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Title: Morphological and Endocrine Correlates of Dominance in Male

  Ring-necked Pheasants (Phasianus colchicus)

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An investigation of the correlation between a number of behavioral,
morphological and physiological parameters and dominance status of male
Ring-necked Pheasants (Phasianus colchicus) was undertaken. Dominant
males performed significantly more aggressive behaviors than
subordinates and a higher proportion of these behaviors was directed
toward distantly ranked subordinates. Animals could also be ranked in a
subordinance hierarchy with subordinate males performing submissive
behaviors and vocalizations at highest frequencies and directing the
largest proportion of these behaviors toward distantly ranked dominants.

A number of morphological characters were measured and their
correlations with dominance status were investigated. Several
significant correlations between certain body and wattle measurements
were found. Experimental manipulations of the wattles were conducted to
attempt to change behaviors and dominance status. Wattles of dominant
birds were painted black to make them look subordinate. Wattles of
subordinate birds were painted red to make them look dominant. Two of
the dominant birds received more aggressive behaviors from true
subordinates, after their wattles were painted. Two of the subordinate

birds received fewer aggressive behaviors from true dominants, after their wattles were painted.

Plasma levels of testicular hormones were measured during hierarchy establishment and in stable hierarchies. No correlations were found between testosterone levels and dominance status or frequencies of any of the agonistic behaviors measured. Exogenous hormones (estradiol, dihydrotestosterone, corticosterone, $ACTH_{4-10}$ and α-MSH) were injected to attempt to alter behaviors and change dominance status. These attempts were unsuccessful.

My data conform to previously published reports on the use of morphological characters as signals of dominance status. My data also corroborate the absence of correlations of testicular hormone levels with dominance status and behavioral frequencies in other species of birds. The advantages of a status signalling system are discussed and reasons for living in a group and remaining subordinate are examined.

Morphological and Endocrine Correlates of Dominance
in Male Ring-necked Pheasants (Phasianus colchicus)

by

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MORPHOLOGICAL AND ENDOCRINE CORRELATES OF DOMINANCE IN
MALE RING-NECKED PHEASANTS (PHASIANUS COLCHICUS)

INTRODUCTION

The concept of social dominance has intrigued behaviorists since the seminal work of Schjelderup-Ebbe (1922, translated in Schein, 1975). Schjelderup-Ebbe (1935) investigated the ability of domestic fowl to recognize other individuals as dominants or subordinates and the effect this social ranking had on subsequent social interactions. Later investigations attempted to elucidate the function of dominance, most frequently described in terms of priority of access to resources (DeFries and McClearn, 1970; Syme, 1974; Emlen and Oring, 1977; Banks et al. 1979). More recently, behaviorists have asked the question: Of what advantage is it to remain in a group as a subordinate (Barash, 1977; Wilson, 1980; Rohwer and Ewald, 1981)?

While behaviorists and ecologists have elucidated behavioral and environmental correlates and consequences of dominance, endocrinologists have investigated the role of hormones in the expression of dominant-subordinate relationships particularly the role of the gonadal and the adrenal hormones.

Early endocrine investigations demonstrated the importance of gonadal hormones in the expression of sexual and aggressive behaviors and dominance. Castration of male domestic fowl abolished sexual and aggressive behaviors and testosterone replacement restored them (Davis and Domm, 1943). More recent research has focused on the hormone

specificity of various sexual and aggressive behaviors (Adkins-Regan, 1981a) and the effects of social interactions on circulating hormone levels (Harding, 1981).

The pituitary-adrenal axis may exert an effect on aggressive behavior and dominance via the antagonistic interaction between adrenal secretions and the pituitary-gonadal axis. Castration of male ducks produces an increase in corticosterone, the major adrenal hormone in birds. Treatment of these castrates with testosterone reduces corticosterone levels below precastration levels (Jorgensen, 1976). Adrenocorticotrophic hormone (ACTH) may also act on the central nervous system to affect behavior independent of the release of corticosteroids from the adrenal glands (deCatanzaro et al., 1981).

The ability of an animal to recognize other individuals and to retain this recognition over time is essential for establishing and maintaining a dominance hierarchy. Schjelderup-Ebbe (1922) speculated that recognition in birds is primarily visual but did not address the question of whether certain morphological features could be used to assess fighting potential. Recognition of individuals could be based on various morphological structures including body color (Salzen and Cornell, 1967; Miskelly, 1981) head shape and comb structure (Guhl and Ortman, 1953) and plumage variability (Marler, 1955; Rohwer, 1975).

Vocalizations are also important in signalling status. The use of songs or calls in establishing and maintaining territories is well documented (Falls, 1969; Thielcke, 1976). Often, the order in which a vocalization is given, relative to other conspecifics, signals social rank (Crawford, 1942; Davies and Halliday, 1978; Kroodsma, 1979).

The social structure of the male Ring-necked Pheasant (Phasianus colchicus) provides a good system for investigating hormonal and morphological correlates of dominance. Male pheasants are gregarious in winter, setting up small groups (6-9) with stable dominance hierarchies (Collias and Taber, 1951). Observed hierarchies are linear peck rights (terminology of Bekoff, 1977) in which there is a stepwise regression of dominance status and aggression occurs in only one direction between any pair of birds. Reversals in dominance are rare. In the spring, groups begin to break up as males establish territories and attract harems. Males at or near the top of the winter dominance hierarchy are the same males that succeed in establishing breeding territories. Low ranking subordinates rarely defend territories.

Ring-necked Pheasants are highly sexually dimorphic, the males having brightly colored plumage and paired wattles surrounding the eyes. Adult pheasants undergo one molt per year, a postnuptial molt in the fall. Therefore if morphological cues based on plumage are being used to signal status, the cues used in the winter, during hierarchy formation, remain unchanged in the spring when territories and breeding harems are established. It is possible that the cues that males use to assess potential dominance status in the winter are the same cues that females use in the spring when choosing mates.

Agonistic (aggressive and submissive) behaviors and vocalizations in wild populations of Ring-necked Pheasants have been thoroughly described (Taber, 1949; Heinz and Gysel, 1970). The intimidation display given by a dominant cock to a subordinate, is very similar to the courtship display. The displaying bird orients himself laterally, fluffs his

feathers and inflates his wattles. This exaggeration of wattle size and shape in both agonistic and sexual displays suggests that it is an important secondary sexual characteristic and may play a role in signalling status.

This study presents the results of an investigation of correlates of dominance in a laboratory colony of adult male Ring-necked Pheasants. It is one of the most complete controlled experimental studies of morphological signals of status.

MATERIALS AND METHODS

<u>Animals.</u> Adult male Ring-necked Pheasants, <u>Phasianus colchicus,</u>
were used for all experiments in this study. Animals were obtained from
the E.E. Wilson Game Farm north of Corvallis, Oregon in July, 1980. The
animals were one year old when obtained and had completed one breeding
cycle under semi-domesticated conditions. Animals were maintained
indoors in 1.2 meters wide x 2.4 meters long x 1.5 meters high plywood
aviaries. All aviaries were housed in a single room with constant
temperature control (65°F) and flourescent lighting provided the sole
source of illumination. Photoperiod was maintained at 16L:8D for the
entire study. Diet consisted of Purina Turkey Growena and Purina Hen
Scratch fed <u>ad libitum.</u> Water was available at all times. Straw or hay
was used as bedding.

Each individual was marked with a pair of blue vinyl patagial wing
tags bearing a unique letter-numeral identification. I attempted to
make the bands as uniform as possible. All bands were of the same
length, shape and color. All animals were identified by both a letter
and a numeral. It has been suggested that when more than one banding
color or pattern is used, certain bands confer preferential treatment on
the bearers (Balding, 1967; Burley, 1981; Burley et al., 1982; S.I.
Rothstein, personal communication).

Behavioral Observations during Hierarchy Establishment

Twelve animals were randomly assigned to one of two experimental groups. All animals were placed in separate cages for fourteen days before testing began. Birds were visually isolated from each other during this period. To determine dominance rank, each member of an experimental group (n=6) was paired with every other member. For testing, animals were placed in a 1.2 meter wide x 1.2 meter long x 1.5 meter high aviary that was novel to both animals. Behavior was observed through a one-way glass window. The frequencies of aggressive and submissive behaviors were recorded using an Esterline-Angus 40-channel event recorder. Each pair was tested for ten minutes per day on three consecutive days (Group II) or on three alternating days (Group I). The order of testing was determined using a random number table. Time of day at which observations were made was alternated between morning and afternoon to eliminate any effects of diurnal variations in activity. The sum of the frequencies of aggressive and submissive behaviors for all three tests was used for analysis.

Five behaviors and three vocalizations were quantified in this study. They are described in the Results section. The dominant animal of a pair was considered to be the animal that showed the highest frequency of aggressive behaviors or the animal that elicited the greatest frequency of submissive behaviors from its opponent. In all cases dominance was easily determined. After dominance status was assigned to every pair in the hierarchy, rank within the hierarchy was

assigned according to the number of members each bird dominated or was dominated by.

Morphological Parameters

Prior to the first behavioral tests, the following physical measurements were taken on each individual: body weight, wing length, tail length, spur length, bill width and bill length. Wattle color was determined by comparing the wattle to the Munsell Color Atlas (1907). There was very little variation in the hue of the wattle. Apparent differences were due instead to the presence or absence of black feathers in the fleshy area of the wattle. Initially, the only wattle measurements taken were: longest horizontal and vertical measurement on right and left sides and the longest horizontal and vertical measurement of the black eyeline within the wattle. When these measurements were compared with dominance status a relationship emerged of increasing wattle size with higher status. Based on this preliminary observation a more thorough measurement of all wattle components was undertaken. Color slides were taken of the wattles of each individual. The following measurements were taken using a Zeiss MOP-3 System for Quantitative Digital Image Analysis: total area of the wattle, total area minus the area of the eye and nude skin surrounding the eye, area of the eye line, area of the red erectile tissue within the wattle (total area minus the eye, nude skin and eye line), the area of black feathering within the wattle, the percent of the wattle that is composed

of black feathers and the percent of the wattle that is composed of black feathers and the eye line (Figure 1).

Wattle Manipulations. To test the hypothesis that wattle size and the area of red tissue in the wattle is correlated with dominance, I performed a series of manipulations in which the wattles were altered in color and size. Wattles of subordinate animals were made to look like a dominant's by painting the wattle with red nail polish. All of the black feathering within the wattle was painted red. The total area was enlarged by extending the margins of the wattle with red polish. Wattles of dominant animals were made to look like a subordinate's by painting them with dark brown nail polish. Dark spots were added to the red portion of the wattle to increase the apparent black feathering in it. The total area was reduced by darkening the margins of the wattle. Each manipulated animal was tested against every other member of the hierarchy using the pair-wise testing regime previously described. So that each animal could serve as its own control the wattles were painted with clear polish. Each control animal was again tested against every other member of the hierarchy by pair-wise testing. The effects of manipulation were determined by quantifying the number of aggressive and submissive behaviors occurring before and after manipulation. The sequence of presentation of the manipulated bird was alternated. In half the manipulations, animals encountered the control first; in the other half the manipulated bird was encountered first. This was done to eliminate the possibility of sequence effects.

Statistical Methods. Behavior frequencies of the two hierarchies were arranged in matrix form. Separate matrices were made for aggressive behaviors, submissive behaviors and for submissive vocalizations. Spearman's rank correlation tests were performed on all behavioral data to test the hypothesis that higher frequencies of behavior are directed toward animals more distant in rank. Tests were one-tailed since a predicted response was being tested (Steel and Torrie, 1980).

Landau's index of dominance was used to test the degree of linearity of a hierarchy (Landau, 1951). A perfect linear hierarchy has an index of 1.0. A value less than 1.0 indicates the presence of intransitive triads in which a lower ranking animal dominates a higher ranking one or dominance is undetermined among one or more pairs of animals (Bekoff, 1977).

Analysis of morphological data was done in three ways. First, the hierarchy was divided into the dominant half composed of the three top ranking members and the subordinate half composed of the three lowest ranking members. Mean values for each parameter measured were generated for each group. The means of the two groups were compared using a Students t-test, one-tailed (Steel and Torrie, 1980).

The second analysis involved splitting the hierarchy into three groups: dominants, composed of the two top ranking individuals; intermediates, composed of the two middle ranking birds and subordinates, consisting of the two lowest ranking birds. A mean value was generated for each group and the three means were analyzed using a one-way analysis of variance. Any parameter having a significant F value was then analyzed with a Student-Newman-Keuls' test to determine

which means were significantly different (Steel and Torrie, 1980).
Finally, Spearman's rank correlation tests were performed to determine
whether any correlations exist between dominance status and any of the
parameters measured. This was also a one-tailed test since predictions
were made.

Results of the wattle manipulation experiments were analyzed in one
of three ways depending upon the type of data generated. Data from each
manipulation were organized in 2 x 2 contingency tables in which the
number of aggressive and submissive behaviors performed were scored
before and after manipulation. Each table contained the total frequency
of each behavior for all paired encounters. If only one of the cells
had a frequency of less than 5, a chi square was generated to test
whether the frequencies of the two types of behaviors were independent
of manipulation. If more than one cell had a frequency of less than 5
but at most one cell had a frequency of zero, a Fisher's Exact Test was
performed to test whether there was a significant departure from random
expectation. If two cells had a frequency of zero, the percent change
after manipulation was determined. These percentages were used for
comparative purposes. There are no statistical tests appropriate for
testing whether the changes in behaviors were significantly different
from random expectations (Steel and Torrie, 1980).

All calculations were performed on a Hewlett-Packard 97
calculator. Spearman's rank correlations, Students t-tests, one-way
analyses of variance and 2 x 2 contingency tables were performed using
programs provided by Hewlett Packard in the standard statistical

package. Fisher's Exact Tests were performed using a program provided to Hewlett Packard Company by F. Reid Creech.

Behavioral Testing for Behavioral Endocrinology Experiments

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The first behavioral endocrinology experiment performed was an investigation of the endocrine correlates of dominance. Nine birds were randomly assigned to one of three aviaries to live in triads. The establishment of a dominance hierarchy was monitored for each triad using the same behavioral criteria used in the investigation of morphological correlates of dominance. Vocalizations were not quantified during these tests. Birds were introduced just before the dark phase of the light cycle to give them a chance to acclimate to the aviary, yet keep interactions at a minimum. Observations began the day after the triads were established (Day 1). Each triad was observed for ten minutes during which behaviors were quantified and qualitative notes were taken. Additional observations were made on Days 3, 11 and 13 after triad establishment. Blood was drawn from each animal immediately following each behavioral observation. All observations and bleedings were performed at the same time of day to eliminate confounding effects of diurnal fluctuations in hormone levels.

In the second experiment the effects of living in a stable dominance hierarchy on hormone levels were investigated. Two stable triads (greater than three months coexistence) were used in this experiment. Blood samples were drawn on four different days to use in the determination of baseline hormone levels in birds experiencing little or

no fighting. To determine the effects of fighting on these birds, food
was removed for 24 hours. Encounters were staged by introducing food
into the center of the cage in a bowl large enough for one bird to feed
at a time. Animals would fight for an opportunity to feed.
Observations were conducted for 10 minutes after food was introduced.
Behaviors were quantified as in previous experiments. In addition, the
length of time each bird spent feeding was quantified. Vocalizations
were not quantified. Three encounters were staged with each triad.
After each encounter, blood was taken from each bird.

Venepuncture and Sample Processing

Blood was removed from the brachial vein using a 1 cc tuberculin
syringe with a 25 g. 5/8-inch needle. Before venepuncture the bore of
the syringe and needle were lubricated with heparin (159 USP K units per
ml saline). Syringes were held on ice until all samples were
collected. Each sample was removed to a 12 x 75 mm borosilicate glass
tube and centrifuged for 10 minutes at 1500 g at 4°C (Beckman TJ-6
centrifuge). Plasma was aspirated with a Pasteur pipette and stored in
polypropylene microcentrifuge tubes at -20°C until assayed.

Radioimmunoassay

Individual plasma samples were column chromatographed to separate
testosterone and dihydrotestosterone fractions. Each fraction was
subjected to radioimmunoassay (RIA). Chromatography and RIA were

performed using a modification of the procedure described by Wingfield and Farner (1975, Appendix A).

Validation of the assay for male Ring-necked Pheasant plasma was performed on non-chromatographed plasma. The sensitivity of the assay was 6.25 picograms per tube (t = 13.63, 2 d.f., p <0.01). The precision of the assay as measured by the within assay coefficient of variation was 3.6%. The between assay coefficient of variation was 7.1% for the assays reported. To determine the parallelism between the standard curve and pheasant plasma a pool of plasma from all males in the colony was prepared. A dilution curve of this pool was run and a linear regression of the logit transformation of the counts per minute of each sample on the log of the volume of plasma was performed. The correlation coefficient was -0.99. The equation for the regression line was $y = 3.58 - 2.05x$. The correlation coefficient for the regression line describing the standard curve was -0.99. The regression equation was $y = 2.97 - 1.68x$. The slopes of the two lines were not significantly different when compared with an F test ($F_{1,10} = 2.86$; $.05F_{1,10} = 4.96$, N.S.; Sokal and Rohlf, 1981). Parallelism of the dilution curve with the standard curve indicates that the immunoreactivity in pheasant plasma with my antiserum is not significantly different from the immunoreactivity of synthetic testosterone. The accuracy of the assay was measured by spiking the plasma pool with five different levels of testosterone standard. The amount of testosterone measured was regressed against the amount added. The correlation coefficient for the regression line was 0.998. The equation of the line was $y = 15.33 + 1.31x$. Perfect accuracy of

measurement would generate a line with a slope of one. The slope of the line generated was significantly different from one when compared with the 95% confidence interval for a slope of one (Neter and Wasserman, 1974). The low accuracy of the assay suggested the presence of plasma factors that were not removed by benzene-hexane extraction. These factors, probably protein or lipid in nature, may have been interfering with accurate measurement of endogenous steroids, perhaps by cross reacting with the antiserum particularly at lower levels. I decided to use dichloromethane extraction followed by column chromatography. Recovery of tracer following this procedure ranged from 70 to 80%.

The dihydrotestosterone assay was not validated due to extremely low levels of endogenous dihydrotestosterone.

Administration of Exogenous Steroids

A third experiment was performed to test the effects of various exogenous hormones on behavior and dominance status of males living in established hierarchies. The three triads from the experiment on endocrine changes during hierarchy formation were used.

Initially, Silastic tubing implants were used to deliver exogenous hormones (Moore, 1981). Implants were prepared from Silastic tubing (I.D. 0.58 in x O.D. 0.77 in x 20 mm in length). Each implant was packed with crystalline hormone or left empty to serve as a control. Implants were inserted subcutaneously between the scapulae. They were difficult to insert owing to extreme fragility of the skin. Because of this problem, the remaining experiments used intramuscular injections

into the pectoral muscle. The injection site was alternated from left side to right to minimize bruising.

Steroid injections were prepared by grinding the crystalline steroid with half its volume of acacia (gum arabic, J.T. Baker) and three drops of 100% ethanol. This mixture was suspended in 0.9% saline. Peptide hormones were dissolved directly in saline. Four injection regimes were used:

1. Each bird in a triad received one of the following injections daily for 22 days:

a. estradiol 17-β (Sigma). 0.05 mg in 0.1 ml saline.

b. 5-α-dihydrotestosterone (Sigma). 1.0 mg in 0.1 ml saline.

c. control. 0.1 ml saline.

Behavior was observed for ten minutes, starting sixty minutes after injection.

2. One bird of each triad was injected with 0.5 mg corticosterone (Sigma) in 0.1 ml saline, daily for five days. In one triad the dominant bird was injected; in the second triad, the intermediate was injected; in the third triad, the subordinate was injected. Behavior was observed 60 minutes after injection for 10 minutes.

3. Each bird in the triad received one of the following injections:

a. control. 0.1 ml saline.

b. corticosterone. 0.5 mg in 0.1 ml saline.

c. $ACTH_{4-10}$ (Peninsula Laboratories, Inc.). 10 µg in 0.1 ml saline.

Injections were delivered daily for three days. Behavior was observed 60 minutes after injection.

4. Each bird in the triad received one of the following injections daily for two days:

a. control. 0.1 ml saline.

b. corticosterone. 0.5 mg in 0.1 ml saline.

c. α-MSH (Sigma). 10µg in 0.1 ml saline.

Injection doses for sex steroids were based on the injection regime used on Japanese quail by Adkins and Pniewski (1978). Injection dosages for corticosterone were based on work by Deviche (1979) on Rouen ducks and adjusted for body weight. Dosages for $ACTH_{4-10}$ and α-MSH were based on work done on guinea pigs by Rodriguez-Sierra et al. (1981).

RESULTS

Behaviors

The agonistic behaviors and vocalizations used to determine
dominance in this study have been described in wild populations of Ring-
necked Pheasants (Taber, 1949; Heinz and Gysel, 1970). To my knowledge,
this is the first report of these behaviors and vocalizations in a
laboratory colony of Ring-necked Pheasants.

To determine dominance status five behaviors and three vocalizations
were quantified. Each behavior and vocalization could be categorized as
either aggressive or submissive. The aggressive behaviors observed
were:

Pursuit. - One male walks or runs toward another male and attacks or
displaces him.

Peck. - One male strikes his opponent with the tip of the beak,
generally directing it toward the head, nape or back. Frequently
feathers are pulled out from these areas. During very intense
encounters, the dominant male may also attempt to spur his opponent
by leaping onto his back and gouging with the tarsal spurs.

Intimidation Display. - The displaying animal orients his body
horizontally to the ground, tail feathers flared, wings slightly
drooped, contour feathers fluffed, pinnae raised and wattles

engorged. This display may be given with a frontal orientation to the opponent but is most often given in a lateral orientation. Occasionally a hoarse growling call, the antagonistic call (Heinz and Gysel, 1970), is given during this display. Since it was only heard as a part of the intimidation display in this study, it was not quantified separately.

The submissive behaviors observed were:

Flee. - One male walks or runs from a displaying or attacking male. Occasionally, a subordinate animal would flee from a dominant that approached too closely in a non-threatening manner, such as backing into or walking in the direction of the subordinate.

Fly Up. - This behavior consists of a spring into the air from a sitting, standing or running position and vigorous flapping of the wings. This behavior was performed by a subordinate to avoid the approach or attack of a dominant. It was also performed by a dominant as a displacement behavior during an attack or intimidation display. High frequencies of submissive behaviors or vocalizations by the subordinate also elicited this behavior from the dominant bird.

The only aggressive vocalization quantified was the crow. This vocalization was given frequently by isolated birds but rarely heard

during paired encounters. It is a harsh, disyllabic call that is
thought to be used in advertising the presence of a male.

The submissive vocalizations quantified were:

Alarm Call. - Predominantly mono- or disyllabic occasionally,
trisyllabic, the alarm call has been called the "tucket" or
"tucketuck" call. It was uttered by dominants and subordinates but
most frequently by subordinates. It was given in response to a
pursuit, peck, intimidation display or to a perceived threat such as
the non-threatening approach of a dominant.

Pecked Call. - The pecked call is a high pitched squeak uttered by
males while being pecked. This call was also uttered when a bird
was threatened either by a male exhibiting an intimidation display
or merely by the presence of a dominant in the test cage.

Hiss. - This call was given by a bird in various intimidating
situations. In this study it was heard only when birds were
approached by humans such as during feeding or handling. It was not
heard during any agonistic interactions and so was not quantified.

Establishment of the Hierarchy

The frequencies of aggressive behaviors performed by each member of
the two hierarchies are summarized in Table 1.

In Group 1, the alpha bird, B2, directed aggressive behaviors toward all members of the hierarchy. Higher frequencies were directed against members of lowest rank. The beta bird, B1, never displayed any aggressive behaviors during these tests. His rank was accepted by the four lower ranking birds and conceded by the performance of submissive and avoidance behaviors toward him. A3, the gamma bird, displayed low frequencies of aggressive behaviors toward the three lower ranking birds. The three lowest ranking members never performed any aggressive behaviors during these tests. This hierarchy is a linear peck right hierarchy (Bekoff, 1977) in which assertions of dominance occur only in one direction. This explains the lack of data points below the diagonal drawn through the matrix. Linearity, as measured by Landau's index of dominance, was established after only three encounters (Table 2).

In Group II (Table 1) the alpha bird, D3, also performed aggressive behaviors at high frequencies. The trend noted in Group I, in which higher frequencies were displayed against more distantly ranked members, is evident in Group II. A2, the beta bird, performed aggressive behaviors at a low frequency. C2 the gamma bird, was most aggressive towards lower ranking members. E1, the delta bird, was initially dominant to A2, the beta bird, thus the entry of behaviors below the matrix diagonal. This dominance was reversed in subsequent trials and maintained throughout the rest of the experiment. The two lowest ranking birds performed no aggressive behaviors. This hierarchy is also a linear peck right, with linearity being achieved after only two encounters (Table 2).

To test the hypothesis that high ranking individuals performed aggressive behaviors at higher frequencies than low ranking individuals, a Spearman's rank correlation test was run on individual totals for all aggressive behaviors displayed to other members of the hierarchy. In Group I the correlation was marginally significant ($r = 0.71$, $t = 2.04$, 4 d.f., $p = 0.058$). In Group II the correlation was significant ($r = 0.76$, $t = 2.34$, 4 d.f., $p < 0.05$).

The frequencies of submissive and displacement behaviors performed by each member of the two hierarchies are summarized in Table 3.

In Group I the occurrence of data points predominantly below the matrix diagonal illustrates the one-way nature of submissive behaviors. The occurrence of four data points above the diagonal represents displacement behavior, not submissive behavior. A pattern similar to Table 1 is evident in which submissive behaviors are displayed only toward higher ranking members. These behaviors are displayed with higher frequency toward animals that are more distant in rank compared to frequencies displayed toward closely ranked individuals. A Spearman's rank correlation test on these data showed a highly significant correlation between frequency of submissive behaviors performed and status ($r = 0.943$, $t = 5.67$, 4 d.f., $p < 0.005$).

In Group II (Table 3) a similar pattern was found. Most submissive interactions occurred only in one direction. Four of the five data points above the diagonal represent displacement behavior. The fifth data point (E1-A2) represents an initial dominance by E1 that was reversed. The trend toward higher frequencies of behaviors displayed toward more distantly ranked members is evident in this Group. A

Spearman's rank correlation test on Group II data showed a poor correlation between status and frequency of submissive behaviors performed ($r = 0.43$, $t = 0.95$, 4 d.f., $p < 0.2$). This low correlation is due primarily to the fact that the omega bird, C3, showed a low overall frequency of behavior.

A summary of submissive vocalizations may be found in Table 4. In Group I (Table 4) the vocalization matrix is very similar to the submissive behavior matrix. Interactions were again primarily in one direction with birds vocalizing at higher frequencies toward more distantly ranked birds. A Spearman's rank correlation test on these data shows a significant correlation between status and the frequency of submissive vocalizations ($r = 0.886$, $t = 3.82$, 4 d.f., $p < 0.01$).

In Group II (Table 4) the one way nature of these interactions is evident but the trend noted in Group I is less pronounced. Animals C2 and E1 display this trend. A Spearman's rank correlation test on Group II data shows only a moderate correlation between rank and vocalization frequency ($r = 0.60$, $t = 1.5$, 4 d.f., $p < 0.1$).

A summary of the data from both experimental groups reveals that the alpha birds performed the highest frequencies of aggressive behaviors and were most aggressive toward birds of low rank. The beta birds displayed very little aggression, in spite of their high rank. The gamma birds performed aggressive behavior at low frequencies and were most aggressive to distantly ranked birds. The three lowest ranking birds showed no aggression once their status was determined.

The subordinance matrices for both groups were similar. Submissive behaviors were displayed only toward higher ranking members. The

highest frequencies of submissive behaviors were shown toward animals
distant in rank. The matrices of subordinate vocalizations show a
pattern similar to that of submissive behaviors.

Throughout the rest of this study the term "aggressive behaviors"
includes the aggressive vocalizations described. The term submissive
behaviors includes the submissive vocalizations described.

Morphological Parameters and Dominance

During observations of hierarchy formation, when two birds were
placed in the observation chamber, they inspected each other visually
and one animal quickly conceded the position of dominance to the
other. It seemed likely that animals were using some morphological
character as a cue to an individual's potential status. The following
morphological parameters were measured and analyzed for correlations
with dominance status: body weight, wing length, tail length, left and
right spur length, bill width and bill length. These measurements are
summarized in Table 5.

The following wattle measurements were analyzed for correlations
with dominance status: total area of the wattle, total area minus the
area of the eye and bare skin surrounding the eye, area of the eye line,
area of the red erectile tissue within the wattle (total area minus the
eye, bare skin and eye line), the area of black feathering within the
wattle, the percent of the wattle that is composed of black feathers and
the percent of the wattle that is composed of black feathers and the eye

line (Figure 1). These measurements are summarized in Table 6 (Group I) and Table 7 (Group II).

A Student's t-test was used to compare the mean value of each parameter in the three top ranking birds (dominants) with the mean value for the three lowest ranking birds (subordinates). In Group I wing length was significantly longer in the dominant birds ($t = 2.65$, 4 d.f., $p < 0.025$). In Group II total wattle area (right side) was significantly larger in the dominant birds ($t = 2.12$, 4 d.f., $p < 0.05$).

Since animals in the middle ranks of the hierarchy are not really dominant or subordinate, the data were split into three groups: the dominant mean, generated by averaging the values of each parameter for birds 1 and 2; the intermediate mean which was the average of each parameter for birds 3 and 4; the subordinate mean which was the average of each parameter for birds 5 and 6. The three means were analyzed with a one-way analysis of variance.

In Group I, two parameters showed significant differences between the three groups; left spur length ($F_{2,3} = 12.38$, $p < 0.05$) and left eye line ($F_{2,3} = 16.22$, $p < 0.025$). Analysis of left spur length by the Student-Newman-Keuls' test revealed that dominant birds ($\bar{x} = 16.5$ mm) had significantly longer spurs than intermediates ($\bar{x} = 6.5$ mm) and subordinates ($\bar{x} = 6.0$ mm). Analysis of the left eye line means showed that subordinates ($\bar{x} = 100$ mm^2) had significantly larger eye lines than intermediates ($\bar{x} = 53.85$ mm^2) and dominants ($\bar{x} = 54.85$ mm^2). One way analysis of variance testing of all the morphological parameters in Group II revealed no significant differences.

Finally, Spearman's rank correlation tests were run on each of the parameters to determine whether the size of any morphological characteristics could be used to predict status.

In Group 1, four of these parameters were statistically significant: wing length ($r = 0.89$, $t = 3.90$, 4 d.f., $p < 0.01$); tail length ($r = 0.77$, $t = 2.41$, 4 d.f., $p < 0.05$); left spur length ($r = 0.76$, $t = 2.34$, 4 d.f., $p < 0.05$) and percent black feathering plus eye line, left side ($r = 1.0$). In Group II none of the morphological parameters were significantly correlated with rank.

Visual inspection of wattle measurements suggested that the wattle may be an important cue in assessing an individual's potential status. Total area of the left wattle in Group 1 declines with decreasing status. Only one bird, E2, is out of the predicted order. The same trend is present in the measurements of total area minus the eye and bare skin of the left wattle. The eye lines on both right and left sides, are largest in the subordinates (Table 6). In Group II the area of black feathers in the right wattle increases with decreasing status with only the omega bird, C3, being out of the predicted order.

Examination of the morphological parameters that are significantly correlated with dominance suggests that the wattle may be an important status signal. In Group I there was a perfect correlation between status and the percentage of black feathering plus the eye line (left side). As status decreases, the percentage of black in the wattle increases. Although the correlation is not significant there is a trend toward a decrease in total wattle area and total area minus the eye and bare skin (left side) with decreasing status. The eye lines on both

sides are largest in subordinates. In Group II the total wattle area on the right side was significantly larger in dominant birds. The area of black feathers in the right wattle increases with decreasing status but the correlation is not significant. These correlations and trends suggest that larger redder wattles signal high status and smaller blacker wattles signal low status.

Wattle Manipulations - Group I

The observations of behavioral and morphological correlates of dominance led to the following predictions: (1) if a dominant animal is painted to look subordinate (wattles darkened and made smaller) the frequency of submissive behaviors shown by subordinates should decrease; (2) there may be an increase in aggressive behaviors leading to a reversal in dominance involving an animal very close in rank; (3) there may be an increase in aggressive behaviors by the painted dominant male, in response to the change in behavior of subordinates; (4) a subordinate, painted to look dominant (wattles painted red and made larger) should receive lower frequencies of aggressive behaviors from higher ranking birds; (5) a painted subordinate may respond to the change in the dominants' behavior by performing more submissive or displacement behaviors.

To test these predictions a series of experiments was performed in which the size and color of the wattles were manipulated and the effects on behavior quantified.

Only the two highest ranking and two lowest ranking birds were chosen for manipulation. Since behavioral differences were most pronounced between birds of widely separate status, I felt that if manipulating wattles produced any behavioral effects, these effects would be most pronounced among members at the extreme ranks of the hierarchy.

In Group I, E2, the fifth ranking bird was out of the predicted place in the hierarchy based on wattle size (see Table 6). C1, the fourth ranked bird, was manipulated in his place.

Results were analyzed by combining responses of all birds dominant to the manipulated bird and all responses of birds subordinate to him. Predicted results were made based on the behavior patterns observed during hierarchy formation (Tables 1, 3 and 4). Table 8 summarizes the predicted and observed results of the manipulation of the dominant and subordinate birds of Group 1. Also see Appendix B for a summary of the raw data used in compiling Table 8.

In three of the four birds, manipulation of wattle size and color produced significant changes in behavior in other members of the hierarchy.

When B2, the alpha bird, was manipulated to look subordinate, other subordinates responded with the predicted increase in aggressive behaviors and an unpredicted increase in submissive behaviors. Their change in behavior was highly significant. The manipulation of the other dominant, B1, to look subordinate produced a four-fold increase in the frequency of aggressive behaviors in the other dominant, B2. Other subordinates displayed the predicted increase in frequency of aggressive

behaviors with a reversal of status occurring with the third ranked bird, A3. No change in the frequency of submissive behaviors occurred but the overall change in behavior was highly significant. When the intermediate (C1) was manipulated to look dominant, other dominants displayed aggressive behaviors (x^2 = 0.08,N.S.). Other subordinates showed a three-fold increase in the frequency of submissive behaviors. Following the manipulation of the lowest ranked bird, B3, dominants displayed significantly fewer aggressive and submissive behaviors.

The individual response of each member of Group 1 to the manipulations was also examined (Tables 9-12; Appendix C summarizes the raw data used in compiling these tables). In the combined data the manipulation of B2 (darkened wattle) produced a predicted increase in aggressive behaviors by the other birds. This increase was due to the response of one bird, A3. A3 showed a highly significant increase in aggressive and submissive behaviors. Three of the other birds, B1, C1 and B3 showed an increase in submissive behaviors, 36%, 11% and 82% respectively. None of these data are analyzable. Only E2 showed the predicted decrease in submissive behaviors (38%, Table 9).

To determine whether these unpredicted responses were due to differences in B2's behavior after darkening the wattle the responses of the manipulated birds were examined. Data were combined to yield responses to all birds dominant to and subordinate to the manipulated bird (Appendix D summarizes the raw data for these analyses). Responses of the manipulated bird to each member were also examined (Tables 9-12; Appendix E presents the raw data used in compiling Tables 9-12).

B2 showed an 11% increase in aggressive behaviors toward other birds after manipulation. Analyses of his responses to individuals reveal that this increase was displayed to B1(40%), A3 (seven-fold increase) and C1 (52%), the birds closest in rank to B2. B2 responded to the lowest ranking birds, E2 and B3, with a decrease in aggressive behaviors, 61% and 39%, respectively (Table 9).

In summary, the manipulation of the alpha bird, B2, to look subordinate produced a marked response by all members except C1. They responded with an increased frequency of agonistic behaviors. The unexpected increase in submissive behaviors displayed toward B2 may be a response to the increase in aggressive behaviors directed by B2 toward the three birds immediately below him in rank.

As discussed previously, painting B1 to look subordinate produced an increase in aggressive behaviors by subordinates and by the other dominant, B2. This increase in aggressive behaviors by subordinates was due to the challenge and reversal in dominance by A3, his immediate subordinate (Table 10). The only dominant, B2, responded to the manipulation of B1 with a predicted increase in aggressive behaviors (greater than four-fold).

B1's responses to other members before and after his wattles were darkened are not statistically analyzable but definite trends are present (Table 10). B1 displayed an increase in submissive behaviors after manipulation (71-fold increase) to the other dominant, B2. He displayed an increase in both aggressive and submissive behaviors to other subordinates. His behavior changed only toward the two members closest to him in rank, B2 and A3. He displayed an

increased frequency of submissive behaviors to both animals (71-fold increase to B2; 0 to 96 acts to A3) and an increase in aggressive behaviors to A3 (0 to 21 acts; Appendix D).

The overall pattern of the change in response to the manipulation of B1 to look subordinate is highly significant (Table 8). Changes occurred in the predicted direction and were of the greatest magnitude in closely ranking birds.

The manipulation of the intermediate, C1, to look dominant produced a non-significant decrease in aggressive and submissive behaviors, by other dominants and an increase in submissive behaviors by other subordinates. Individual responses to C1's manipulation are summarized in Table 11. Two of the three animals dominant to him, B2 and A3, displayed less aggression to him after his manipulation. One of his subordinates, E2, showed an increase in submissive behaviors (three-fold).

C1's response to other dominants after his wattles were painted red was a decrease in submissive behaviors (18%). His change in response to other dominants was due to his response to two birds, B2 and A3. He displayed a 45% increase in submissive behaviors toward A3 the bird immediately above him in rank. He responded to B2 with a decrease in submissive behaviors (31%, Table 11). He showed no change in behavior toward other subordinates.

In summary the response of Group I to the manipulation of C1 is a nonsignificant change in the predicted direction. Birds closest in rank showed the greatest magnitude of response.

The manipulation of the lowest ranking bird, B3, to look dominant,

produced a significant decrease in aggressive and submissive behaviors from other members of the hierarchy. This decrease was most evident in the response of B2 and E2. A3 displayed an increase in submissive behaviors (53%). C1 responded with a decrease in submissive behaviors (33%) and B1 showed no change in response. Table 12 summarizes the individual responses to B3's manipulation.

B3 responded to other birds with an increase in submissive behaviors (70%) after his wattles were painted red. An examination of his response to each member (Table 12) reveals that this increase characterized his response to four of the other birds. The increase in submissive behaviors was greatest toward E2 and C1, the animals closest in rank to B3 (Table 12). He responded to the fifth bird, B1, with a slight decrease in submissive behaviors (12%).

The overall response to the manipulation of B3, the lowest ranking bird, was highly significant. All birds except one showed a marked response, a decrease in agonistic behaviors, to his apparent increase in status. The two birds closest to him in rank did not show the predicted response.

Wattle Manipulations - Group II

In the Group II hierarchy, the two most dominant and two most subordinate birds were chosen for manipulation. Unlike Group I the correlations between each wattle measurement and status were not significant in this group. There was a distinct trend toward an increase in the percentage of black feathers in the wattle (left and

right) with decreasing status. On this basis I chose to manipulate Group II in the same way as Group I. The two dominant birds were manipulated by darkening their wattles. The two subordinates were manipulated by adding red to their wattles.

Table 13 summarizes the predicted and observed results for the manipulation of the Group II hierarchy (see also Appendix F for raw data used in compiling Table 13). Only one of the four manipulations performed produced significant behavioral changes.

Manipulation of D3, the alpha bird, produced an unpredicted increase in submissive behaviors by the other birds (Table 13). The response to the manipulation of the other dominant, A2, to look subordinate was not in the predicted direction. The alpha bird, D3, showed a decrease in aggressive behaviors and the other subordinates responded with an increase in submissive behaviors (Table 20). Painting the subordinate, A1, to look dominant produced no significant change in the behavior of birds dominant to him. The only subordinate, C3, showed no response to A1's manipulation. The manipulation of C3, the lowest ranking bird, to look dominant, produced the only significant change in behavior in this group. The other members showed the predicted increase in submissive behaviors and decrease in aggressive behaviors (Table 13).

Individual responses to each manipulation were examined (Tables 14-17; Appendices G and I present the raw data used in compiling Tables 14-17). Although the increase in submissive behaviors by other subordinates to D3's manipulation (wattles darkened) was not predicted, every individual showed this response (Table 14). Only those data from the D3 vs A1 encounters could be statistically analyzed, but the

observed increase was not significant (Table 14). Three of the other subordinates, A2, C2 and C3, showed marked increases in submissive behaviors.

D3's behavior to the other birds was analyzed (Appendix H presents the raw data for these analyses). He displayed a significant increase in both aggressive and submissive behaviors (p = 0.039, Fisher's exact test). D3 displayed an increase in aggressive behaviors toward three of the five birds; A2, C2 and A1. D3 showed less aggression to E1 and C3 (Table 14).

In summary, painting D3 to look subordinate produced no significant change in the behavior of the other birds in Group II. There was a definite trend of increased frequency of submissive behaviors shown to D3 after his manipulation with the closest ranking birds (A2, C2) showing the greatest response. This unexpected trend, can be explained by the fact that D3 showed significantly more aggressive and submissive behaviors after his manipulation.

When A2 was painted to look subordinate, D3, the only dominant, showed a decrease in aggressive behaviors. The other subordinates showed an unexpected increase in submissive behaviors in the combined data (Appendix F presents the raw data for these analyses). This trend was evident in only two of the four subordinates; A1 and C3 (Table 15). The other two subordinates, C2 and E1, showed the predicted decrease in submissive behaviors.

The combined responses of A2 before and after his wattles were darkened reveal little change in his behavior. A2 displayed a 75% decrease in submissive behaviors displayed toward the only dominant,

D3. However, the frequency of behavior was very low to begin with (4 acts). His response to all other subordinates after manipulation was not significantly different (p = 0.652, Fisher's exact test). His individual responses to three of those animals, C2, E1 and A1 showed no change (Table 15). He displayed a 45% decrease in aggressive behaviors toward C3, the lowest ranking bird.

The response in Group II to the apparent decrease in rank of A2 is characterized by a nonsignificant decrease in aggressive behaviors by the other dominant and a nonsignificant increase in submissive behaviors by the other subordinates. Those birds closest in rank to A2 (C2 and E1, but also C3) showed the greatest magnitude response.

Individual responses to the manipulation of A1 (wattles painted red) are summarized in Table 16. In the combined data, the dominants showed no significant change in behavior to A1's manipulation. When the individual responses are examined it can be seen that one of the dominants, C2, showed the predicted decrease in aggressive behaviors. The other three dominants showed an increase in aggressive behaviors.

A1 showed strong changes in behavior after manipulation. The combined data reveals a 132% increase in submissive behaviors shown toward other dominants. This trend was very evident in his responses to D3, C2 and E1 (Table 16). A1 displayed reduced submissive behaviors toward the fourth dominant, A2 (Table 16).

The response of Group II to the apparent elevation in rank of A1 was not significant. The animal showing the largest change in response was a closely ranked animal, C2. D3, the most dominant bird also showed a marked response to A1's manipulation.

Table 17 summarizes the individual responses of Group II to the manipulation of the lowest ranking bird, C3. The manipulation of C3 to look dominant produced a significant decrease in aggressive behaviors and an increase in submissive behaviors by other group members. Three of the five dominants showed a decrease in aggressive behaviors; D3, A2 and C2. E1 showed an increase in submissive behaviors.

The combined data for C3's response to other dominants after his wattles were painted red shows a 28% increase in submissive behaviors. When his response to each individual is analyzed (Table 17) it is evident that the increase in submissive behaviors observed in the combined data is due to the six-fold increase displayed toward A2. He responded to D3, the alpha bird, with a 38% decrease in submissive behaviors.

The apparent increase in rank of C3, the lowest ranking bird, was the only manipulation to produce significant behavioral changes in Group II. The changes were in the predicted direction. Of the four birds showing a behavioral change, three were of large magnitude (greater than 40%). The response of largest magnitude occurred in a closely ranked bird, E1.

To summarize, four of the wattle manipulations performed produced significant changes in the behavior of other group members (Table 8 and Table 13). In Group I both of the dominant birds that were painted to look subordinate received significantly more aggression from their true subordinates after manipulation. In one case, submissive behaviors also increased. Painting the two most dominant birds in Group II to look subordinate caused no significant change in the behavior of other group

members. Painting the omega bird in each group to look dominant produced significant changes in the behavior of other group members. Both birds received less aggression after manipulation. Painting the other subordinate in Group II, A1, to look dominant produced no significant change in the behaviors of other group members. An intermediate from Group I, C1, was painted to look dominant. Although other dominants displayed less aggression toward him after manipulation, the difference was not significant.

Endocrine Changes during Hierarchy Establishment

Behavioral Observations. - Status was assigned based on the frequency of aggressive and submissive behaviors displayed by each bird (Appendix J). In every case the dominant bird performed the highest frequency of aggressive behaviors. The intermediate occasionally showed aggression (Triads 1 and 2) and it was always directed toward the subordinate bird. The intermediate also showed submissive behaviors toward the dominant bird. The subordinates never displayed any aggressive behaviors. They displayed submissive behaviors toward both of the other birds in the triad.

The total number of agonistic acts performed per day was determined by totaling all behaviors performed by each bird in the triad each day. Figure 2 displays the results of this analysis. Triad 1 showed high frequencies of interactions on Day 1. By Day 3, interactions had dropped to nearly one-third of the initial level. Frequencies of interactions did not differ on Day 11. By Day 13, all aggression had ceased.

Triad 2 (Figure 2) showed an unusual pattern. On Day 1, no interactions were observed. On Days 3 and 11, interactions increased from five to seven, respectively. By Day 13, interactions were still occurring, at the highest frequency recorded for this group (10 acts). Eventually all aggression ceased.

Triad 3 (Figure 2) established a hierarchy rapidly. On Day 1, eight interactions were observed and dominance was easily determined. No subsequent interactions were observed. Many agonistic behaviors may have occurred during the first 24 hours, prior to the first observation.

Endocrine Parameters

Due to problems with the assay (to be discussed) an incomplete profile of testosterone levels is presented in Table 18.

In Triad 1, on Day 3, the dominant bird, E1, and intermediate, D3, had the highest testosterone levels (Table 18). Testosterone levels in the subordinate, C1, were 30 to 40% lower.

In Triad 2, a different pattern emerged. On Day 3, the dominant bird, E2, and intermediate, C2, had lower testosterone levels than the subordinate, A2. By Day 11, testosterone levels in the dominant and intermediate birds had dropped below the sensitivity of the assay. The subordinate, A2, still had an extremely high level at Day 11.

In Triad 3, testosterone levels in all birds were below the sensitivity of the assay on Day 1. On Day 3, the subordinate, B3, still had undetectable levels of testosterone. The dominant, A1, showed the

highest level. The intermediate, C3, showed much lower levels of testosterone.

Based on these limited data, there does not appear to be a correlation between frequency of aggressive behaviors and testosterone levels. High testosterone levels were found in an animal showing a low frequency of these behaviors (A1, 4.99 ng/ml testosterone, 0 acts, Day 3).

In Triads 1 and 3 the two top ranking animals had the highest testosterone values. In Triad 2, the subordinate, A2, had the highest testosterone levels measured. He also displayed low frequencies of behaviors.

Although the testosterone profile is incomplete and the sample size is small these data suggest that neither high dominance status nor high frequencies of aggressive behaviors can be correlated with high testosterone levels.

Dihydrotestosterone levels were below assay sensitivity for all samples.

Difficulties with the Assay

After the assays (described above) were performed I began to experience difficulties with between assay replicability of the pooled plasma standard that was measured in every assay. Levels dropped rapidly from the mean value (0.635 ng/ml) measured in the first two assays to levels that were undetectable. It appeared that during the long-term storage of these samples testosterone had been degraded or

metabolized. It may be possible that at the storage temperature (-20°C) another product had formed that interfered with measurement of the steroid. It is generally thought that steroids are very stable when stored at -20°C for long periods of time (up to two years). However, the effects of long-term storage on steroid levels in biological fluids has not been extensively studied (Abraham et al. 1977). Plasma from the rough-skinned newt, Taricha granulosa and the vole, Microtus montanus are stored routinely at -20°C for up to two years without steroid loss (Frank Moore, personal communication). My data indicate that changes occur in pheasant plasma stored for long periods of time (greater than six months). Immediate assay of plasma or storage at -80°C until assays are performed may be necessary for accurate measurements.

As a result of these difficulties, no endocrine measurements were obtained for the experiment investigating the effect of forced agonistic encounters on hormone levels of males in an established hierarchy.

Forced Agonistic Encounters in a Stable Dominance Hierarchy

Table 19 (Triad A and Triad B) summarizes the behavioral response to the presentation of food to animals that had been deprived of food for 24 hours.

In Triad A, A3, the alpha bird, directed aggression only toward A1, the lowest ranking bird. A1 was not allowed to feed during the observation periods. Although the beta bird, A2, was not threatened by A3, he was not able to feed for very long.

In Triad B, the alpha bird, B2, attacked both of his subordinates. He spent more than one-third of the total observation time feeding. Both of the subordinates spent little time feeding.

Effects of Exogenous Hormones on Behavior

Injection of gonadal steroids. -- Only one triad showed a stimulation of behaviors after the injection of gonadal steroids. Before the injections the hierarchy was stable and members were not performing any agonistic behaviors. Table 20 summarizes the treatment and its effect for each member of the triad. Eight observations were conducted during the course of treatment. Interactions were observed only during three of those periods. The alpha bird, E1, showed an increase in aggressive behaviors when injected with estradiol-17-β. Aggression was directed only toward the lowest ranked bird C1. C1 was missing feathers from the nape, an obvious sign of continued attack by a dominant.

Injection of corticosterone, $ATCH_{4-10}$ and α-MSH. -- Corticosterone, $ACTH_{4-10}$ and α-MSH caused no change in the frequencies of any behaviors monitored. It was noted that at the end of the treatment, the corticosterone treated birds were lethargic and less reactive to stimuli.

DISCUSSION

Establishment of the Hierarchy

The alpha bird in both of the hierarchies used in this study showed the highest frequencies of aggressive behaviors. However, the performance of aggressive behaviors was not necessary to confer high rank since the beta birds in both hierarchies displayed low frequencies of aggressive behaviors. Still, the correlation between status and frequencies of aggressive behaviors performed was marginally significant in Group I and significant in Group II. My data suggest that among male Ring-necked Pheasants demonstration of fighting ability is an effective but not necessary means of attaining high dominance rank. In a study investigating dominance relationships of Dark-eyed Juncos, Ketterson (1979a) also shows that expression of high frequencies of aggressive behaviors is not requisite for high dominance status. In fact she shows that rank in the hierarchy and the proportion of interactions won are not completely congruous. A bird with high rank may win a lower proportion of its interactions than birds lower in rank while competing for food. Juncos forage in large flocks with the dominant birds feeding close together in the center of the flock and subordinates more widely separated at the periphery. Dominant birds, being closely spaced, encounter each other more frequently and are thus exposed to animals capable of defeating them more frequently.

In both groups of pheasants there is a trend among those animals performing aggressive behaviors to show higher frequencies toward

animals more distant in rank. This trend may reflect a way of demonstrating dominance status with low personal risk. If an animal shows more aggression toward low ranking subordinates, he is able to demonstrate his fighting abilities with low potential for suffering physical harm. Presumably a low ranking subordinate would be less likely to injure him. An attack by a dominant on a low ranking subordinate may act as a signal of dominance to other conspecifics that are in visual or auditory range (Cox, 1981).

Rohwer (1975) shows that Harris Sparrows practice despotic fighting in which dominant animals (studlies) concentrate their aggressive attacks on animals much subordinate to them (unstudlies). Rohwer believes that this pattern of fighting might be expected if there is active regulation of numbers through dominance behavior. "If dominance behavior confers fitness through access to resources, the best strategy for a studly bird should be to persecute the unstudlies because they eat as much as other birds and are much less likely to fight back." I disagree with this opinion. Banks et al. (1979) report that high dominance rank confers priority of access to food. Dominant hens and roosters feed longer and more frequently than do subordinates. In the experiments in which I starved triads of birds living in stable hierarchies and forced agonistic encounters by providing food, I also showed that dominant birds feed for longer periods of time than subordinates. If food is a limiting resource and high ranking birds are consuming more than lower ranking birds, it might be best to persecute a close ranking dominant even though the chances of defeat are greater. Although Searcy (1979) does not address the fact, his Red-winged

Blackbird hierarchies show a similar trend. Birds more distant in rank engage in higher frequencies of encounters than birds close in rank.

The frequency with which submissive vocalizations and behaviors were performed was significantly higher in lower ranking pheasants in Group I but not in Group II although a definite trend is present in Group II. Submissive behaviors or vocalizations were performed even when the dominant bird performed no aggressive behaviors. These data suggest that the existence of subordinate hierarchies may be as important as dominance hierarchies in establishing relative ranking of individuals in a social group. Rowell (1966), in a study of hierarchy formation in captive baboons, showed that the behavior of subordinate animals in approach-retreat interactions correlated best with rank; agonistic behavior initiated by animals of high status was less well correlated. Most frequently one monkey would avoid another without any detectable communication taking place between them. Agonistic interactions were usually determined and often initiated by the subordinate's behavior (Rowell, 1974).

Submissive vocalizations may be used to communicate the intentions of the sender in an agonistic encounter. If an animal perceives its opponent as being more likely to win an agonistic encounter, it would be to his advantage to communicate his concession of dominance and possibly circumvent an encounter. Crawford (1942) was able to reliably predict dominance status among pairs of female chimpanzees on the basis of vocalizations; the subordinate almost always vocalized first. Jarvi et al. (1980) found that male Willow Warblers are more likely to sing a special type of song (A-song) just before attacking an opponent.

Playbacks of these A-songs to other males causes them to retreat. Countersinging duels of male Marsh Wrens are ritualized expressions of dominance-subordinance relationships (Kroodsma, 1979). The subordinate male (as determined by aggressive-submissive tendencies), sings after the dominant and mimics his song type. West et al. (1981a, b) show that male Brown-headed Cowbirds acoustically alter their songs early in the spring to reduce the amount of aggression received from other males. Once high rank is achieved by agonistic interactions, the male begins singing an unaltered song which is more effective in stimulating female copulatory behavior. Their data indicate that dominance must be earned before these sexually "potent" songs can be sung. Song appears to be a substitute for the more energetic and risky forms of agonistic behavior in many avian species (Falls, 1969).

Linearity of the pheasant hierarchies was established rapidly in both groups. Hierarchies characterized by intransitive triads or more complicated networks are less stable than linear hierarchies. There is evidence (Wilson, 1980; pg. 137) that linear hierarchies are more efficient. When triads of hens exist in a linear hierarchy a certain amount of food is quickly consumed by the alpha bird sometimes assisted by the beta bird. When the hierarchies are circular the hens feed warily, birds frequently displace each other and food is consumed more slowly.

Morphological Parameters and Dominance

Both wing length and tail length were positively correlated with dominance rank in Group I. During the lateral facing intimidation display used by male Ring-necked Pheasants the wings and tail contribute significantly to the total size of the bird. Drooping of the wings and flaring of the tail and tail coverts exaggerates these features. Since this display figures prominently in agonistic and sexual encounters it seems likely that larger size, as measured by wing and tail length, would enhance the effectiveness of this display. Searcy (1979) shows that wing length is significantly positively correlated with dominance rank in adult and first year male Red-winged Blackbirds. Due to daily fluctuations in body weight, Searcy (1979) believes that wing length is a more accurate measure of body size.

Left spur length was also significantly positively correlated with status in Group I. Since the tarsal spurs are used during intense agonistic encounters, larger spurs would convey a distinct advantage to the bearer.

In Group I subordinates had significantly larger eye lines (left side) and a significantly larger percentage of the wattle occupied by black feathers and the eye line (left side). There was a trend in this group toward a decrease in total wattle area (left side) with decreasing rank. Dominants in Group II had significantly larger wattles (right side) than subordinates. Group II shows a trend toward an increase in the area of black feathers in the wattle (right side) with decreasing rank. The variability in wattle appearance cannot be due to age

differences since all birds were of the same age cohort. These data suggest that a large wattle or a wattle with little black coloration is a signal of high status. The wattle is brightly colored and can be inflated to increase the surface area. It functions prominently in the intimidation display which is usually performed with a lateral orientation, making the wattle plainly visible to the opponent.

There are a number of studies demonstrating correlations between dominance status and some morphological parameters. Rohwer (1975) shows that among winter flocks of Harris Sparrows, birds with the largest amount of black feathering on the neck and crown (studlies) are dominant to those having less black (unstudlies). This variation in plumage extends across age and sex classes. Myhre (1980) shows that in captive Willow Grouse, the dominant males in paired encounters had higher comb serrations than the subordinates. All of the males used in her study were the same age so variation was not due to age differences. Miskelly (1981) observing dominance relationships among Buff Wekas, finds that dominant birds have intensely pink-red legs and that there is a continuous gradation to pale orange-pink, the color of the lowest ranking birds. This color gradation extends across age classes. Ketterson (1979b) shows that Dark-eyed Juncos do not have a morphological characteristic that signals status. Juncos do show small but significant differences in wing, tail, tarsal and bill length and bill depth between sex and age classes. There is also variation in plumage coloration and eye color within sex and age classes. Her data indicate that juncos may use this information to determine the sex and age of an opponent and indirectly the potential dominance status. Males

dominate females and adults of both sexes tend to dominate subadults. Balph et al. (1979) also show that hood darkness in Dark-eyed Juncos is a poor indicator of social status apart from its association with sex.

Wattle Manipulations

Four of the eight manipulations performed resulted in significant changes in the behaviors displayed by other group members and all changes were in the predicted direction. A fifth manipulation produced a strong trend in the predicted direction. Only one manipulation produced no change in behaviors. The manipulation of the alpha birds of both hierarchies to look subordinate, produced marked changes in most other members. The manipulation of the alpha bird of Group I produced a significant increase in aggressive and submissive behaviors by subordinates. Manipulation of the alpha bird of Group II produced a nonsignificant increase in submissive behaviors by subordinates. This increase in submissive behaviors was not predicted. Since birds displayed less submissive behavior toward lower ranking birds during hierarchy establishment I expected the subordinates to be less submissive to the alpha bird after manipulation. This unexpected increase may be due in part to changes in the response of the manipulated birds to others in the group, particularly close ranking members. It may be that other subordinate birds perceived the change in signalled status in the dominant bird and responded differently to him. The manipulated bird, perceiving this differential treatment, attempted to reinforce his established rank by increasing aggression

toward closely ranked members. There are two other explanations for this unpredicted increase. First, the other subordinates may have perceived the incongruence between the signalled status and the behavior of the manipulated bird. They responded with an increase in submissive and displacement behaviors. It is also possible that the painted wattles changed the appearance of the bird to the extent that he was recognized as a stranger by other group members. This could also cause an increase in submissive and displacement behaviors.

The manipulation of the omega bird in each hierarchy to look dominant produced significant changes in behavior of other group members and changes were in the predicted direction. Since less aggression was directed toward higher ranking birds during hierarchy establishment I predicted that the omega birds would receive less aggression from other birds if they were painted to look dominant. I also predicted an increase in submissive behaviors especially from closely ranked birds who might perceive the omega bird as a dominant after manipulation. This occurred in Group II but not in Group I. These data suggest that, within this testing regime, the other members accepted the apparent change in status of the manipulated bird and changed their behavior accordingly. In both hierarchies, the animals that did not respond in the predicted direction were close-ranking birds. It is likely that the highest ranking birds still perceived the omega bird as a subordinate after manipulation but less distant in rank than before manipulation. They responded with the predicted decrease in aggression. Closely ranked birds may have perceived that the omega birds had wattles signalling higher status, but also other morphological and behavioral

cues signalling subordinance. They continued to regard the manipulated bird as a subordinate and so did not respond to the manipulation as predicted.

When birds in the middle ranks of both hierarchies were manipulated, responses were greatest in closely ranked birds and these changes were in the predicted direction. It is likely that variation in the cues used in status signalling is a continuum across the hierarchy. Apparent differences will be greatest between birds widely spaced in rank. The wattle is certainly only one cue used in assessing another birds dominance potential. Other morphological and behavioral characteristics surely figure into this assessment. Therefore, it is unlikely that changing the color of the wattle could produce a change of greater than one or two ranks. Birds at the extreme ends of the hierarchy would be less affected by manipulations on middle ranking individuals. Birds close in rank to these individuals or close to their apparent rank after manipulation would be expected to react most strongly. This is what was found.

Other studies have succeeded in experimental deceptions of dominance status. Guhl and Ortman (1953) altered the contour and/or color of White Leghorn pullets and observed the effects on treatment by other flock members. Darkening of the body feathers leads to loss of rank and alteration of the hackle feathers produces strong behavioral changes in flock members. Denudation or darkening of these feathers elicited challenges by subordinates. One pullet had the neck contour changed by gluing red feathers on the nape giving the appearance of a raised hackle, an aggressive posture, and she became the alpha bird.

Alterations of the comb were the most effective in causing behavioral changes. Both changes in comb contour and color cause increased frequency of agonistic encounters. The problems with this study are the small sample sizes used, lack of controls for the alterations and the biological insignificance of some of the changes made. The alterations made were not always of a nature that the birds would normally encounter. Therefore, it is difficult to determine whether behavioral changes by flock members were due to total loss of recognition of the individual, perceived change in status or simply a recognition of the altered bird as "abnormal."

Marler (1955) studied the social structure of mixed-sex flocks of Chaffinches. Chaffinches are highly sexually dimorphic, with the most conspicuous difference being the reddish-orange underparts of the male. Winter flocks are characterized by peck right hierarchies with males dominant to females. To determine the effects of coloring on status, females were painted to look like males and tested under several experimental regimes. Marler shows that female Chaffinches, with the underparts dyed red, win most aggressive encounters with normal females, and are dominant to them. Males still dominate all females whether painted or not, but the painted females in these hierarchies still are dominant to unpainted females.

Peek (1972) darkened the epaulets of male Red-winged Blackbirds to determine its effects on the ability to maintain a territory. His data show a seasonal effect of painting. When epaulets are darkened during the premating season, males lose all or part of their territories and have difficulty maintaining the remainder. If painting is done during

the postmating season there is almost no effect. Unfortunately these data are difficult to interpret because of the lack of controls.

Rohwer (1977) and Rohwer and Rohwer (1978) studied status signalling in Harris Sparrows. As mentioned previously Harris Sparrows exhibit continuous plumage variability extending across sex and age classes. Variability is in the amount of black versus white feathering on the throat and crown. When dominant birds or studlies (large amount of black feathering) are bleached to look subordinate they no longer enjoy passive wins or avoidance behavior by subordinates. They must increase the amount of aggression displayed to other birds to maintain their status. When subordinates are dyed to look dominant, they suffer severe persecution by true dominants. If these animals are dyed and given testosterone they experience dramatic increases in social status. Apparently dyed animals exhibit incongruence between signalled status and behavior and testosterone administration reduces this incongruence. The major drawbacks of Rohwer's work are the use of small sample sizes and lack of controls for the effects of dying and bleaching.

Fugle et al. (1982) investigated the use of external markers to signal dominance status in Gambel's White-crowned Sparrow. In winter, adult birds have black and white striped crowns while immatures have brown and tan striped crowns. Among adults, males show greater contrast between stripes than females. Adults dominate immatures and males dominate females. When immature females are painted to resemble adults, they dominate normal appearing controls. When adult females are painted to resemble males, they dominate normal appearing adult females. Within

an age or sex group, natural variation in crown brightness does not correlate with dominance rank. The amount of variation is very small within groups. These experiments indicate that status signals in this species correlate with a birds' age and sex and feather colors are utilized as indicators of potential dominance on this basis.

If the variation in appearance of male Ring-necked Pheasant wattles serves to signal status, the question is raised as to why an animal would signal subordinance. High social status has been shown to confer a reproductive advantage in this species (Taber, 1949; Collias and Taber, 1951). It seems paradoxical that any bird would display a highly visible signal of low rank. Rohwer and Ewald (1981) explain the compensating benefits of subordinance with the "shepherds hypothesis". They suggest that dominants (shepherds) and subordinates (sheep) coexist because it is mutually beneficial. Dominants defend space in good habitats for subordinates and subordinates act as food finders for the dominants. This hypothesis may explain in part the presence of status signals in male Ring-necked Pheasants. Another explanation may be that subordinate birds are sometimes able to enjoy the same benefits as dominant birds. As previously discussed, male Ring-necked Pheasants exist in stable dominance hierarchies during the winter and in spring cocks become territorial. Only the dominant cocks are successful in establishing territories and attracting harems (Taber, 1949; Collias and Taber, 1951). However, non-territorial cocks have been observed sneaking food and copulations from unattended hens while the territorial cock was occupied with maintaining territorial boundaries (Taber, 1949). Reproductive success of the non-territorial subordinate

cock is probably low but not zero.

In a study of the New Zealand Pukeko, a communal gallinule, Craig (1976) determined that subordinate birds take shelter behind dominant birds during encounters with other Pukeko groups and enjoy full access to any foraging ranges secured by them. Although subordinates rarely acquire mates and reproduce, a subordinate has a greater chance of breeding if it remains with the group awaiting the death of a dominant.

It may be advantageous for an animal to signal its rank if it lives near its kin. If an animal is likely to be subordinate a highly visible signal of low rank might prevent physical encounters with dominants who are likely to be related. Aggression directed against a related subordinate would decrease the fitness of the aggressor. Radesater (1976) has evidence that juvenile Canada Geese establish a firm rank order during the first week of life and that a gosling can recognize members of its own sibling group when only a few days old. Rank is established during the first week of life by biting and fighting. From five or six days of age rank order is demonstrated by appeasing movements from the subordinate goslings.

It may simply be more advantageous to live in a group than to live alone and signalling ones status may contribute to group stability by reducing aggression. Bertram (1978) believes that prey animals that live in groups may be more efficient at detecting and avoiding predators. While there may be liabilities associated with low rank it may still be more advantageous to give the signals of subordinance if that is ones likely status anyway (Ketterson, 1979b).

Endocrine Changes during Hierarchy Establishment

Dominant pheasants performed the highest frequencies of aggressive behaviors in all three triads. This pattern has been observed in a variety of species from Red-winged Blackbirds (Searcy, 1979) to elephant seals (Cox, 1981). In two of the pheasant triads, agonistic interactions were high when birds were first introduced and declined as they became familiar with each other and their relative dominance ranks. The third triad displayed a slight increase in agonistic interactions over time. I cannot explain this unusual pattern. It may be that these low levels of agonistic behaviors simply represent baseline levels of behaviors. Status was easily determined in this group and remained stable for months after observations ceased. Both the alpha and beta birds severely persecuted the omega bird. Persecution by the beta bird may have been perceived as a threat to his status by the alpha bird and he may have responded by becoming more aggressive.

Testosterone measurements in these triads showed no correlation with either dominance status or frequencies of aggressive behaviors performed. Selmanoff et al. (1977) found no consistent correlation of dominance with serum testosterone levels in male white mice. However, Machida et al. (1981) report that dominant male mice have significantly higher testosterone levels than subordinates. The difference in these studies may be due to strain differences. Keverne (1979) and Eberhart et al. (1980) show that in mixed sex social groups of talapoin monkeys,

dominant males have significantly higher testosterone levels than subordinates. If these same males are removed to isolation or to all male groups, there is no difference in testosterone levels with rank. Dominant males in mixed sex groups display higher frequencies of sexual behaviors than subordinates. Higher testosterone levels in these males represent an endocrine response to these behavioral interactions.

Plasma levels of gonadal hormones are not related to dominance status in birds. Berry and Burnham (1962) were unable to demonstrate a correlation between blood androgen level and dominance in White Leghorn cockerels. In free ranging winter flocks of Harris Sparrows, there is no correlation between dominance status and testosterone (Rohwer and Wingfield, 1981). Male Japanese Quail were ranked in order of level of aggressive behaviors performed. Order of aggressiveness is not correlated with plasma testosterone levels (Tsutsui and Ishii, 1981). No systematic relationship exists between androgen level and dominance status in pairs of male Ring Doves (Feder at al., 1977).

Other studies with birds failed to demonstrate that the frequency of aggression is correlated with testosterone levels. Tsutsui and Ishii (1981) castrated male Japanese Quail whose dominance rank had been established and castration abolished all aggressive behaviors. Testosterone replacement restored behaviors to pre-castration levels. Different doses of testosterone had no effect on frequencies of aggressive behavior or rank. Male Lesser Sheathbills showing territorial behavior have levels of testosterone similar to birds showing no territorial behavior. Territorial aggression was not limited to the time of year when testosterone levels were high (Burger and

Millar, 1980). Starlings maintained under short days during the breeding season displayed higher levels of aggression than birds maintained on long days. Testes of short day birds were aspermic and showed little evidence of androgen production (Vandenbergh, 1964). Temple (1974) reports low testosterone levels in Starlings at this time. Balthazart (1978) found no correlation between any measure of aggressive or sexual behavior and plasma testosterone in male Domestic Ducks. Dessi-Fulgheri et al. (1976) found no correlation between plasma testosterone levels and frequency of aggressive behavior in male white mice.

However, performance of aggressive behaviors can produce an endocrine response. Male Red-winged Blackbirds have significantly lower luteinizing hormone (LH) and androgen (testosterone plus dihydrotestosterone) after engaging in an aggressive encounter compared to non-aggressive, foraging males (Harding and Follett, 1979). Male Lesser Sheathbills that had performed a Bob Call display (a mutual pair territorial display) shortly before being sampled had higher testosterone levels than non-displaying males (Burger and Millar, 1980).

It is interesting to note the extremely low endogenous levels of androgen in male Ring-necked Pheasants. Levels were generally 1 ng/ml or less and often undetectable. Purohit (1976, 1978) also reports very low values for male Ring-necked Pheasants. He measured 0.0061 ng/ml in short day birds (10L:14D). Birds exposed to two different stimulatory photoperiods experienced a large increase to 0.24 ng/ml on a 14L:10D photoperiod and a smaller increase to 0.05 ng/ml on a 20L:4D

photoperiod. Purohit's values are probably erroneously low. He did not

chromatograph plasma samples to remove lipids and he used a two-labeled

competitor, ^{3}H-1, 2 testosterone, which is less sensitive than the four

labelled competitor used in my assay. Even if the percent error of his

measurements is large his data still suggest low endogenous levels of

testosterone.

Ottinger and Brinkley (1979) report higher values (9-16 ng/ml) for a

close relative of pheasants, the Japanese Quail (family Phasianidae).

Three different strains of domestic fowl (family Phasianidae) have

testosterone levels ranging from 4.5 to 7.3 ng/ml (Benoff et al.

1978). Stokkan and Sharp (1980) measured 2.5 ng/ml testosterone in

captive male Willow Ptarmigan during the breeding season (family

Tetraonidae). It is possible that male Ring-necked Pheasants have a

different biologically active androgen. Male Pigeons have low plasma

values of testosterone and high values of androstenedione (Rivarola et

al., 1968).

Effects of Exogenous Hormones on Behaviors

Neither dihydrotestosterone nor estradiol produced any changes in

frequency of the behaviors measured. There are many studies that

demonstrate the effectiveness of testosterone in stimulating aggressive

behavior in intact birds (Bennett, 1940; Trobec and Oring, 1972; Rohwer

and Rohwer, 1978; Searcy and Wingfield, 1980; Silverin, 1980; Watson and

Parr, 1981). Adkins-Regan (1981b) investigated the relative

effectiveness of testosterone and its metabolites, estradiol and

dihydrotestosterone, to stimulate sexual and aggressive behavior in Japanese Quail. Dihydrotestosterone and testosterone, but not estradiol, stimulated aggressive behaviors. Finney and Erpino (1976) and Gorzalka and Caira (1979) demonstrated a synergistic effect of estradiol and dihydrotestosterone on the maintenance of aggression in male mice. The lack of results in the present study could be explained in several ways. The dosages administered may have been too low to stimulate behavior. Another testosterone metabolite such as androstenedione may be responsible for stimulating aggression. It is possible that the unesterified steroids used may have been ineffective. Adkins-Regan (1981b) found that the propionated forms of testosterone and dihydrotestosterone were more effective in stimulating behaviors due to their greater biological half life. Presumably estradiol benzoate would be more effective than estradiol for the same reason.

Corticosterone had no effect on any of the behaviors measured in the pheasants. Deviche (1976) found that corticosterone injected into adult male Domestic Ducks had no effect on given or received aggressive behavior. Rohwer and Wingfield (1981) measured a negative correlation between plasma corticosterone and dominance status in free ranging winter flocks of Harris Sparrows under snow-free conditions. When sampled under heavy snow cover a positive correlation (though not statistically significant) was found. Subordinate behavior can be induced in rabbits after exposure to anesthesia which usually activates the adrenal cortex causing the release of corticoids. This increase in glucocorticoids may act to induce subordinate behavior by stimulating

the fear response and reducing the aggressive response (Brain, 1971).
Plasma corticosterone levels are not significantly different between
aggressive and nonaggressive male mice, although there is a trend
suggesting aggressive animals may have lower baseline levels (Politch
and Leshner, 1977). It is possible that observed differences in
corticosterone levels in mice are a function of differential response by
dominants and subordinates to the stress of agonistic encounters.
Differences are then a result of the behavioral interactions and not the
cause of them.

$ACTH_{4-10}$ (a fragment of adrenocorticotrophic hormone) injections had
no effect on any of the behaviors measured. This sequence of the
peptide lacks steroidogenic activity, so any effects from its
administration are presumably through action on the central nervous
system. $ACTH_{4-10}$ is known to be important in learning and memory
(Smotherman and Levine, 1980). ACTH depresses isolation induced
aggressive behavior in white mice (Brain, 1971). ACTH stimulates
precopulatory behaviors but not aggressive behaviors in male Domestic
Ducks (Deviche, 1976). This effect is surprising in view of the
antagonistic relationship between the pituitary-adrenal and -gonadal
axes. $ACTH_{4-10}$ reduces tonic immobility in _Anolis_ lizards (Stratton and
Kastin, 1976). Its action may be due to activation of the central
nervous system and reduction of the fear response.

MSH, melanocyte stimulating hormone, is present in the anterior lobe
of the avian pituitary. Its function and structure in birds are unknown
(Sturkie, 1976). Although I found no effect on pheasant behavior, MSH
can exert behavioral effects in other animals. MSH decreases aggressive

behavior in male white mice (Paterson et al., 1978). Nowell et al. (1980) report that α-MSH causes the release of an aggression promoting odor. Subordinate male mice injected with α-MSH experience higher frequencies of aggression from dominant animals. Panksepp et al. (1976) injected α-MSH into male Leghorn chicks and found that avoidance behavior was higher in the injected birds at one day of age, but at three days of age the effect was reversed. There is evidence that MSH exerts its effects on behavior via the central nervous system (LaHoste et al., 1980). Panksepp et al. (1976) speculate that MSH may modulate autonomic tone in the central nervous system via control of pigmented cells of the central autonomic system, the locus ceruleus. This cell group has been implicated in the basic maintenance of cortical arousal. This is consistent with the hypothesis that MSH increases attention. Effects of this nature may be difficult to quantify because behavioral changes are slight and in many situations are stabilized rather than shifted in a new direction.

Summary

Male Ring-necked Pheasants (Phasianus colchicus) establish linear dominance hierarchies. Dominant birds perform aggressive behaviors at higher frequencies than subordinates and direct the largest proportion of these behaviors toward distantly ranked subordinates. Subordinates perform submissive behaviors and vocalizations at higher frequencies than dominants and direct the greatest proportion of these behaviors toward distantly ranked dominants.

Although correlations were found between several morphological characters and dominance status only the wattle was chosen for experimental manipulations to try to alter behaviors and dominance status. Both the variation in the area of the wattle and the percentage of the wattle covered with black feathers appear to be important in the status signalling function of the wattle. Manipulations in which these variations were altered with painting produced statistically significant behavioral changes in other group members in four of the manipulations and strong trends in three others. Only one manipulation produced no behavioral changes.

During hierarchy establishment, two of the three triads observed displayed a decrease in agonistic interactions over time. There was no correlation between plasma testosterone levels and dominance status or the frequencies of any behaviors measured in these triads. I was unable to alter dominance status or behaviors by injecting exogenous gonadal or adrenal hormones.

One advantage of dominance in the winter hierarchies of male Ring-necked Pheasants is probably preferential access to food. Birds living in a stable hierarchy were deprived of food and food was introduced after 24 hours. Birds had to fight for a chance to feed and dominants fed more often and for longer periods of time.

Figure 1. Morphology of the wattle of an adult, male Ring-necked
           Pheasant. Wattle structures measured include red erectile
           tissue (A), black feathers (B), the eye line (C), the eye (D)
           and the bare skin surrounding the eye (E).

Figure 1.

Figure 2. Number of agonistic acts performed per day by each triad

during hierarchy formation. Number of agonistic acts was

calculated by totaling all aggressive and submissive

behaviors performed by all triad members each day.
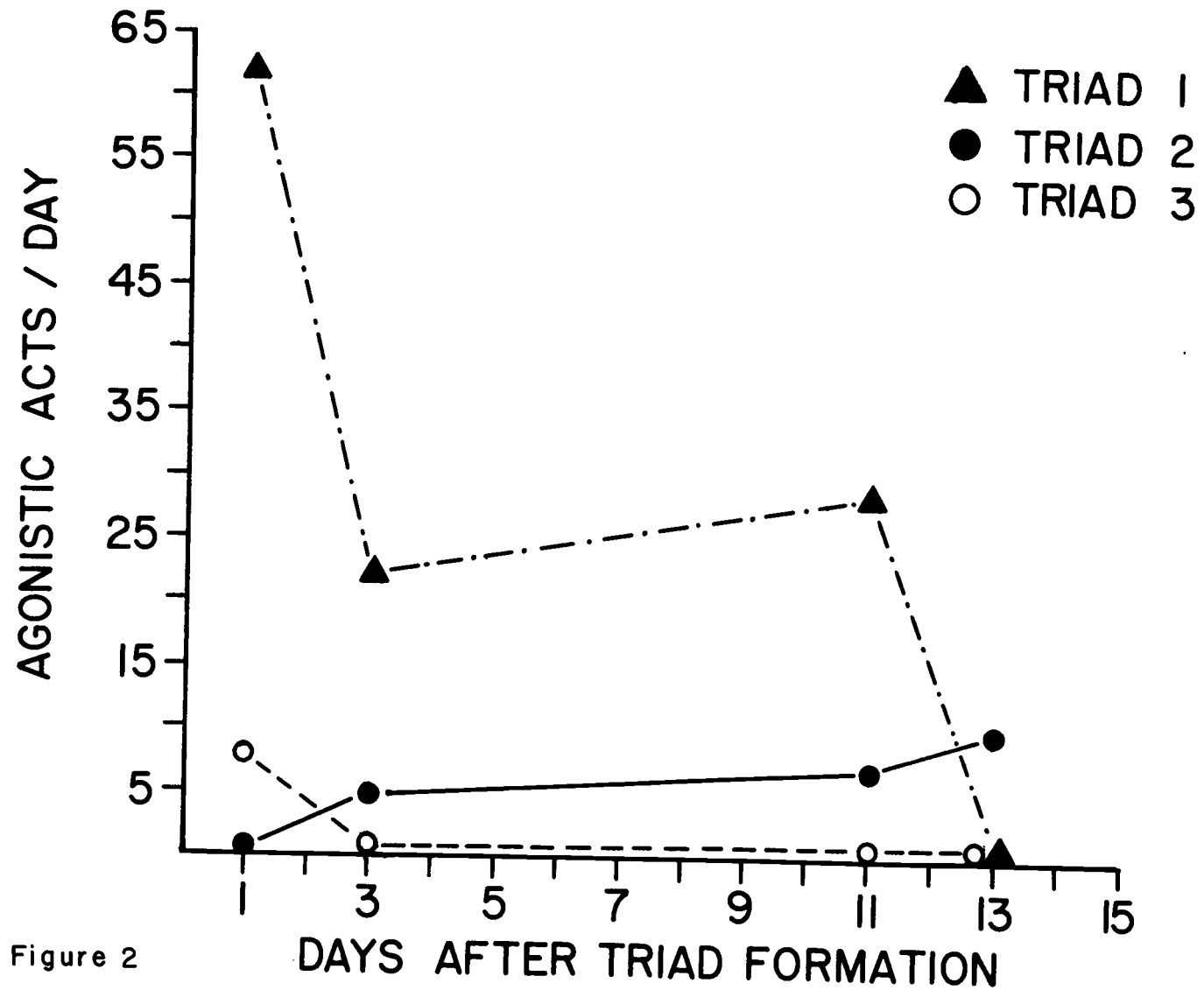
Figure 2

Table 1. Dominance hierarchy for adult, male Ring-necked Pheasants in Group I (a) and Group II (b). Number of aggressive behaviors performed are scored to the right of the dominant bird and below the subordinate. Aggressive behaviors scored include pursuit, peck and intimidation display. (See text for a description of these behaviors.)

a.

Dominants		B2	B1	Subordinates A3	C1	E2	B3
Dominants	B2		21	1	55	54	58
	B1			0	0	0	0
	A3				3	2	5
	C1					0	0
	E2						0
	B3						

b.

Dominants		D3	A2	Subordinates C2	E1	A1	C3
Dominants	D3		4	90	49	101	11
	A2			1	0	0	2
	C2				0	3	23
	E1		32			0	0
	A1						0
	C3						

Table 2.   Establishment of linearity of the dominance hierarchy of Group I and Group II over time. Aggressive and submissive behaviors were scored. Status was assigned based on the amount of aggression given or received or the amount of submissive behavior given or received. (See text for details.) Landau's index of dominance (h) estimates the degree of linearity of the hierarchy. 1 = perfect linearity and suggests a stable hierarchy.

	Date of Encounter	h Value
Group I	19/20 March, 1982	0.77
	22/23 March, 1982	0.88
	25/26 March, 1982	1.0
	27/28 March, 1982	1.0
Group II	29 May 1982	0.88
	30 May 1982	1.0
	31 May 1982	1.0

Table 3. Subordinance hierarchy for adult, male Ring-necked Pheasants in Group I (a) and Group II (b). Number of submissive behaviors performed are scored to the right of the subordinate and below the dominant bird. Behaviors scored include flee and fly up. (See text for a description of these behaviors.)

a.

			Dominants			
	B2	B1	A3	C1	E2	B3
Subordinates B2						
B1	10					
A3	8	11		11	48	67
C1	40	0	8			1
E2	48	0	6	0		
B3	144	20	22	2	3	

b.

			Dominants			
	D3	A2	C2	E1	A1	C3
Subordinates D3		10	15	8	8	
A2	5			35		
C2	117	8				
E1	61	2	1			
A1	69	3	5	1		
C3	16	7	25	4	0	

Table 4. Submissive vocalizations hierarchy for adult, male Ring-necked Pheasants in Group I (a) and Group II (b). Number of submissive vocalizations performed are scored to the right of the subordinate and below the dominant bird. Vocalizations scored include alarm call and pecked call. (See text for a description of these vocalizations.)

a.

		Dominants					
		B2	B1	A3	C1	E2	B3
Subordinates	B2						
	B1	58					
	A3	38	8				
	C1	124	23	68		1	1
	E2	84	34	70	0		
	B3	195	61	52	85	23	

b.

		Dominants					
		D3	A2	C2	E1	A1	C3
Subordinates	D3						
	A2	1			42		
	C2	174	0				
	E1	143	11	12		2	
	A1	1	58	157	26		
	C3	10	1	69	0	0	

Table 5. Measurements of morphological parameters In Group I (a) and Group II (b). Body weight Is In kilograms. Wattle colors are scored according to the Munsell Color System. All other measurements are In millimeters. Wattle and eye line measurements are listed as greatest horizontal measurement x greatest vertical measurement. Birds are listed in order of decreasing status.

	body weight	wing length	tail length	left spur length	right spur length	bill width	bill length	left wattle	right wattle	left eye line	right eye line	left wattle color	right wattle color
(a)													
B2	1.4	255	460	15	14	12	25	45x32	44x34.5	13x7	20x8	R5/10	R5/10
B1	1.8	240	430	18	18	14	30	44x34	40x30	18x6	18x6.5	R5/10	R5/10
A3	1.35	250	240	5	5	13	28	42x38	45.5x33	20x6	15.5x5	R5/10	R5/10
C1	1.5	230	340	8	12.5	15	25	43x34	48x32	17x4.5	15x5.5	R5/10	R5/10
E2	1.5	235	380	8	7	11	26	43x34	44x37.5	22x8	21.5x6.5	R5/10	R5/10
B3	1.15	210	170 (broken)	4	9	15	26	40x30	36x31.5	22x8	23x9	R4/10	R4/9

Table 5. (continued)

	body weight	wing length	tail length	left spur length	right spur length	bill width	bill length	left wattle	right wattle	left eye line	right eye line	left wattle color	right wattle color
(b)													
D3	1.8	240	430	15	12	16	27	42x29	41x31	23x7	23.5x6	R5/10	R5/10
A2	1.5	230	360	16	8	15	25	43x31	44x31	22x6	22x7.5	R5/9	R4/10
C2	1.4	240	390	4	5	15	24	45x36	42x33	19x5	18x6	R5/10	R5/10
E1	1.45	235	435	11	23	14	23	41x32	37x30	23x8	30x8	R4/10	R4/10
A1	1.9	250	415	15	6	16	25	43x39	40x33	21x5	20x5.5	R4/10	R4/10
C3	1.2	215	430	10	12	18	30	39x23	38x22	16x6	19x5.5	R5/8	R5/10

Table 6. Wattle measurements of Group I left wattle (a) and right wattle (b). All measurements are In mm^2. The last two columns represent percentages of total area of the red portion of the wattle. Birds are listed in order of decreasing status.

a

	total area (TA)	TA-eye, skin	eye line	TA-eye, skin, eye line	area of black	% black	% (black + eye line)
B2	832.3	766.5	47	719.5	28.1	3.7	9.8
B1	821.4	691.2	62.7	628.5	7.4	1.1	10.1
A3	767.4	663.7	62	601.7	17.6	2.7	12.0
C1	765.1	654.2	45.7	608.5	35.8	5.5	12.5
E2	845.9	732.5	99.3	633.2	18.1	2.5	16.0
B3	662.1	551.2	100.7	450.5	39.5	7.2	25.4

Table 6 (continued)

b

	total area (TA)	TA-eye, skin	eye line	TA-eye, skin, eye line	area of black	% black	% (black + eye line)
B2	693	602	74.9	527.1	7.7	1.3	13.7
B1	766.8	642.2	51.4	590.8	11.1	1.7	9.7
A3	813.3	708.2	69.5	638.7	4.7	1.0	10.5
C1	960.2	810.7	62.8	747.9	22.7	2.8	10.5
E2	791.9	674.5	80.7	593.8	4.4	1.0	12.6
B3	655.7	544.3	103.0	441.3	62.8	11.5	30.5

Table 7. Wattle measurements of Group II left wattle (a) and right wattle (b). All measurements are in mm^2. The last two columns represent percentages of total area of the red portion of the wattle. Birds are listed in order of decreasing status.

a

	total area (TA)	TA-eye, skin	eye line	TA-eye, skin, eye line	area of black	% black	% (black + eye line)
(a)							
D3	704.3	603	89.9	513.1	13.8	2.3	17.2
A2	854.3	738.4	107.9	630.5	38.5	5.2	19.8
C2	834.7	725	68.4	656.6	30.0	4.1	13.6
E1	879.9	770.6	144.7	625.9	53.2	6.9	25.7
A1	880.5	745.1	76.5	668.6	53.4	7.2	17.4
C3	546.8	427.4	71.3	356.1	5.8	1.4	18.0
(b)							
D3	726.2	588	80.5	507.5	16.7	2.8	16.5
A2	854.4	727.6	89.7	637.9	17.9	2.5	14.8
C2	784.8	658.9	48.8	610.1	22.5	3.4	10.8
E1	590.0	496.7	98.4	398.3	34.5	6.9	26.8
A1	734.1	629.6	61.2	568.4	66.4	10.5	20.3
C3	423.9	321.0	39.4	281.6	6.2	2.0	14.2

Table 8. Expected and observed results of wattle manipulations of the two dominants, one intermediate and one subordinate of Group I. Wattles of the two dominants were painted to look blacker and smaller. Wattles of the intermediate and subordinate were painted to look larger and redder. Manipulated birds acted as their own controls in which the wattles were painted with clear paint. $\uparrow$ = increase, $\downarrow$ = decrease (Also see Appendix B).

Animal	Actual Status	Treatment	Predicted response of other dominants	Predicted response of other subordinates	Observed response of other dominants	Observed response of other subordinates
B2	1/6	painted to look subordinate		$\downarrow$ submissive behaviors; $\uparrow$ aggressive behaviors by closely ranked subordinates		$\uparrow$ aggressive and submissive behaviors x^2=19.16 1 d.f. p <0.005
B1	2/6	painted to look subordinate	$\uparrow$ aggressive behaviors	$\downarrow$ submissive behaviors; $\uparrow$ aggressive behaviors by closely ranked subordinates	4 x $\uparrow$ aggressive behaviors	$\uparrow$ aggressive behaviors; no change in submissive behaviors; 1 reversal in dominance x^2 = 77.19, 1 d.f., p <0.005
C1	4/6	painted to look dominant	$\downarrow$ aggressive behaviors; $\uparrow$ submissive behaviors by closely ranked birds	$\uparrow$ submissive behaviors	$\downarrow$ aggressive behaviors x^2 = 0.08, N.S.	3 x $\uparrow$ submissive behaviors

Table 8. (continued)

Animal	Actual Status	Treatment	Predicted response of other dominants	Predicted response of other subordinates	Observed response of other dominants	Observed response of other subordinates
B3	6/6	painted to look dominant	↓aggressive behaviors; ↑submissive behaviors by closely ranked birds		↓aggressive and submissive behaviors $x^2 = 7.13$, 1 d.f. p <0.01	

Table 9. Individual responses of members of Group I hierarchy to the manipulation of B2, the alpha bird. The wattles of B2 were painted black to look like those of a subordinate. Changes in response to manipulation were determined by comparing responses after manipulation to those of controls in which the wattles of B2 were painted with clear paint. ↑ = Increase, ↓ = decrease.

paired birds	response of non-manipulated bird	response of manipulated bird (B2)
B2 vs. B1	36% ↑ submissive behaviors	40% ↑ aggressive behaviors
B2 vs. A3	↑ aggressive behaviors, ↑ submissive behaviors (p = 0.000473, Fisher's exact test)	7 x ↑ aggressive behaviors
B2 vs. C1	11% ↑ submissive behaviors	52% ↑ aggressive behaviors
B2 vs. E2	38% ↓ submissive behaviors	61% ↓ aggressive behaviors
B2 vs. B3	82% ↑ submissive behaviors	39% ↓ aggressive behaviors

Table 10.   Individual responses of members of Group I hierarchy to the manipulation of B1, the beta bird.   The wattles of B1 were painted black to look like those of a subordinate.   Changes in response to manipulation were determined by comparing responses after manipulation to those of controls in which the wattles of B1 were painted with clear paint.   ↑ = increase, ↓ = decrease

paired birds	response of non-manipulated bird	response of manipulated bird (B1)
B1 vs B2 (B2 dominant)	4 x ↑ aggressive behaviors	71 x ↑ submissive behaviors
B1 vs A3 (A3 subordinate)	↑ aggressive and submissive behaviors (p = 0.00015 Fisher's exact test)	↑ aggressive behviors (0 → 21 acts) ↑ submissive behaviors (0 → 96 acts)
B1 vs C1 (C1 subordinate)	72% ↓ submissive behaviors (p = 0.242, Fisher's exact test)	no change
B1 vs E2 (E2 subordinate)	39% ↑ submissive behaviors	no change
B1 vs B3 (B3 subordinate)	no change	no change

Table 11. Individual responses of members of Group I hierarchy to the manipulation of C1, the delta bird. The
wattles of C1 were painted red to look like those of a dominant. Changes In response to manipulation
were determined by comparing responses after manipulation to those of controls In which the wattles
of C1 were painted with clear paint. ↑ = increase, ↓ = decrease.

paired birds	response of non-manipulated bird	response of manipulated bird (C1)
C1 vs B2 (B2 dominant)	24% ↓ aggressive behaviors	31% ↓ submissive behaviors
C1 vs B1 (B1 dominant)	no change	no real change (4 →0 submissive acts)
C1 vs A3 (A3 dominant)	38% ↓ aggressive behaviors; 60% ↓ submissive behaviors (p = 0.299, Fisher's exact test)	45% ↑ submissive behaviors
C1 vs E2 (E2 subordinate)	3 x ↑ submissive behaviors	no real change (3 →0 submissive acts)
C1 vs B3 (B3 subordinate)	no change	no change

Table 12. Individual responses of members of Group I hierarchy to the manipulation of B3, the omega bird. The wattles of B3 were painted red to look like those of a dominant. Changes in response to manipulation were determined by comparing responses after manipulation to those of controls in which the wattles of B3 were painted with clear paint. ↑ = increase, ↓ = decrease.

paired birds	response of non-manipulated bird	response of manipulated bird (B3)
B3 vs B2	80% ↓ aggressive behaviors	19% ↑ submissive behaviors
B3 vs B1	no change	12% ↓ submissive behaviors
B3 vs A3	53% ↑ submissive behaviors	50% ↑ submissive behaviors
B3 vs C1	33% ↓ submissive behaviors	8 × ↑ submissive behaviors
B3 vs E2	46% ↓ submissive behaviors (P = 0.654, Fisher's exact test)	16 × ↑ submissive behaviors

Table 13. Expected and observed results of wattle manipulations of the two dominants and two subordinates of Group II. Wattles of the two dominants were painted to look blacker and smaller. Wattles of the two subordinates were painted to look larger and redder. Manipulated birds acted as their own controls in which the wattles were painted with clear paint. ↑ = increase, ↓ = decrease (Also see Appendix F).

Animal	Actual Status	Treatment	Predicted response of other dominants	Predicted response of other subordinates	Observed response of other dominants	Observed response of other subordinates
D3	1/6	painted to look subordinate		↓ submissive behaviors; ↑ aggressive behaviors by closely ranked subordinates	.	↑ submissive behaviors (p = 0.646, Fisher's exact test)
A2	2/6	painted to look subordinate	↑ aggressive behaviors	↓ submissive behaviors; ↑ aggressive behaviors by closely ranked subordinates	↓ aggressive behaviors (4 → 0 acts)	↑ submissive behaviors no change in aggressive behaviors (p = 0.302 Fisher's exact test)
A1	5/6	painted to look dominant	↓ aggressive behaviors; ↑ submissive behaviors by closely ranked birds	↑ submissive behaviors	no significant change (p = 0.266, Fisher's exact test)	no change

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Table 13. (continued

Animal	Actual Status	Treatment	Predicted response of other dominants	Predicted response of other subordinates	Observed response of other dominants	Observed response of other subordinates
C3	6/6	painted to look dominant	↓ aggressive behaviors; ↑ submissive behaviors by closely ranked birds		↓ aggressive behaviors; ↑ submissive behaviors (p = 0.016, Fisher's exact test)	

Table 14. Individual responses of members of Group II hierarchy to the manipulation of D3, the alpha bird. The wattles of D3 were painted black to look like those of a subordinate. Changes in response to manipulation were determined by comparing responses after manipulation to those of controls in which the wattles of D3 were painted with clear paint. ↑ = increase, ↓ = decrease.

paired birds	response of non-manipulated bird	response of manipulated bird (D3)
D3 vs A2	5 x ↑ submissive behaviors	↑ aggressive and submissive behaviors (p = 0.032, Fisher's exact test)
D3 vs C2	2.5 x ↑ submissive behaviors	↑ aggressive and submissive behaviors (p = 0.286, Fisher's exact test)
D3 vs E1	8% ↑ submissive behaviors	↓ aggressive behaviors, ↑ submissive behaviors (p = 0.096, Fisher's exact test)
D3 vs A1	90% ↑ submissive behaviors (p = 0.657, Fisher's exact test)	↑ aggressive and submissive behaviors (p = 0.321, Fisher's exact test)
D3 vs C3	80% ↑ submissive behaviors	↓ aggressive behaviors, ↑ submissive behaviors (p = 0.165, Fisher's exact test)

Table 15. Individual responses of members of Group II hierarchy to the manipulation of A2, the beta bird. The wattles of A2 were painted black to look like those of a subordinate. Changes in response to manipulation were determined by comparing responses after manipulation to those of controls in which the wattles of A2 were painted with clear paint. ↑ = increase, ↓ = decrease.

paired birds	response of non-manipulated bird	response of manipulated bird (A2)
A2 vs D3 (D3 dominant)	↓ aggressive behaviors (4 → 0 acts)	75% ↓ submissive behaviors
A2 vs C2 (C2 subordinate)	75% ↓ submissive behaviors; no change in submissive behaviors (p = 0.27, Fisher's exact test)	no change
A2 vs E1 (E1 subordinate)	91% ↓ submissive behaviors (p = 0.115, Fisher's exact test)	no change
A2 vs A1 (A1 subordinate)	63% ↑ submissive behaviors	no change
A2 vs C3 (C3 subordinate)	2 x ↑ submissive behaviors (p = 0.368, Fisher's exact test)	45% ↓ aggressive behaviors (p = 0.648, Fisher's exact test)

Table 16. Individual responses of members of Group II hierarchy to the manipulation of A1, the epsilon bird. The wattles of A1 were painted red to look like those of a dominant. Changes in response to manipulation were determined by comparing responses after manipulation to those of controls in which the wattles of A1 were painted with clear paint. ↑ = increase, ↓ = decrease.

paired birds	response of non-manipulated bird	response of manipulated bird (A1)
A1 vs D3 (D3 dominant)	↑ aggressive (0→8 acts) and submissive (0 → 3 acts) behaviors	5 x ↑ submissive behaviors
A1 vs A2 (A2 dominant)	↑ aggressive behaviors (0 →2 acts)	81% ↓ submissive behaviors
A1 vs C2 (C2 dominant)	93% ↓ aggressive behaviors (p = 0.938, Fisher's exact test)	40% ↑ submissive behaviors
A1 vs E1 (E1 dominant)	↑ aggressive behaviors (1 →3 acts)	11 x ↑ submissive behaviors
A1 vs C3 (C3 subordinate)	no change	no change

Table 17. Individual responses of members of Group II hierarchy to the manipulation of C3, the omega bird. The wattles of C3 were painted red to look like those of a dominant. Changes in response to manipulation were determined by comparing responses after manipulation to those of controls in which the wattles of C3 were painted with clear paint. ↑ = increase, ↓ = decrease.

paired birds	response of non-manipulated bird	response of manipulated bird (C3)
C3 vs D3	50% ↓ aggressive behaviors, 60% ↓ submissive behaviors (p = 0.441, Fisher's exact test)	38% ↓ submissive behaviors
C3 vs A2	41% ↓ aggressive behaviors	6 x ↑ submissive behaviors
C3 vs C2	↓ aggressive behaviors (2 → 0 acts)	no change
C3 vs E1	10 x ↑ submissive behaviors	no change
C3 vs A1	no change	no change

Table 18. Testosterone (T) levels during hierarchy establishment compared with status and frequencies of behaviors. Testosterone measured in ng/ml. N.D. = not detectable; – = not measured.

Triad	Animal and Status	T levels Day 1	Behavioral frequencies Day 1	T levels Day 3	Behavioral frequencies Day 3	T levels Day 11	Behavioral frequencies Day 11
	E1 (1)	--	--	0.92	11 aggressive behaviors	--	--
1	D3 (2)	--	--	1.07	1 submissive behavior	--	--
	C1 (3)	--	--	0.64	11 submissive behaviors	--	--
	E2 (1)	--	--	1.23	3 aggressive behaviors	N.D.	1 submissive behavior
2	C2 (2)	--	--	1.39	0	N.D.	5 aggressive behaviors
	A2 (3)	--	--	10.44	2 submissive behaviors	16.28	1 submissive behavior
	A1 (1)	N.D.	2 aggressive behaviors	4.99	0	--	--
3	C3 (2)	N.D.	1 submissive behavior	0.67	0	--	--
	B3 (3)	N.D.	5 submissive behaviors	N.D.	0	--	--

Table 19. Effects of forced agonistic encounters on behavioral frequencies and feeding times in Triad A and Triad B. Frequencies represent totals for three 10-minute observation periods. Status is indicated in parentheses after animal number. Feeding times are in minutes.

| | Triad A | | | Triad B | | |
	A3(1)	A2(2)	A1(3)	B2(1)	C1(2)	B3(3)
aggressive behaviors	4	0	0	10	0	0
submissive behaviors	0	0	4	0	3	6
time feeding	1.1	.13	0	10.73	2.9	3.63

Table 20. Changes in behavioral frequencies after injection of exogenous steroids. This was a stable hierarchy so pre-injection behavioral frequencies were zero. (Estradiol, = E2, dihydrotestosterone = DHT, saline = S).

Animal	Status	Steroid Injected	Aggressive Behaviors post injection	Submissive Behaviors post injection
E1	1	0.05 mg E2 in 0.1 ml S	8	0
D3	2	0.1 mg DHT in 0.1 ml S	0	1
C1	3	0.1 ml S	0	9

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APPENDICES

APPENDIX A

Chromatography and Radioimmunoassay

Celite Columns

Celite was heated to 540° C for 24 hours prior to use. A water trap was packed in each column (5 ml disposable glass pipette) supported by a glass bead. The water trap mixture consisted of 4.5 gm celite plus 1.5 ml double distilled water per ten columns. The mixture was ground in a mortar and packed to the 4.5 ml mark on the pipette. The stationary phase mixture consisted of 9 gm celite plus 4.5 mls propylene glycol: ethylene glycol 1:1 per ten columns. This mixture was ground in a mortar and packed to the 3 ml mark on the pipette. Two 4 ml aliquots were eluted through this mixture at a rate of 1 drop/7 seconds under nitrogen pressure.

Plasma Preparation

One hundred microliter plasma aliquots plus 400 ul double distilled water were pipetted into glass tubes. Water blanks consisted of 500 ul double distilled water. Tritiated testosterone and dihydrotestosterone (1,000 cpm/25 ul in redistilled ethanol) were added to all samples for recovery determinations. Water blanks did not get steroids. Samples equilibrated with tracer for 3 to 12 hours at 4°C. Each sample was extracted with 5 ml dichloromethane at room temperature for one hour.

The organic layer was aspirated and dried under air at 40°C. Dried extract was taken up in a total of 1.5 ml of 2% ethyl acetate in iso-octane and layered on the columns.

Chromatography

Plasma extracts were run into the column at a rate of 1 drop/7 seconds under nitrogen pressure. This rate was maintained throughout the assay. Progesterone was eluted with 4 ml iso-octane, dihydrotestosterone with 4.5 ml 10% ethyl acetate in iso-octane and testosterone with 20% ethyl acetate in iso-octane. Extracts were evaporated with air at 40°C. All extracts were taken up in 1 ml of the appropriate mobile phase solvent. Two hundred microliters were removed to determine recovery; the remaining 800 ul was divided in half, dried under air at 40°C and assayed for steroid content.

Radioimmunoassay

For the standard curve, duplicate tubes of each standard were prepared. One hundred microliter aliquots of testosterone or dihydrotestosterone, ranging from 0 to 2000 pg./100 uls redistilled ethanol were used. These were evaporated under air at 40°C. Dried sample extracts and standard tubes received 200 ul antiserum (diluted 1:40,000 in phosphate buffered saline with gelatin (PBS-G) for testosterone and 1:30,000 for dihydrotestosterone). All tubes were allowed to equilibrate for 20 minutes at room temperature. To all

tubes, a 100 ul aliquot of the respective tritiated steroid was added (12,500 cpm/100 ul PBS-G). In addition, three duplicate sets of banks were prepared. Two pair contained 200 ul PBS-G and 100 ul tritiated steroid. These represent non-specific binding tubes and total count tubes. The third pair contained 200 ul antiserum and 100 ul tritiated steroid. This blank represents 100% binding. All tubes were incubated at 4°C for 16-22 hours.

To stop the reaction, tubes were placed on ice for 5 min. A 1 ml aliquot of dextran coated charcoal was added to all sample and standards tubes except total counts tubes, to precipitate any unbound hormone. The total counts tubes (PBS-G plus tritiated steroid) received 1 ml of phosphate buffered saline (PBS) so that counts in the supernatant represent total counts added to the assay. Non-specific binding tubes (PBS-G plus tritiated steroid) received charcoal; counts in the supernatant represent non-specific binding to elements in the buffer and residual free counts not precipitated by the charcoal. The 100% binding tubes (antiserum plus tritiated steroid) also received charcoal; counts in the supernatant reflect maximal binding achievable in the assay. After a 10 min. incubation in charcoal, all tubes were centrifuged at 2500 g for 10 min. at 4°C. A 0.4 ml aliquot of supernatant was mixed with 3.6 ml scintillation fluid and counted for 4 min. or to 2% accuracy (Packard Tri-Carb Liquid Scintillation System).

Calculations

The standard curve was generated by correcting all starndards for non-specific binding. Data were transformed before performing a linear regression. Concentrations of standards were transformed to log values. Counts of standards were logit transformed as follows:

$$\text{logit } (B_i) = \ln \frac{B_i - NSB}{B_o - B_i}$$

Where - NSB = average counts of non-specific binding tubes

B_o = average counts for zero standard

B_i = average counts of ith standard

Logit transformed counts were regressed on log of standard concentration and a regression equation was generated. The average counts of each plasma unknown were logit transformed and fitted to the regression line to determine the concentration of steroid. All values for plasma unknowns were adjusted for recovery and values expressed as ng/ml.

Reagents and Materials

Chromatography

Celite 503 (J.T. Baker)

Propylene glycol (J.T. Baker)

Ethylene glycol (J.T. Baker)

Iso-octane (2,2,4-trimethylpentane; spectrophotometric grade - Mallinckrodt)

Ethyl acetate (HPLC grade, Fisher)

Plasma Extraction and Recovery Efficiency

1,2,6,7 - ^{3}H-5α-dihydrotestosterone (New England Nuclear)

1,2,6,7 - ^{3}H-testosterone (New England Nuclear)

dichloromethane (HPLC grade, Fisher)

Radioimmunoassay

Testosterone (Sigma)

5α-Dihydrotestosterone (Sigma)

Antiserum - Anti-testosterone-11-BSA(S-250)
    from Gordon Niswender, Colorado State University

Phosphate Buffered Saline (PBS)
    .39 gm NaH_2PO_4 (Mallinckrodt)
    .80 gm Na_2HPO_4 (Mallinckrodt)
    8.20 gm NaCl (Mallinckrodt)
    1.0 gm Na N_3 (J.T. Baker)
    Dissolve in 1 liter distilled water. Adjust to pH 7.0 with 5 N
NaOH.

Phosphate Buffered Saline with Gelatin (PBS-G)
    Dissolve 1.08 gm Knox gelatin per liter PBS at 37°C.

Dextran coated charcoal

Add 0.25 gm Dextran T-70 (Pharmacia) and 2.50 gm Neutralized Norit (Sigma) to one liter PBS. Mix and chill to 4°C overnight before use.

Scintillation Fluid:

Dissolve 21.0 gm 2,5-diphenyloxazole (PPO; Sigma) in 2 liters toluene (American Scientific). Add 1 liter Triton X-100 (Sigma).

Appendix B. Combined data for the responses of other dominants and subordinates to each manipulation in Group I. The wattles of the two dominant birds, B2 and B1, were painted black to look like those of a subordinate. The wattles of the intermediate C1, and the subordinate B3, were painted red to look like those of a dominant. Changes in response to manipulation were determined by comparing responses after manipulation to those of controls in which the wattles of the manipulated bird were painted with clear paint.

Manipulated Bird	Response of other dominants		Response of other subordinates	
	before	after	before	after
B2				
Aggressive behaviors			0	27
Submissive behaviors			734	1023
			$X^2 = 19.16$ 1 d.f.	
			$p < 0.005$	
B1				
Aggressive behaviors	3	13	0	116
Submissive behaviors	0	0	64	66
	4X↑		$X^2 = 77.19$ 1 d.f.	
			$p < 0.005$	
C1				
Aggressive behaviors	55	40	0	0
Submissive behaviors	29	19	12	39
	$X^2 = 0.08$, 1 d.f., N.S			3x ↑
B3				
Aggressive behaviors	32	6		
Submissive behaviors	107	67		
	$X^2 = 7.13$, 1 d.f.			
	$p < 0.01$			

Appendix C. Responses of individuals of Group I to the manipulations of members of their hierarchy. The wattles of the dominant birds, B2 and B1, were painted black to look like those of a subordinate. The wattles of the intermediate, C1 and the subordinate B3, were painted red to look like those of a dominant. Changes in response to manipulation were determined by comparing responses after manipulation to those of controls in which the wattles of the manipulated bird were painted with clear paint.

	B2 manipulations		B1 manipulations	
	before	after	before	after
B2 vs B1			**B1 vs B2**	
Aggressive	0	0	3	13
Submissive	66	90	0	0
	36% ↑		4 x ↑	
B2 vs A3			**B1 vs A3**	
Aggressive	0	27	0	115
Submissive	118	346	4	12
	P = 0.000473		p = 0.00015	
	(Fisher's exact test)		(Fisher's exact test)	
B2 vs C1			**B1 vs C1**	
Aggressive	0	0	0	1
Submiswsive	227	253	25	7
	11% ↑		p = 0.242	
			(Fisher's exact test)	
B2 vs E2			**B1 vs E2**	
Aggressive	0	0	0	0
Submissive	212	132	33	46
	38% ↓		39% ↑	
B2 vs B3			**B1 vs B3**	
Aggressive	0	0	0	0
Submissive	111	202	2	1
	82% ↑			

Appendix C. (continued)

	C1 manipulations		B3 manipulations	
	before	after	before	after
C1 vs B2			**B3 vs B2**	
Aggressive	50	38	30	6
Submissive	0	0	0	0
	24% ↓		80% ↓	
C1 vs B1			**B3 vs B1**	
Aggressive	0	0	1	0
Submissive	0	1	0	0
C1 vs A3			**B3 vs A3**	
Aggressive	5	2	0	0
Submissive	29	18	30	46
	p = 0.299 (Fisher's exact test)		53% ↑	
C1 vs E2			**B3 vs C1**	
Aggressive	0	0	0	0
Submissive	12	39	6	4
	3 x ↑		33% ↓	
C1 vs B3			**B3 vs E2**	
Aggressive	0	0	1	0
Submissive	0	0	84	45
			p = 0.654 (Fisher's exact test)	

Appendix D. Combined data for the response of each manipulated bird of Group I to other dominants and subordinates. The wattles of the two dominant birds, B2 and B1, were painted black to look like those of a subordinate. The wattles of the intermediate, C1, and the subordinate, B3, were painted red to look like those of a dominant. Changes in behavior after manipulation were determined by comparing the behavior of the manipulated bird after he was painted to his behavior during control tests in which the wattles were painted with clear paint.

Manipulated Bird	Response toward other dominants		Response toward other subordinates	
	before	after	before	after
B2				
Aggressive behaviors			155	172
Submissive behaviors			0	0
			11% ↑	
B1				
Aggressive behaviors	0	0	0	21
Submissive behaviors	1	71	0	96
	71x ↑			
C1				
Aggressive behaviors	0	0	0	0
Submissive behaviors	319	261	3	0
	18% ↓			
B3				
Aggressive behaviors	0	0		
Submissive behaviors	165	280		
	70% ↑			

Appendix E. Responses of the manipulated birds of Group I to members of their hierarchy. The wattles of the two dominant birds, B2 and B1, were painted black to look like those of a subordinate. The wattles of the intermediate C1, and the subordinate, B3, were painted red to look like those of a dominant. Changes in behavior after manipulation were determined by comparing the behavior of the manipulated bird after he was painted to his behavior during control tests in which the wattles were painted with clear paint.

	B2 manipulations		B1 manipulations	
	before	after	before	after
B2 vs B1			B1 vs B2	
Aggressive	10	14	0	0
Submissive	0	0	1	71
	40% ↑		71 x ↑	
B2 vs A3			B1 vs A3	
Aggressive	9	64	0	21
Submissive	0	0	0	96
	7 x ↑			
B2 vs C1			B1 vs C1	
Aggressive	29	44	0	0
Submissive	0	0	0	0
	52% ↑			
B2 vs E2			B1 vs E2	
Aggressive	69	27	0	0
Submissive	0	0	0	0
	61% ↓			
B2 vs B3			B1 vs B3	
Aggressive	38	23	0	0
Submissive	0	0	0	0
	39% ↓			

Appendix E (continued)

	C1 manipulations			B3 manipulations		
	before	after		before	after	
C1 vs B2			**B3 vs B2**			
Aggressive	0	0		0	0	
Submissive	257	177		112	133	
		31% ↓			19% ↑	
C1 vs B1			**B3 vs B1**			
Aggressive	0	0		0	0	
Submissive	4	0		33	29	
					12% ↓	
C1 vs A3			**B3 vs A3**			
Aggressive	0	0		0	0	
Submissive	58	84		10	15	
		45% ↑			50% ↑	
C1 vs E2			**B3 vs C1**			
Aggressive	0	0		0	0	
Submissive	3	0		7	55	
					8 x ↑	
C1 vs B3			**B3 vs E2**			
Aggressive	0	0		0	0	
Submissive	0	0		3	48	
					16 x ↑	

Appendix F. Combined data for the responses of other dominants and subordinates to each manipulation of Group II. The wattles of the two dominant birds, D3 and A2, were painted black to look like those of a subordinate. The wattles of the two subordinates, A1 and C3, were painted red to look like those of a dominant. Changes in response to manipulation were determined by comparing responses after manipulation to those of controls in which the wattles of the manipulated bird were painted with clear paint.

Manipulated Bird	Response of other dominants		Response of other subordinates	
	before	after	before	after
D3				
Aggressive behaviors			0	1
Submissive behaviors			207	376
			p = 0.646 (Fisher's exact test)	
A2				
Aggressive behaviors	4	0	3	3
Submissive behaviors	0	0	128	164
			p = 0.302 (Fisher's exact test)	
A1				
Aggressive behaviors	15	14	0	0
Submissive behaviors	1	3	0	1
	p = 0.266 (Fisher's exact test)			
C3				
Aggressive behaviors	33	18		
Submissive behaviors	6	12		
	p = 0.016 (Fisher's exact test)			

Appendix G. Responses of individuals of Group II to the manipulations of members of their hierarchy. The wattles of the dominant birds, D3 and A2, were painted black to look like those of a subordinate. The wattles of the two subordinates, A1 and C3, were painted red to look like those of a dominant. Changes in response to manipulation were determined by comparing responses after manipulation to those of controls in which the wattles of the manipulated bird were painted with clear paint.

| | D3 manipulations | | A2 manipulations | |
	before	after	before	after
D3 vs A2			A2 vs D3	
Aggressive	0	0	4	0
Submissive	4	20	0	0
	5 x ↑			
D3 vs C2			A2 vs C2	
Aggressive	0	0	2	2
Submissive	37	93	8	2
	2.5 x ↑		p = 0.27 (Fisher's exact test)	
D3 vs E1			A2 vs E1	
Aggressive	0	0	0	1
Submissive	63	68	23	2
	8% ↑		p = 0.115 (Fisher's exact test)	
D3 vs A1			A2 vs A1	
Aggressive	0	1	0	0
Submissive	93	177	91	148
	p = 0.657 (Fisher's exact test)		63% ↑	
D3 vs C3			A2 vs C3	
Aggressive	0	0	1	0
Submissive	10	18	6	12
	80% ↑		p = 0.368 (Fisher's exact test)	

Appendix G. (continued)

| | A1 manipulations | | C3 manipulations | |
	before	after	before	after
A1 vs D3			C3 vs D3	
Aggressive	0	8	4	2
Submissive	0	3	5	2
			p = 0.441	
			(Fisher's exact test)	
A1 vs A2			C3 vs A2	
Aggressive	0	2	27	16
Submissive	0	0	0	0
			41% ↓	
A1 vs C2			C3 vs C2	
Aggressive	14	1	2	0
Submissive	1	0	0	0
	p = 0.938			
	(Fisher's exact test)			
A1 vs E1			C3 vs E1	
Aggressive	1	3	0	0
Submissive	0	0	1	10
			10 x ↑	
A1 vs C3			C3 vs A1	
Aggressive	0	0	0	0
Submissive	0	1	0	0

Appendix H. Combined data for the responses of each manipulated bird of Group II to other dominants and subordinates. The wattles of the two dominant birds, D3 and A2, were painted black to look like those of a subordinate. The wattles of the two subordinates, A1 and C3, were painted red to look like those of a dominant. Changes in behavior after manipulation were determined by comparing the behavior of the manipulated bird after he was painted to his behavior during control tests in which the wattles were painted with clear paint.

Manipulated Bird	Response toward other dominants		Response toward other subordinates	
	before	after	before	after
D3				
Aggressive			58	125
Submissive			23	75
			p = 0.039	
			(Fisher's exact test)	
A2				
Aggressive	0	0	59	32
Submissive	4	1	1	0
	75% ↓		p = 0.652	
			(Fisher's exact test)	
A1				
Aggressive	0	0	0	1
Submissive	87	202	0	0
	132% ↑			
C3				
Aggressive	0	0		
Submissive	18	23		
	28% ↑			

Appendix I. Responses of the manipulated birds of Group II to members of their hierarchy. The wattles of the two dominant birds, D3 and A2, were painted black to look like those of a subordinate. The wattles of the two subordinates, A1 and C3, were painted red to look like those of a dominant. Changes in behavior after manipulation were determined by comparing the behavior of the manipulated bird after he was painted to his behavior during control tests in which the wattles were painted with clear paint.

| | D3 manipulations | | A2 manipulations | |
	before	after	before	after
D3 vs A2			**A2 vs D3**	
Aggressive	10	16	0	0
Submissive	1	13	4	1
	p = 0.032		75% ↓	
	(Fisher's exact test)			
D3 vs C2			**A2 vs C2**	
Aggressive	7	35	0	0
Submissive	3	17	0	0
	p = 0.286			
	(Fisher's exact test)			
D3 vs E1			**A2 vs E1**	
Aggressive	30	14	1	0
Submissive	2	4	0	0
	p = 0.096			
	(Fisher's exact test)			
D3 vs A1			**A2 vs A1**	
Aggressive	7	58	0	0
Submissive	2	18	0	0
	p = 0.321			
	(Fisher's exact test)			
D3 vs C3			**A2 vs C3**	
Aggressive	4	2	58	32
Submissive	15	23	1	0
	p = 0.165		p = 0.648	
	(Fisher's exact test)		(Fisher's exact test)	

Appendix I (continued)

	A1 manipulations		C3 manipulations	
	before	after	before	after
A1 vs D3			C3 vs D3	
Aggressive	0	0	0	0
Submissive	9	45	13	8
	5 x ↑		38% ↓	
A1 vs A2			C3 vs A2	
Aggressive	0	0	0	0
Submissive	16	3	2	12
	81% ↓		6 x ↑	
A1 vs C2			C3 vs C2	
Aggressive	0	0	0	0
Submissive	55	77	1	1
	40% ↑			
A1 vs E1			C3 vs E1	
Aggressive	0	0	0	0
Submissive	7	77	0	0
	11 x ↑			
A1 vs C3			C3 vs A1	
Aggressive	0	1	0	0
Submissive	0	0	2	2

Appendix J. Frequencies of behaviors during hierarchy formation. Each table represents the total aggressive (A) and submissive (S) behaviors performed by each animal of a triad during a ten minute observation period. Day 1, 3, 11 and 13 are days after formation of the triad. Birds are listed in order of descending rank.

Triad		Day 1 A	S	Day 3 A	S	Day 11 A	S	Day 13 A	S
	E1(1)	33	0	11	0	13	0	0	0
1	D3(2)	2	14	0	1	0	1	0	0
	C1(3)	0	13	0	11	0	14	0	0
	E2(1)	0	0	3	0	0	1	4	0
2	C2(2)	0	0	0	0	5	0	2	1
	A2(3)	0	0	0	2	0	1	0	3
	A1(1)	2	0	0	0	0	0	0	0
3	C3(2)	0	1	0	0	0	0	0	0
	B3(3)	0	5	0	0	0	0	0	0