A FACTOR ANALYSIS OF SEASONAL, BEHAVIORAL, HORMONAL AND BODY WEIGHT CHANGES IN ADULT MALE BARHEADED GEESE, ANSER INDICUS

by

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(With 3 Figures)
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Correlations between the circulating levels of hormones and the frequencies of behavior have been used to study behavioral hormonal interactions by a number of authors with both positive and negative results (BALTHAZART, 1976; BALTHAZART & HENDRICK, 1976; GORMAN, 1977; HARDING & FEDER, 1976; LESHNER, 1978, for a review; PRÖVE, 1978; TSUTSUI & ISHII, 1981). One of the most important aspects of these experiments is that they produce a framework within which many other experiments manipulating the peripheral levels of hormones and behavior can be interpreted.

In this paper, results of a previous study on adult male barheaded geese (DITTAMI, 1981) have been taken and subjected to statistical analysis to determine if the circulating levels of various hormones and the frequencies of behavior were related on an annual or seasonal basis. The calculations of correlation coefficients were augmented by a factor analysis to reduce several mutually dependent correlations to a small number of independent factors. This method also allows one to examine whether a combination of hormones might explain more of the variance in the data relating endocrinological variables to behavior.

Methods

The population of geese, behavioral observations, bleeding techniques and hormonal assays have all been described in DITTAMI (1981). For this analysis, sets of data on individual males for whom behavioral and hormonal data in a given time period (the calendar month or phase of reproduction) were available have been used. For the behavioral data individual averages were calculated over the time period. These were then combined with the weight and hormonal data from the same period. If more than one set of hormonal and weight data were available averages were calculated. The following hormones were taken for the analysis: testosterone, luteinizing hormone (LH), thyroxine

(T4) and prolactin. The behaviors analysed were pair-bond displays (PBD), attacks (ATT) and courting (COURT). Body weight was also put into the calculations.

Initially data from the entire year, excluding incubation (phases 4 and 5 DITTAMI, 1981) were analysed. Means of the data used are shown in Fig. 1. The data were then broken up into two groups: from March to the beginning of incubation and secondly from hatching through summer, fall and winter up to the following March. The rationale for this breakup was as follows: in the spring data, pairs were not accompanied by goslings and the levels of reproductive hormones (LH, testosterone) were relatively high. In the remainder of the year successful adults were together with their goslings and the levels of reproductive hormones were lower.

As neither hormone titers nor the frequencies of behavior were normally distributed, the original data were subjected to a square-root transformation. After this transformation most variables no longer differed from a normal distribution ($p > 0.10$; Lillifors modification of the Kolmogorov-Smirnov one sample test, SACHS, 1978). The transformation did not have a pronounced effect as the heavily skewed original data had produced the same results.

The actual factor analysis was based on Pearson correlation coefficients between all variables. For computation we used SSP program FACTO of IBM with subsequent VARIMAX rotation. According to a common rule, initially only factors with an eigenvalue of ≥ 1 were extracted (VAN GEER, 1971; BALTHAZART, 1973; ASPEY & BLANKENSHIP, 1977). This resulted in three separate factors for each of the two smaller time periods but only two factors for the whole year. To make the comparison of results easier a third factor with an eigenvalue of 0.9 was extracted for the whole-year sample. Following a suggestion by ASPEY & BLANKENSHIP (1977) only factor loadings ≥ 0.45 were considered relevant, but even with loadings as low as 0.35 the results did not change with one minor exception (see below).

As the same individuals were sampled repeatedly the data are not completely independent. Still, the use of correlations is justified as seasonal variation was much greater than inter-individual differences in a given time period. The factor analysis is thus primarily based on variation in time.

Results

Results from the factor analysis of the whole data and the two time periods are in Fig. 2 and 3. In all three analyses the three factor solutions explained a very high amount of variance (70.1-75.4%) and heavy loadings existed between parameters and factors. In the analysis of the data from the whole year (Fig. 2) Factor I was characterized by strong positive relationships with attacks (ATT) and pair-bond displays (PBD), somewhat weaker, positive correlations with changes in the hormones testosterone and LH and a negative one with prolactin. Courting (COURT) separated out independently of ATT and PBD in Factor II but was still positively correlated with LH and testosterone. The last Factor (III) showed a negative correlation with body weight and a positive one with T4 and prolactin.

The components of the factors changed when the data were split into two time periods. Examining the data from the breeding season (Fig. 3, left) the weight/prolactin/T4 factor from the previous analysis was

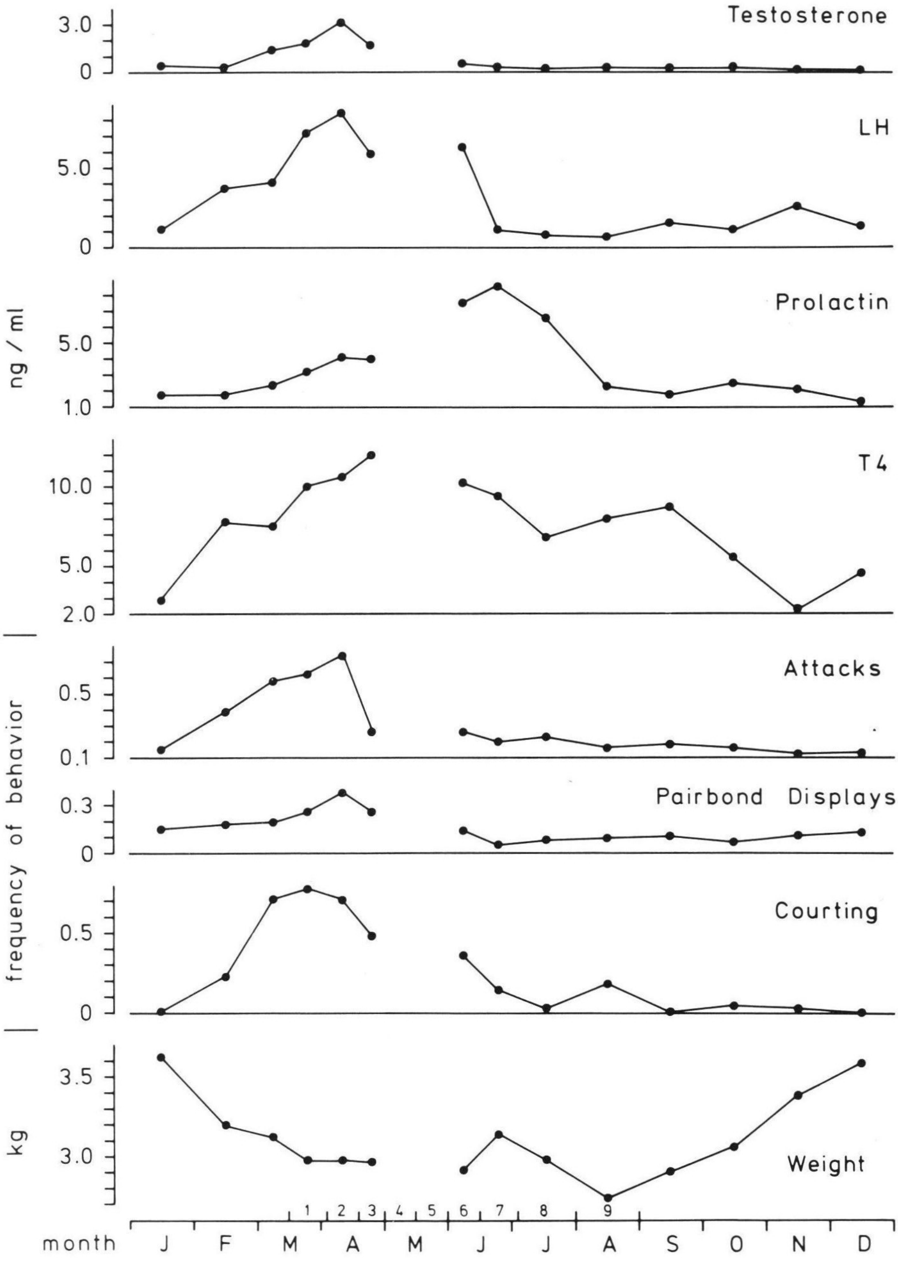

Fig. 1. Seasonal changes in testosterone, luteinizing hormone (LH), prolactin, thyroxine (T4), attacks (/min), pair-bond displays (/min), courting (% observational periods) and body weight in adult, male bar-headed geese from Dittami (1981). Data from breeding have been plotted according to the phase of reproduction and those from nest incubation (phase 4 and 5) have been left out. Means of the data used in the factor analyses are plotted.

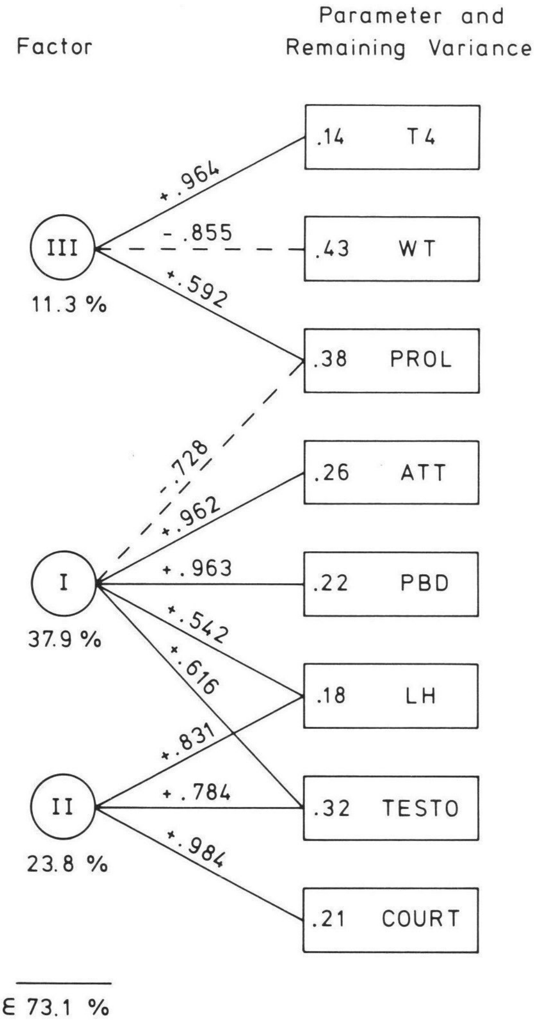

Fig. 2. Results of the factor analysis on data from the whole year excluding incubation. Numbers under the factors represent the percentage of total variance explained by a particular factor. Numbers on the connecting lines between factors and parameters are the factor loadings represented as correlation coefficients between the two after VARIMAX rotation. Negative correlations are represented by dashed lines. The numbers in the parameter boxes give the remaining variance after the analysis. The parameters are: T4 = thyroxine, WT = body weight, PROL = prolactin, ATT = attacks, PBD = pairbond displays, LH = luteinizing hormone, TESTO = testosterone and COURT = courting.

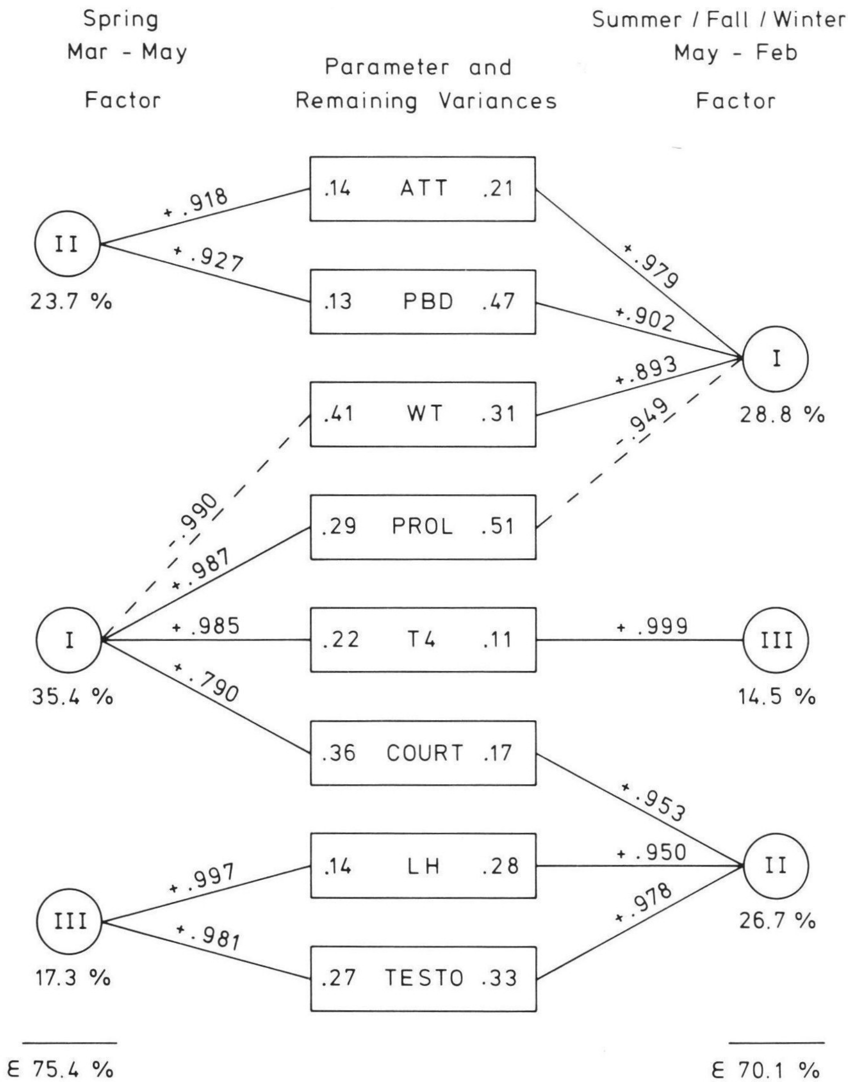

Fig. 3. Same as Fig. 2 except two analyses have been performed for the different time periods; on the left spring and on the right summer, fall and winter.

associated with COURT (Factor I) which was no longer associated with testosterone or LH. These two hormones split off from ATT and PBD also and constituted a factor of their own, Factor III. ATT and PBD were found in Factor II. So in effect the parameters which had been found together in factors on an annual basis fell apart into a ATT/PBD, an LH/testosterone and a weight/prolactin/T4/courting factor in spring.

In the off-season data the associations were again different. T4 fell out alone as an independent Factor (III) although a weak negative association with weight could be detected if factor loadings between 0.35 and 0.45 were considered as well. LH, testosterone and COURT were well correlated with Factor II as in the whole year analysis. The association between ATT and PBD remained as did that between prolactin and body weight but now all four variables were accounted for by the same Factor (I).

TABLE 1. The occurrence of various parameters in a common factor a (b, c)

	PBD	Court	Weight	Testo	LH	Prol.	T4
Agg.	+(++)	o(oo)	o(o+)	+(oo)	+(oo)	-(o-)	o(oo)
PBD		o(oo)	o(o+)	+(oo)	+(oo)	-(o-)	o(oo)
Court			o(-o)	+(o+)	+(o+)	o(+o)	o(+o)
Weight				o(oo)	o(oo)	-(--)	-(-o)
Testo					+(++)	-(oo)	o(oo)
LH						-(oo)	o(oo)
Prol.							+(+o)

a: on an annual basis; b: in spring; c: outside breeding; o: no relation; +: a positive correlation; -: a negative correlation.

A summary of the associations between variables is in Table 1, where the occurrence and directions of various parameters in a common factor can be seen. A number of points can be made from it:

1) Attacks and pair-bond displays were positively correlated with the same factor in all three analyses.

2) Courting never occurred in the same factor with either of the above, implying that it was controlled by other factors.

3) Testosterone and LH were always associated with the same factor.

4) Body weight changes were always negatively related to prolactin and never related to testosterone or LH.

5) T4 was never correlated to a factor controlling ATT and PBD or testosterone and LH. It showed a seasonally dependent, negative relationship with body weight and a positive one with prolactin.

6) Courting, testosterone and LH were correlated with the same factor on an annual basis and in the off-season but not during breeding.

7) Prolactin was negatively correlated with the ATT/PBD factor in the off-season and on an annual basis and, positively with T4 on an annual basis and in spring.

8) A number of other relationships were found between parameters which occurred only on an annual basis or in one of the smaller time periods investigated. This implies that the reliance of these parameters on a common factor were less pronounced. Good examples were testosterone/LH to ATT/PBD, prolactin/T4 to courting and weight to ATT/PBD.

Discussion

The most obvious result of the factor analysis was that the relationships between some of the parameters seemed to change depending on which time period was analyzed. Still, there were other parameters which were constantly associated with one another irrespective of the data breakup. The most pronounced were attacks (ATT) and pair-bond displays (PBD) which were always linked to the same factor with very heavy loadings. This is in line with investigations on pair-bond displays in greylag geese, *Anser anser*, by FISCHER (1965) where these displays were found to help individuals during aggressive interactions in the flock. The fact that no relationship was found between courting and pair-bond displays/attacks in the factor analysis here also fits the results from grey-lag geese as no common motivational basis has been described for courting and pairbond displays. This lends some credibility to the analysis as the seasonal fluctuations in these parameters were quite parallel.

Testosterone and LH were another pair of parameters which were always positively correlated to the same factor. This is in agreement with other experimental work in birds by MAUNG & FOLLETT (1978) and PAULKE & HAASE (1978) demonstrating that the peripheral levels of androgens were under the control of LH. In other bird studies, testosterone has been shown to be negatively correlated with body weight (AKESSON & RAVELING, 1981) and thyroid function (JALLAGEAS & ASSENMACHER, 1974, 1979). The latter discrepencies have been discussed in a separate paper (DITTAMI & HALL, 1983). The lack of a negative relationship between testosterone and body weight is not surprising as the major body weight decreases occurred from January to February while the androgens first increased in March. Although the raw data from AKESSON & RAVELING (1981) are quite similar to those described here, the negative relationship may have resulted from their examining the time period from January to May alone.

The constant negative relationship between prolactin and body weight was rather surprising. If anything, experimental work has pointed towards a positive relationship between weight increases and prolactin, especially in migratory birds (see NICOLL, 1974, and ENSOR, 1978 for reviews). Still, more recent field work on the rook (LINCOLN, RACEY, SHARP & KLANDORF, 1980) and the starling (DAWSON & GOLDSMITH, 1982 for prolactin; GWINNER, DITTAMI, GÄNSHIRT, HALL & WOZNIAK, in press, for weights) has demonstrated that prolactin increases on a circulating level were contemporal with body weight losses. So the fact that prolactin levels were always negatively correlated with the weight factor might either represent a physiological role of prolactin which has not been investigated or may be the result of some seasonal processes which link the two factors but do not imply a causal relationship.

The clumping of endocrine and behavioral parameters in the same factors were less reliable. The testosterone-courting relationship which has been described in many species (BALTHAZART & HENDRICK, 1976; ADKINS-REGEN, 1981; GORMAN, 1974; PRÖVE, 1978; WADA, 1982, among others) seemed to exist on an annual basis and outside of the breeding season, but in spring when the circulating levels were highest, no relationships were found. This leads one to believe that perhaps above a certain threshold level of circulating androgens no corresponding behavioral changes are to be expected as the peaks may have more to do with some physiological phenomena.

The positive correlations between factor I on an annual basis and testosterone/LH and ATT/PBD were in agreement with results on ducks by BALTHAZART & HENDRICK (1976). It is of interest that the relationship did not hold up on a seasonal basis. The coupling between these hormonal and behavioral parameters seems to be rather loose. Indeed, rather contradictory results exist about the role of androgens in controlling aggressive behavior (see BRAIN, 1977; LESHNER, 1978 for reviews) and even in Canada geese (AKESSON, pers. comm.) the association was not constant.

The relationships between prolactin and behavior seem as complex as the description of its physiological functions (see NICOLL, 1974, and ENSOR, 1978 for reviews). Its positive relationship with courting in spring may reflect the augmenting action of prolactin in androgen stimulation in males (NICOLL, 1974). On the other hand, the negative relationship with aggressive behavior may represent the result of a seasonally dependent antigonadal function as has been described for thyroid effects (WIESELTHIER & VAN TIENHOVEN, 1972) and is indicative of the assumed role of prolactin in parental behavior.

In general the results presented in this paper are in agreement with many manipulation experiments which have been undertaken in vertebrates even though the data were collected from a free-living population, where many circumstantial factors which could not be taken into account play a role in the expression of behavior. The linking of testosterone with courting and aggression is what one would expect, however, the fact that the two behaviors separated out into independent factors shows that their relationship with the steroid plasma titer goes beyond a simple question of concentration. It could result from seasonal changes in their relationship or from differences on an individual basis in the motivation for the respective behaviors. These relationships did not occur at very high plasma titers of testosterone. It may be that above a certain threshold no corresponding changes in behavior can be expected with increasing plasma concentrations of steroids. Those increases, right before female egg laying may be related more to either physiological phenomena like spermatogenesis or to specific behaviors like copulations which were not included in the analysis as the frequency of their occurrence was too low.

Summary

Individual measurements of courting, aggression, pairbond displays, body weights and the circulating levels of testosterone, LH, T4 and prolactin in male barheaded geese were subjected to a factoral analysis. Data from the whole year were analysed and then broken up into pre-breeding and post-breeding components and re-analysed. Some parameters remained clumped in the same factors throughout like aggression and pair-bond displays, LH and testosterone, and prolactin and body weight. Others, especially behavioral and endocrinological parameters were only linked on either an annual or seasonal basis.

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Zusammenfassung

Bei adulten Streifengansmännchen wurden mit Hilfe einer Faktoranalyse Zusammenhänge zwischen folgenden Parametern untersucht: Balzaktivität, Angriffshäufigkeit, Häufigkeit des Triumphgeschreis, Körpergewicht und den Plasmatitern von Testosteron, LH, Thyroxin und Prolaktin. Zunächst wurden die Daten des gesamten Jahreszyklus