the undulatory phase of copulation and that the horns of the penis head remove sperm from the spermatheca.

Scanning electron microscopy (*13*) revealed several morphological features of the penis that could aid in sperm displacement. First, the flexible head of the penis (Fig. 2A, *ph*) is probably extensible by internal fluid pressure (*14*) and may aid in scooping or displacing sperm from the bursa copulatrix. In Fig. 2B a mass of sperm (*sm*) is held under the distal flange (*fl*) of the penis head shown folded back on the venter of the penis. The backward pointing hairs on the venterolateral surfaces of the base of the penis head (Fig. 2B, *h*) aid in removing the sperm mass. Removal of sperm from the spermathecal tubes involves backward pointing hairs on the horns of the penis head (Fig. 2B), seen at higher magnification (Fig. 2C) to be holding a clump of entangled sperm.

The penis of *Calopteryx maculata* thus serves the dual function of sperm removal and sperm transfer. It appears that such a dual function has not previously been reported for the intromittent organ of any animal.

The postcopulatory behavior of the Odonata falls into three general classes: (i) no postcopulatory association of mates, (ii) oviposition in tandem, and (iii) noncontact guarding of an ovipositing mate (*15*). The first class involves oviposition by females in hidden locations, or away from male activity, or after the daily or seasonal period of male activity. These behaviors can be viewed as means of avoiding disturbance during oviposition and, especially in the second and third classes, prevention of take-over and sperm displacement by other males (*1, 16*).

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9. Females were tethered on monofilament (No. 6 test) fishing line, with a drop of Duco cement on the thorax or between the front wings. Tethered females placed on or moved near the oviposition site in a male's territory elicited courtship and tandem formation. The tandem pair was then allowed to fly up to nearby bushes or the observer's hand for completion of copulation.
10. In damselflies (Odonata), sperm transfer to the female is indirect. The male first transfers sperm from a storage reservoir associated with his testes in abdominal segment 8 to the bulbous sperm vesicle of the copulatory complex on the venter of abdominal segment 2. The organs of this complex are not homologous with copulatory organs of other insects. Sperm is transferred from the sperm vesicle to the female's bursa copulatrix by injecting it into the sperm channel (Fig. 2A, *sc*) on the dorsal surface of the penis (*14*).
11. The estimate of 88 percent was derived by dividing the average index of sperm volume for females in tandem (at premating) by that of females from interrupted copulation (at postdisplacement). Since the interrupted pairs were still in the process of sperm removal, it should be considered a minimum. In 5 of 24 females, 100 percent of the sperm was removed from the bursa copulatrix and spermatheca.
12. Males copulating with tethered females were kept in copula by decapitation with dissecting scissors. The female's abdomen was then cut at segment 6 and the male's abdomen at segment 4 and at the thorax. The remaining abdomens and engaged genitalia were immediately placed in alcohol for storage until dissection.
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Hormone Changes Triggered by Aggression in a Natural Population of Blackbirds

Abstract. *The concentrations of hormones in the plasma of male red-winged blackbirds caught at the height of an aggressive encounter are significantly different from those in males that have not recently engaged in aggressive behavior. Concentrations of luteinizing hormone in the plasma are decreased in the aggressive males, whereas androgen concentrations are affected in a more complex manner. Concentrations of corticoids do not appear to be affected by aggressive behavior.*

Aside from seasonal variation in reproductive function, circulating steroid and gonadotropin concentrations in male vertebrates were once thought to be relatively stable or tonic. However, recent research has shown that circulating hormones can be rapidly and profoundly affected by an animal's social interactions. In a variety of species in captivity, copulation or mere exposure to a conspecific female increases the concentration of testosterone in the male's plasma (*1–4*). Increases in plasma luteinizing hormone (LH) after copulation have also been reported (*5*). Other workers (*6–7*) have found striking changes in circulating hormones in animals that have participated in aggressive interactions, the general pattern being that the adrenal corticoids increase, whereas LH and testosterone decrease. The rapidity with which these hormonal changes can occur during a social interaction suggests that the endocrine system may have a more important role in the individual's minute-to-minute response to critical social stimuli than was previously realized. This possibility is strengthened by the finding that preventing the normal changes in circulating hormone concentrations during an aggressive encounter significantly altered the behavior of the individual that was being attacked (*8*).

How applicable these laboratory findings are to animals living under natural conditions is unclear. In studies of aggression it is not usually possible to separate the effects of aggression from the effects of social confinement, thus the changes in endocrine function after an aggressive encounter under laboratory conditions may be a normal response to social stimulation or a "stress" response to abnormal social conditions that the animal cannot escape. We present evidence from a natural population of red-winged blackbirds (*Agelaius phoeneceius*), demonstrating that hormone concentrations change rapidly as a function of the animal's ongoing behavior.

Because repeated blood sampling in small animals can obscure the effects of behavior on hormone concentrations, (*9*), our study was designed to compare the concentrations of circulating hormones in two different groups of birds rather than one group examined twice. Males from a breeding population of red-winged blackbirds were caught in the town of Washington, Dutchess County, New York, between 15 April and 21 May 1976 under one of two conditions—that is, when the birds were either at the height of an aggressive interaction or foraging. To elicit aggression, a live decoy male was placed in the central

Table 1. Hormone concentrations in the plasma of male red-winged blackbirds trapped when they were either at the height of an aggressive encounter or foraging. Numbers in parentheses are the number of animals per group.

Group	LH (ng/ml)	DHT (ng/ml)	Testosterone (ng/ml)	Total androgens (ng/ml)	Corticosterone (μg/ml)
Aggressive males*	5.41 ± 0.64 (22)	1.16 ± 0.27 (22)†	2.94 ± 0.55 (22)	4.10 ± 0.80 (22)†	1.06 ± 0.16 (16)
Foraging males	9.13 ± 1.11 (12)	1.52 ± 0.38 (16)	4.07 ± 0.53 (16)	5.75 ± 0.80 (16)	1.09 ± 0.31 (10)
Aggressive males‡	5.73 ± 0.67 (12)	1.10 ± 0.25 (16)†	2.90 ± 0.56 (16)	3.98 ± 0.78 (16)	1.27 ± 0.22 (10)

*Data from all available aggressive males. †Although the means of these groups are not significantly different from the mean of the corresponding foraging group, nonparametric statistics demonstrate that the distribution of these hormone levels is significantly different from that of foraging males. ‡Data from group adjusted to equal numbers of animals.

portion of a male's territory in a spring-loaded net trap, accompanied by the playback of male advertising song (*10*). The "singing intruder" usually elicited a rapid behavioral response from the territorial male, including increased frequency of song and the accompanying species-specific wingspread display, approach, and ultimately attempts to attack the intruder. The behavior of the territorial male was recorded until, in his escalating attempts to drive off the intruder, he hit the trap's trigger mechanism and was caught. On average, these aggressive encounters lasted 19.5 ± 2.4 minutes (mean ± standard error) before the birds were caught. Foraging males were caught in four-celled Potter traps baited with cracked corn and oats. These traps were not placed on individual territories but along the edge of a road running through the study area where males were often observed feeding.

The traps were observed until a bird was caught. A blood sample was then obtained by cardiac puncture as rapidly as possible. The mean latency to obtain a blood sample was 2.58 ± 0.29 minutes. The birds were then weighed, banded, and released. The levels of 5α-dihydrotestosterone (DHT), testosterone, corticosterone, and LH in each plasma sample were measured by radioimmunoassay (*11*).

Originally, we caught more aggressive than foraging males during April; this could have been a source of sample bias if there were any seasonal effects of hormones. We therefore analyzed the data twice, first using all available data and then, more conservatively, by dropping the data from six aggressive males so that data from equivalent numbers of birds were analyzed under both conditions for each week of the experimental period (*12*). Males in the two groups did not differ in the other variables measured such as time of capture, latency to obtain blood sample, weight, territory possession, number of females and active nests on the territory. The territories of the foraging males were often adjacent to those of males caught during an aggressive encounter. An effort was made to avoid retrapping in the feeder traps males caught previously in the aggressive condition; when this occurred, no blood sample was taken.

Table 1 [see (*13*)] shows that aggressive males had significantly lower LH levels than foraging males ($P < .002$, all males; $P < .02$, adjusted to equal numbers per group). Aggressive males also had significantly different DHT concentrations compared to foraging males ($P < .002$, all males; $P < .016$, groups adjusted to equal numbers). This difference was more complex than that found for LH. The concentrations of DHT in aggressive males tended to be much more variable than those of the foraging males. This same trend was apparent in the testosterone and total androgen (DHT + testosterone) data, but was significant only for total androgen concentrations for all males ($P < .027$). Plasma corticoid concentrations did not differ between groups. Levels of LH and androgen were not correlated in the foraging males (LH and DHT: $r = -.393$, LH and testosterone: $r = -.121$), but were significantly correlated in the aggressive males (LH and DHT: $r = .646$, LH and testosterone: $r = .654$; $P < .02$) (see Fig. 1). Concentrations of DHT and testosterone in each individual were significantly correlated in both foraging and aggressive males (.70 and .74, respectively; $P < .02$).

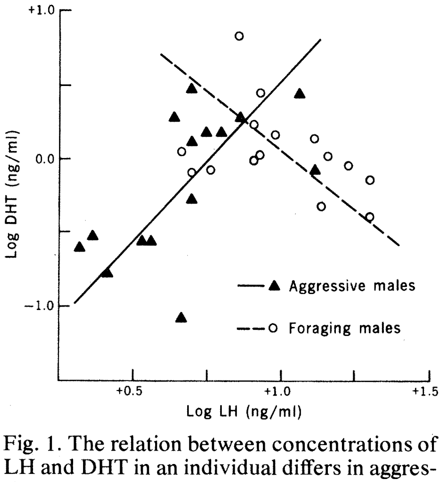

Fig. 1. The relation between concentrations of LH and DHT in an individual differs in aggressive and foraging males. There is a significant positive correlation between LH and DHT in aggressive blackbirds, but not foraging blackbirds. Data from groups adjusted to equal numbers; only 15 data points are given for each group because each group contained one bird for which there were LH data but no DHT data, or vice versa.

Several studies have suggested that LH rather than testosterone is the hormone that modulates intermale aggression in passerine birds (*14*), hence it was interesting to find that LH concentrations were clearly different in aggressive as compared to foraging males. Our finding of lower LH concentrations in the aggressive males is consistent with the laboratory results showing that LH levels in both dominant and subordinate male mice are lower immediately after an aggressive encounter (*6,7*). It has been suggested for mice that frequent or prolonged aggressive interactions lower gonadotropic function to such an extent that the male's reproductive capacity is adversely affected (*15*).

In most studies of androgen and behavior interactions, chromatographic analyses have either been omitted, and total androgens measured, or only the testosterone fraction has been assayed. It is therefore interesting that in the present study the less frequently studied androgen, DHT, was clearly more responsive to behavioral stimulation than testosterone. Circulating hormone with the mobility of DHT has been found in several other passerine species (*16*), but what, if any effect it may have on behavior in these species is unknown (*17*).

The finding that androgen concentrations in the aggressive males tended to be more variable than those of foraging males is not completely surprising. In mammals, different males may show completely different though replicable patterns of hormone secretion in response to the same stimulus animal. The response of male mice to a trained fighter on the other side of a wire mesh barrier is dependent on their previous experience. Previously defeated males respond with greatly increased levels of corticosterone secretion, whereas inexperienced males do not (*17*). Similarly, testosterone concentrations in male guinea pigs after exposure to an estrous female are related to the level of sexual activity the males show when given the opportunity to copulate (*9*).

The lack of correlation between LH and androgen concentrations in foraging males is not surprising. Most studies examining the relation between LH and testosterone have found either no correlation or a sluggish testicular response to LH, with peaks in testosterone secretion lagging behind those of LH by anything from 30 minutes to 3 hours (*16,18,19*). The significant positive correlations between LH and both testosterone and DHT in the aggressive males are therefore all the more interesting and may represent a behaviorally activated neuroendocrine mechanism.

Plasma corticoid concentrations were not increased in the aggressive birds, even in those birds which had interacted with the intruder for 30 to 40 minutes before capture. Laboratory studies with mammals have consistently shown increased corticoid levels in both the dominant and subordinant individuals that have just had an aggressive encounter. Of course, this could be a species difference in the way animals respond to aggressive stimulation; there are no comparable data on redwings in the laboratory, nor on any other bird. Another possibility is that the corticoid levels found in our study reflect a difference between freedom to initiate and pace an aggressive interaction rather than confinement in a small open area with a conspecific.

Our data demonstrate that under natural conditions, an animal's hormone levels may fluctuate rapidly in response to ongoing social interactions. Since the birds were sampled only once, it is unlikely that our data represent maximal deviations from normal concentrations of circulating hormones. There is no question that the changes occur rapidly, however, since the average length of the aggressive interaction was 19 minutes. The rapidity with which both pituitary and steroid hormones may respond to social stimulation suggests that the endocrine system may play a more important role in modulating an animal's minute to minute behavioral responses during social interactions than was previously thought.

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11. Using antibody S-250 (supplied by G. Niswender), we assayed plasma DHT and testosterone as described (*9*) but with the following modifications. Sample chromotography was carried out on columns of Sephadex LH-20 (Pharmacia) with heptane, methanol, and ethyl acetate (900 : 75 : 50 by volume) being used as the solvent. Chromatography solvent was added to each standard in the DHT and testosterone curves to correct for the slight loss of binding in the samples caused by the solvent. The DHT standard curve was run against ^{3}H-labeled testosterone rather than ^{3}H-labeled DHT. Plasma corticoid concentrations were measured against corticosterone according to the method of L. C. Krey, K. H. Lu, W. R. Butler, J. Hotchkiss, F. Piva, E. Knobil, *Endocrinology* **96**, 1088 (1975). After completion of the steroid assays, the samples were shipped frozen to Bangor where plasma LH levels were determined in triplicate at three dilutions by a micromodification of the method outlined by B. K. Follett, C. G. Scanes, and F. J. Cunningham [*J. Endocrinol.* **52**, 359 (1972)].
12. In fact, no significant seasonal trends were found in plasma hormone concentrations during the period studied. The second analysis of the data represents the most conservative view possible of the data. The six birds were not dropped at random, but in the case of the androgen analysis they were the three aggressive males with the lowest and the three males with the highest androgen concentrations, caught during the second half of April. Since the Moses test was being used to examine the possibility that data from the aggressive males tended to fall at the extremes of the distribution, dropping the data from the males that had the most extreme scores actually tended to bias the data against significance—providing a most conservative analysis.
13. The data were analyzed by nonparametric methods as described by S. Siegel [*Nonparametric Statistics* (McGraw-Hill, New York, 1956)]. The Mann-Whitney *U* test (LH data) and the Moses test of extreme reactions (androgen data) were used to compare groups. The Spearman rank correlation coefficient was used to evaluate the relation between concentrations of two hormones in the same individual. Means (± standard error) are also presented.
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20. We thank C. Quimby for assistance in the field, L. Krey and B. McEwen for the use of their laboratory facilities, and P. Marler and H. Feder for advice. Research supported by PHS postdoctoral fellowship GM 01063 01-3 and a grant from the Agricultural Research Council.

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The Gynoecium Winteraceous Plants

While the report by J-F. Leroy (*1*) provides a tantalizing glimpse of floral structure in an enigmatic plant, the provocative title and conclusions are insufficiently supported by the evidence given.

To summarize, Leroy stated that the gynoecium in *Bubbia perrieri* has two carpels fused together at their margins. However, the two placental ridges described are the usual condition for an individual carpel in other winteraceous plants such as *Drimys winteri* (*2*), *D. lanceolata* (*3*), *Pseudowintera axillaris* (*4*) and several species of *Bubbia* (*5*). Bailey and Nast (*5*) illustrated several species of *Bubbia* with short stigmatic regions not greatly different from that illustrated for *B. perrieri*, except that in the latter species the stigmatic crests are laterally pendant over the top of the gynoecial structure. *Bubbia perrieri* was originally described as unicarpellate (*6*), and soli-