of the mouth and the distance above the line bisecting the head determined location. To determine shape of the eye a proportion was calculated between the height and length of the eye; the head shape was determined in the same fashion. Those results closest to 1 were most round; as the resulting numbers approached 2, the eye and/or head shape became more oval. Eye height index (EHI) is the distance from the bottom of the head to the center of eye. The EHI was determined by dividing the distance between the eye's center and the bottom of the head, by the distance between the bottom and top of the head. Eye rearward index (ERI) is the distance from the corner of the mouth to the center of the eye. The ERI was determined by dividing the distance between the eye's center and the corner of the mouth, by the distance between the corner of the mouth and the back of the head. To determine the eye size relative to the head size (E:H) a grid was used. A grid was superimposed over each bird's profile photograph. By counting, within the outline drawn, all squares and fractions of squares occupied by the eye and the head (eye inclusive), the total areas of the eye and head were calculated. A proportion was figured by dividing the eye area by the head area. A smaller number represented a larger eye, while a larger number represented a smaller eye. Next the white area was tallied and a simple percentage of white was figured by dividing the total white area by the total head area (see Appendix C).

Results

Data compilation

After the data were collected scores on the following behaviors were tallied: aggression, display, attraction (to females), weight, wing length, wing width, head and eye shape, E:H (proportions), eye size, EHI, ERI, and white on the face (percentages). After arriving at each male's overall scores, they were compared using the Pearson's correlation method. Behavioral scores for the males were determined in the following manner. Each male and his competitor's behaviors were designated as either aggressive, display, or attractive. The cumulative behavior tallies (BT) of the subject (S) and his competitor (C) were added in each category. For example: $S\ BT + C\ BT = \text{total behavior (TB)}$. Next the BT of each male, per trial, was divided by TB: $S\ \text{(or C)}\ BT / TB = S\ \text{(or C)}\ \% \text{ behavior}$. The percent behavior represents the percentage of points (PP) each male scored per match. This procedure was repeated, for each male and his six competitors, and for each of the three behavioral categories. To determine overall fighting, display, or attractive abilities for a male, the PP for each of his trials was totaled. Next the PP's of his six opponents were totaled. Once again these scores were added ($S\ \text{total PP} + C\ \text{total PP} = \text{overall PP}$). Then S's totals were divided into the overall PP, the procedure was repeated for each of his 6 opponents: $S\ \text{(or C)} / \text{overall PP} = \text{overall degree of ability (ODA)}$ in any given category (dominance, display, and attraction). A table was set up listing the male's ID number along with his ODA and morphological scores. *Statistix* stats software was used to derive linear Pearson's correlations of the measurements.

Statistics

Correlations were determined using Pearson's method (See Table in Appendix D). Significance was set at .05 for a one-tailed test. The $n = 10$; therefore degrees of freedom were 9. At this level, values must lie outside of ± 0.5210 to be considered significant (Fisher & Yates, 1963). There were only six instances of significant correlation between the twelve variables (see Table 1 on page 15). These significant variables were display and weight (-0.8883), wing width and eye shape (-0.7172), wing span and EHI (-0.6281), attractiveness and wing width (-0.5983), E:H and EHI (-0.5890), attractiveness and percent white (0.5710), attractiveness and eye shape (0.6272), and E:H and ERI (0.7305). Two other variable sets were nearly significant, aggressiveness and attractiveness (-0.5126) and weight and eye shape (-0.5189), and deserve some mention. It is interesting to note that correlational significance occurred three times between variable pairs involving attractiveness and variable pairs involving eye shape.

Discussion

Rationale: Subjects and Methods

Subject choice and methods used throughout the study were based on the findings of others. Reasoning behind particular choices or actions taken will be discussed first.

Due to findings of several researchers showing relationships between aggression and age and size, the chicks originated from the same hatch and varied by no more than 1 day in age (Hoberton, Hanano & Able, 1990; Collis & Borgia, 1992). Uniformity of age and origin was important to control for any effects that body size (Hilakivi-Clarke & Lister, 1992; Turner, 1994) or experience in competitive situations (Beacham, 1988; Collis & Borgia, 1992) might have had on the outcomes of male-male competition. The

subjects shared the same environment throughout their lives, thus eliminating any competition advantages gained from prior residency (Hilakivi-Clarke & Lister, 1992; Cristol, Nolan & Ketterson, 1990; Hoberton, Hanano & Able, 1990).

Dominance that might have been asserted prior to puberty was not considered due to the findings of Nol, Cheng & Nichols (1996). These findings showed that juvenile dominance in Japanese quail *Japonica coturnix coturnix* had no relation to adult dominance.

Due to the importance of symmetry in avians, bands were placed on both legs of each bird (Waas & Wordsworth, 1999). Switching from a neutral white band to a series of colored bands was based on multiple findings. Data were found showing that the color of leg bands does not interfere with bird health (Weiss & Cristol, 1999) or dominance status (Cristol, Chiu, Peckham & James, 1992). Color combinations were easier to identify than printed numbers.

The categories of dominance, display, and attraction along with individual behaviors constituting each were compiled from information gained from personal experience and published sources. Two resources on quail mating ritual and strategy were used extensively in determining what behaviors to look for: Bent's monograph on quail found in Life Histories on N. A. Gallinaceous Birds and Armstrong's Bird Display and Behaviour.

The decision to use only one female observer per trial was made in light of Tejedo's findings on the operational sex ratio in toads (1988). Tejedo found that a scarcity of mating partners results in higher levels of aggression. In grouse it was found

that the number of females present inversely affected male behaviors (Hoglund, Johansson & Pelabon, 1997).

Segregation of the males took place to prevent any territorial establishment from taking place and to disrupt the homeostatic balance in the established social hierarchy (Cristol, Nolan & Ketterson, 1990). Though visual segregation was employed, audio isolation was impossible and may have affected the outcome of dominance trials.

Leonard and Horn found that crowing in male domesticated fowl is dominance related (1995). Some of the Bobwhite quail males may have been asserting their superiority long before the trials began.

Explanation of Results

Attraction of the female, to certain morphological traits and behaviors in the male, is the focus of the study. Comment on correlations between variables will pertain to attractive qualities and how these qualities may be genetically desirable. Comment will also be made on the variable pairs that were nearly significant.

The results indicate that a female quail tends to ignore display and dislike dominance. She does not seem to care for heavy birds with big wings. Long wings seem undesirable; even less desirable are wings that are wide. While a somewhat elliptical head is preferred, eye size and location impact choice very little. The shape of the eye, however, does seem to be important. Another important feature is the amount of white present on the male's head. These traits will be discussed in detail below.

Weight and display were most negatively correlated at -0.8883. As body weights increased, the tendency to display dropped. This may be due to a lower level of activity among heavier males. Display may decrease as weight increases because display signals

territorial possession and is not intended to act as an attracting device to females. Weight was positively correlated to aggression, although not significantly. Heavy, aggressive males may invest less time advertising possession because lighter weight males represent less of a dominance threat. This could ultimately result in fewer actual battles for the heavy male, especially involving small males that have had prior losses (Hollis, Dumas, Singh & Fackelman, 1995). In a study of grouse, Gratson found that there was an inverse relationship between weight and attractiveness and weight and display (1993). The slightly inverse relationship between display and female attraction suggests that females are selecting for a male with calmer, less dominance seeking tendencies, in short a homebody. Sapolsky determined in a study of primates that females often passively selected friendlier males (1998). Manson found the same phenomena to be true in a study that showed female rhesus monkeys were more attracted to sub-dominant males (1994). A male less inclined to spend a great deal of time in competition or display may have more time to invest in the rearing of young. Since both the female and male Bobwhite share equally in the raising of young, a tendency to be nurturing is likely more desirable.

Aggression was very close to significant levels and will be addressed. As mentioned above, females preferred calmer males. There were two types of males in the flock. They had traits very similar to types A and B found in humans. In the segregation cages some males seemed more relaxed while others were endlessly seeking a way to escape. In the community pen, certain males would react sooner than others to startling events such as loud noises or sudden movement. Interestingly the most vigilant male was also the most aggressive male, suggesting a tendency to remain at or near "fight or flight" readiness. Cristol and Johnsen found that in blackbirds high levels of T seem to be

precursors to aggressive behavior (1994). High T levels are also related to display, a slightly unattractive trait to females. Conversely, lower T levels are associated with male parental care (Justice & Logan, 1995; Vleck & Dobrott, 1993).

Wing width and eye shape were also highly correlated (-0.7172). As the shape of the wings became narrower the male's eye became more elliptical. While only two males actually demonstrated a wing flap, it is likely that a female is able to judge wing size in its folded state. The attraction to a narrower wing is puzzling; it seems a narrower wing would not provide as efficient lift for the short powerful flights of quail, resulting in a handicap. Female quail may be selecting for a smaller size, and there is an indication that wing size and span increase with weight. A greater dietary demand by heavier and/or larger offspring may be difficult to meet; therefore a female may choose for phenotype that indicates genes that would prevent offspring from becoming too large and demanding of food resources. Because of the low number of males actually displaying wing size, all wing data is potentially misleading.

Two other variables that were significantly correlated to attractiveness were percent white and eye shape (0.5710 and 0.6272 respectively). The percent white on the face had no significant correlation with any other variable, but one trait it was most highly correlated with was eye shape. It seems highly likely that the percent white may be a device to draw the female's attention to the male's eyes. Eyes that were more elliptical were preferred. Birds with more elliptical eyes also tended to be less aggressive, display less, weigh less, and have narrower wings, all traits preferred by females.

Because the birds were not sacrificed for this study, it is unknown whether it was the shape of the lids over the eye or the eye itself that caused the oval shape. If anatomy

of the eye is a factor, then it may be possible that certain eye structures indicate a level of visual acuity. Observations made of the quail indicate that vision is very important in locating food and watching for unusual events. Some artificial "unusual events" were the flying of paper airplanes or introducing strange objects into the pen; usually the same apparently hyper-vigilant birds would call the alarm. Some birds may have better close-range vision while other may have better long-range vision. Close-range vision would aid in foraging while long range vision aids in early predator detection; quail are highly predated, with almost 80% mortality in their first year (Nebraska Game and Parks Commission, n.d.). While Hedrick and Dill, in a study of crickets, found the degree of predation affects their choice in mate selection by lowering their selectivity (1993), it is felt that quail may not be driven to indifference toward the male's suitability quite as easily.

Individuals in the flock may possess their own special niche in the social structure of the flock. On the basis of family units, those birds possessing close-range vision are better providers to a female's offspring, while on the basis of community units, birds having long-range vision are better guards of the flock. While the safety of the entire community is important, a female will most likely be more interested in her genetic contribution or offspring. Small found that "female primates choose mates that care for offspring" (1994). Perhaps the short-sighted males are better able to care for these offspring. In light of the investment quail fathers make in raising the offspring, parental care giving may be what female quail seek, too. Males chosen as mates participate in the rearing of offspring once hatched and will even step in to incubate the eggs should the

female die. Bachelor males may also take on incubation duties should the natural father die, too (Nebraska Game and Parks Commission, n.d.).

It may be possible that the amount of facial whiteness on the male's face was a phenotypic signal to females. An oval eye shape allows for more white area on the head. Because the percentage of facial white was positively related to the eye's tendency towards oval shape (0.3171) and is less correlated to attractiveness, I believe that the white on a male's face is a secondary attractant, acting only to draw attention to the male's eye. A Pavlovian pairing of greater facial white and preferred visual acuity may have become hardwired in the female quail over generations, resulting in an apparently automatic preference for white. Sundberg and Larsson found that in the female yellowhammer, plumage, in the form of a more colorful mate, is a signal of parental quality (1994).

The wing span, position of the eye, head shape, and the eye-to-head size ratio of males seemed to have little impact on his attractiveness. Wingspan was negatively correlated to the EHI (-0.6281). Males having eyes set lower on the head tended to have longer wings. EHI was also somewhat positively correlated to head shape; higher set eyes were related to longer heads. EHI was significantly negatively correlated to the E:H. As eyes became larger, they tended to be set in longer skulls. Eye position is probably related to basic anatomical requirements. As the eye becomes larger the head becomes longer to accommodate sinus and orbital cavities, and the brain.

The explanations of what female quail are seeking in a mate are all highly conjectural, but gain credence through the support of other findings. While the exact reason for female trait choice is not apparent, it seems that they do in fact choose. Choice

seems to be highly related to eye shape and the amount of facial white. There is support that female choice actually drives the genetics behind the dimorphic traits of the males (Ritchie, 1996). There is also evidence supporting the fact that female choice often leads to genetic benefits (Kotiaho, Simmons & Tomkins, 2001). To summarize, it seems that female quail have certain criteria, namely eye shape and percentage of white on the face and male docility that they find attractive. The remaining measures of attraction were very near neutral. These measures were eye size, rearward location of the eye, and vertical location of the eye.

Several new studies could originate from these findings. It would be most interesting to follow up with T levels in attractive vs. unattractive (dominant) males. It would also be of some interest to determine visual acuity and its relationship to eye shape. A longitudinal study of second year males to determine the repeatability of dominance, display, and attraction may show whether these are stable traits over lifespan or whether docility can be learned. Can males who remained unmated due to excessive dominance learn to control these tendencies in successive years? Perhaps with time physiological changes occur. Humans with antisocial personality disorders become calmer with age through changes in neuroanatomy involving cortical development (Robins, 1966). If this is the basis of their aggression, do male quail undergo similar changes? Which males survive the 80% mortality rate to live and mate a second year, is it the more passive males or the dominant males? Results from such experiments would certainly be supportive of the findings of this study.

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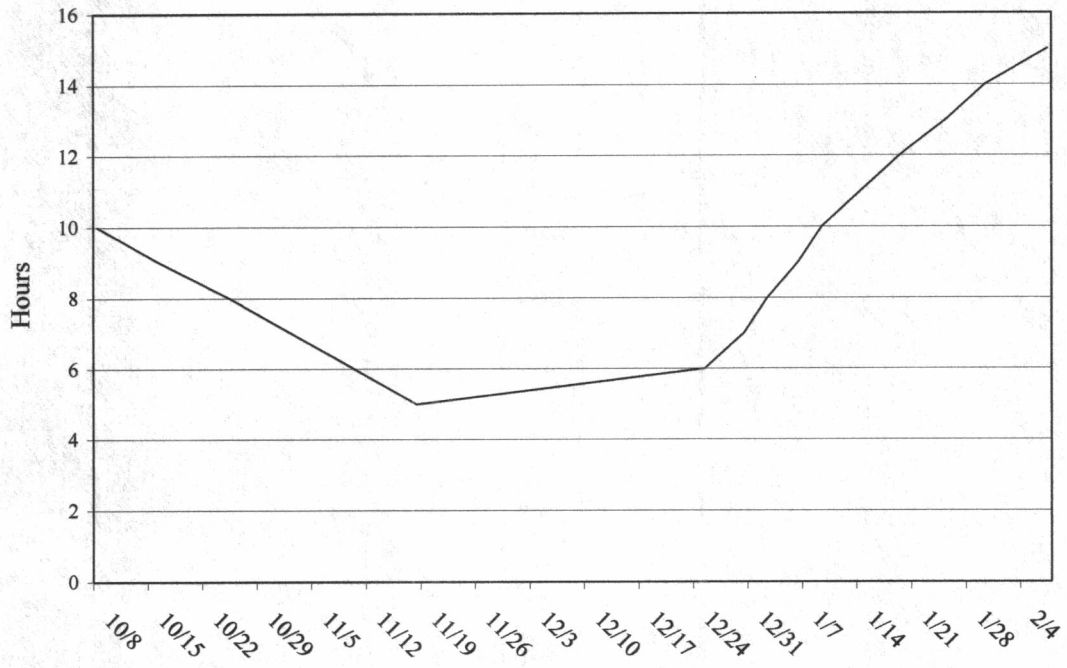
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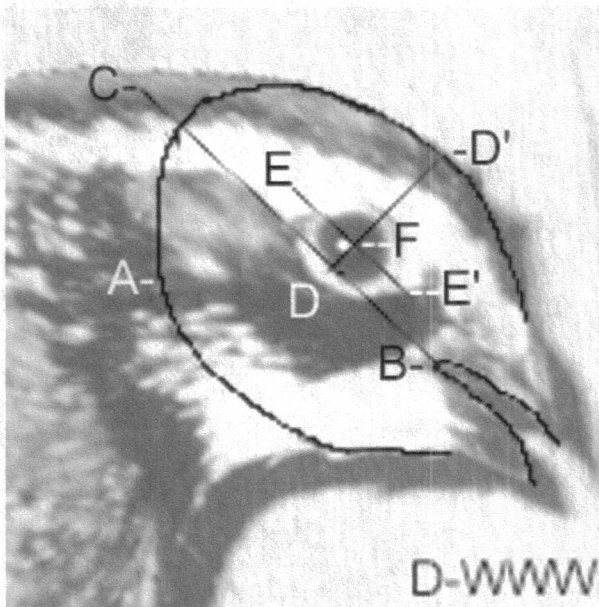
Appendix A

Hours of Light



After February 4 the light remained at a constant of 15.5 hours per day.

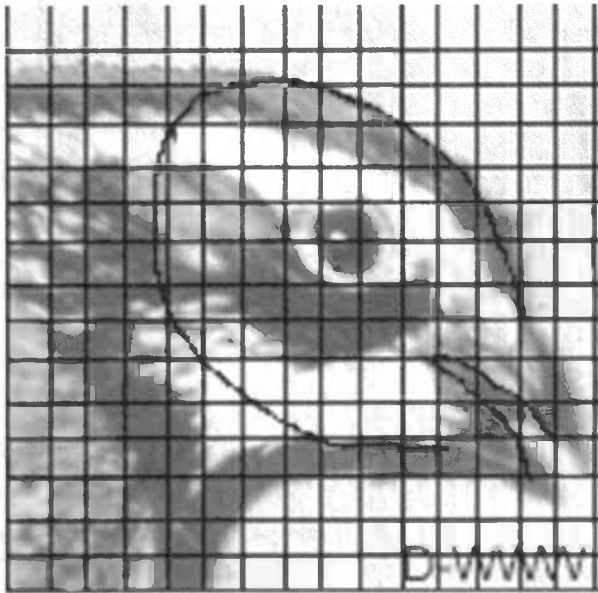
Appendix B



Methods used in creating divisions and points on the head:

- An outline of the skull A was drawn on the head using the jaw line, occipital process, and forehead as guides.
- The corner of the mouth B was located.
- The midpoint of the head between the top of the head and the deepest angle of the cheek was determined, and segment BC was drawn through those points.
- A perpendicular segment DD' was drawn from segment BC through the middle of the eye.
- Another segment EE' was drawn parallel to segment BC and through the middle of the eye. Segment EE' is perpendicular to segment DD' and intersects it at point F.
- Point F is the center of the eye.

Appendix C



Calculation of the percentage of white on the face:

Area of the head was figured by counting the squares and fractions of squares that the area within the skull outline occupied in the grid. A fractional value was assigned to partially involved squares and included in the tally. The eye and white area were tallied using the same method of counting, and a percentage for each was figured by dividing their respective total areas by the total head area. The actual grid used had vertical and horizontal lines every $1/8^{\text{th}}$ of an inch. The grid used in this figure is only a representation.

	Behavioral Measures			Morphological Measures							
	Aggress	Attract	Display	Weight	Wing Span	Wing Width	Head Shape	Eye Shape	E:H	EHI	ERI
Aggression											
Attractive	-0.5126										
Display	-0.4121	-0.1049									
Weight	0.4768	-0.1297	-0.8883								
Wing Span	-0.1178	-0.0565	-0.1405	0.1760							
Wing Width	0.0793	-0.5983	-0.0474	0.0833	0.1150						
Head Shape	-0.1927	0.2021	0.1403	-0.2087	-0.3317	-0.0027					
Eye Shape	-0.3115	0.6272	0.2281	-0.5189	-0.0433	-0.7172	0.0631				
E:H	-0.1365	-0.0907	0.3109	-0.0542	0.1050	-0.3164	-0.3874	0.0353			
EHI	0.0887	0.0254	-0.1800	-0.0407	-0.6281	-0.0050	0.3689	0.1447	-0.5890		
ERI	-0.1931	-0.0732	0.1730	0.0170	0.3776	-0.4650	-0.4482	0.1943	0.7305	-0.3124	
Pct. White	-0.2677	0.5710	0.0015	-0.1596	-0.1722	-0.2101	0.0464	0.3171	0.3616	-0.2282	-0.0940

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