

Within-pair testosterone covariation and reproductive output in Greylag Geese *Anser anser*

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In monogamous animals, reproductive success may vary considerably among pairs. To study this variation, we focussed on reproductive events and the circannual hormonal co-ordination within pairs during the reproductive cycle. Testosterone was chosen as covariable for both sexes because of its mediator function between behaviour and physiology. In a flock of free-living Greylag Geese *Anser anser*, individual faecal samples were collected weekly from 23 pairs over a complete annual cycle. From the faeces, equivalents of testosterone, oestrogen and other steroid hormones were analysed by enzyme immunoassay. In contrast to correlations between male and female testosterone, no correlations were found between oestrogen–oestrogen or oestrogen–testosterone. Therefore, only testosterone (T) is considered here. Sex-specific differences in T were in amplitude rather than in the annual timing of maxima and minima. However, the annual timing varied to some degree between individuals within sexes. Therefore, we examined the degree of annual testosterone correlation (TC) within pairs. Pairs that nested had significantly higher TC over the year than pairs that did not. The higher the within-pair TC, the larger the clutches and the heavier the eggs. Also, TC in the year investigated was positively and significantly correlated with the pairs' long-term reproductive output. No correlation was found between TC and the duration of the pair-bond, individual age, or age difference from pair partner. We suggest that TC is a measure of behavioural synchrony and, therefore, pair-bond quality. We consider whether within-pair TC results from mate choice.

In comparison with other species, few Greylag Goose *Anser anser* pairs reproduce successfully (Black *et al.* 1996, Nilsson & Persson 1994). From 1990, in the goose flock studied here, 81.5% of all adult pairs attempted to nest, 57.5% incubated the clutch, but only 18.0% of all pairs successfully fledged young (Hemetsberger unpubl. data). The decision to nest and breeding success are probably related to numerous individual or pair parameters including conditional, behavioural, physiological and predation risks. Previous studies have considered individual social and life-history parameters, such as social status (Black & Owen 1987, Lamprecht 1986), parental age and the females' breeding experience (Cooke & Rockwell 1988, Lamprecht 1990, Nilsson & Persson 1994,

Raveling 1981). However, in seeking the constraints on reproductive success, in geese, it may be insufficient to focus on only one member of the pair because of the biparental reproductive effort (Choudhury *et al.* 1996). Therefore, dyadic parameters, such as differences in age and size within the pair (Black & Owen 1995, Choudhury *et al.* 1996) or pair-bond duration (Owen *et al.* 1988) have been examined. These studies suggest that reproductive output in geese and other long-term monogamous birds (Black 1996) may not only be a matter of individual quality but may be crucially affected by the 'compatibility' of the pair partners (Black *et al.* 1996, Cézilly *et al.* 1997, Coulson 1972). Barnacle Geese *Branta leucopsis*, for example, pair according to the dominance status of the families from which they originate and according to size, rather than pairing with the largest available individual. The greater the size-mismatch, the lower

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was the reproductive success of the pair (Black & Owen 1995, Choudhury *et al.* 1996, Cooke & Davies 1983).

Sex-specific contributions to reproduction may be complex. Although egg production is clearly a female affair, fertility (clutch size) depends on female nutritional state and may, therefore, be affected by the male's performance during the prenesting period (Cooke *et al.* 1984, Cooke & Rockwell 1988, Raveling, 1979, Schneider & Lamprecht 1990). The eggs are incubated by the female. The males tend to stay some distance from the nest and join the females during their few short incubation breaks. Goslings are not fed, but are brooded by the female during their first few weeks (Schneider & Lamprecht 1990). Males spend much time vigilant, while females and offspring mainly feed. Parents assume complementary behavioural roles and both contribute to the survival of the young to fledging and during the first winter (Schindler & Lamprecht 1987).

Aside from phenotypic matches, it may be expected that successful pairs also show some covariation in physiological parameters, since hormones, behaviour and social status closely interact throughout the complex annual cycle of a pair of geese (Akesson & Raveling 1981, 1983, Dittami 1981, Kotrschal *et al.* 1998). O'Connell *et al.* (1981) suggested that gonadal synchrony between the sexes in Ring Doves *Streptopelia risoria* was a function of behavioural and physiological co-ordination during the reproductive cycle. Bluhm *et al.* (1984) found in Canvasback Ducks *Aythya valisineria* that successful pairs co-ordinate more closely than unsuccessful ones. Behavioural interactions within a pair, and between pair partners and flock members, may contribute to fine-tune the onset of reproduction (Gwinner 1986, Wingfield & Farner 1980). This fine-tuning could be reflected in hormonal parameters. For example, testosterone can regulate sperm production and the activation of sexual behaviour in the male (Becker *et al.* 1992, Brown 1994, Nelson 1995). A peak in female testosterone during the prelaying phase is involved in follicular development and may also affect sexual behaviour (Carter 1992, Furr & Thomas 1970, Johnson 1986, Schwabl 1996). Throughout laying and incubation, testosterone is decreased in both sexes (Figs 1 & 2; Dittami 1981, Hirschenhauser *et al.* 1997, Wingfield & Farner 1977). Hormones affect behaviour, and environmental stimuli feed back on hormonal status. Testosterone, for example, is involved in the feedback-regulation of sexual and aggressive behaviour, competitiveness and parental effort (Akesson &

Raveling 1983, Carter 1992, Dittami 1981, Hegner & Wingfield 1987, Hirschenhauser *et al.* 1997, Ketterson *et al.* 1992, Silverin 1990, Wingfield *et al.* 1990). Androgens may respond to social stimuli (male-male interactions, sexually receptive females; Silverin 1984, 1990, Wingfield *et al.* 1990) and other environmental stimuli (daylength, weather, availability of food, environmental xenobiotics: Assenmacher & Jallageas 1980, Danzo 1997, Dusseau & Meier 1971, Sanderson *et al.* 1997, Silver 1992, Silverin 1984, Wingfield *et al.* 1997).

The analysis of steroid hormones from faeces is non-invasive, and therefore allows repeated long-term sampling from individuals to investigate hormone-related social mechanisms and functions in unrestrained animals (Creel *et al.* 1997, Frigerio *et al.* 1997, Hirschenhauser *et al.* 1997, Kotrschal *et al.* 1998, Lee *et al.* 1995). As the temporal patterns of testosterone may vary markedly among populations and individuals, we chose to scan for within-pair testosterone covariation, as studies increasingly indicate a prominent role of testosterone in the fine-tuning of socio-sexual behaviour. We related these within-pair testosterone correlations to reproductive effort during the year sampled and to the pair's reproductive output over the duration of the pair-bond. Although the evidence is correlational, we argue that the seasonal matching of testosterone between pair partners (no matter whether this is cause or effect) may be a measure of pair-bond quality.

METHODS

Animals and data collection

The free-ranging resident flock of Greylag Geese studied was established in the Upper Austrian valley of the river Alm in 1973 (Lorenz 1988). Birds are individually marked with coloured leg-rings and are habituated to the presence of humans. This enables one to sample individual faeces and behavioural data year-round. Since the flock was established, social interactions within it, and clutch data, have been recorded (three times per week) throughout nesting. Feeding twice a day supplements the birds' natural food, except for times of snow cover when this is their only food source. Animals within this flock compete for food (Kotrschal *et al.* 1993). However, feeding nearly *ad libitum* may release the pairs from energetic constraints acting on geese in the wild and reproductive success or failure may depend more on other factors including individual and/or pair-bond quality.

We studied 23 of the approximately 32 pairs of the flock, because only from these could sufficient faecal samples be gathered. Individual faecal samples from males and females were collected weekly from February 1993 to February 1994 between 08.00 h and 11.00 h after the morning food provisioning, resulting in a total of 501 faecal samples: 249 from males and 252 from females. On average, 11 faecal samples per individual and year were collected.

Age, age difference from the pair partner, and duration of the pair-bond at the onset of the study were considered. Individual age ranged from 2 to 21 years (mean \pm sd = 7.2 ± 4.8) in females and from 3 to 23 years (8.7 ± 4.7) in males. Age differences between partners ranged between 0 and 9 years (2.6 ± 2.4), and pair-bond duration from 1 to 18 years (4.0 ± 4.0).

Five reproductive parameters were examined, four of which are related to reproductive output in the year sampled: clutch size (total number of eggs in the clutch), mean egg weight per clutch, hatching success (percentage of eggs hatched) and fledging success (percentage of hatched goslings fledged). In addition, we assessed the mean annual productivity of the pair (total number of goslings fledged divided by pair-bond duration; Scott 1988). One of the pairs regularly bred at the Bavarian Chiemsee (120 km away) and returned in autumn with their fledged young. Thus, clutch size, egg weight and hatching success, as well as complete annual cycles, were not available for this pair.

Analysis of steroid hormones from faeces

Gut passage time in geese is only 2–3 hours and individuals may defecate more than once per hour. Steroid metabolites are produced in the liver and are excreted via faeces and urine (Macdonald *et al.* 1983, Peter *et al.* 1996). Because a separation of faeces and urea is hardly feasible in goose droppings, they were analysed together (Bercovitz *et al.* 1978). Because they are herbivorous, in geese only a small proportion of the dropping consists of urea. To avoid handling of the birds, blood sampling was not an option. Thus, plasma levels can only be inferred. A parallel excretion study with domestic geese, which received systemic injections of ^3H -labelled steroid revealed that excretion started a few minutes after the injection and peaked 1–2 hours later (Krawany, 1996). In agreement with reports by Bishop & Hall (1991), Cockrem and Rounce (1994), Palme *et al.* (1996) and by Berkeley *et al.* (1997) across a range of species, another series of experiments with domestic geese (Hirschenhauser *et al.* unpubl. data) showed significant correlation between

plasma steroids and metabolites in the faeces. Therefore, faecal samples are assumed to reveal an integrated, proportional record of the plasma steroid levels up to approximately two hours before defecation.

Faecal testosterone was assayed by enzyme immunoassay (Möstl *et al.* 1987) at a methanol dilution of 1:150 using a group-specific antibody against 4-androstene-17 β -ol-3-one-carboxymethyl-oxine-albumine-CMO (raised in rabbits). As label 5 α -androstane-3 β ,17 β -diol-3-hemisuccinate (Palme & Möstl 1993) was used (working dilution 1:200 000). The sensitivity of the assay was less than 2 pg, concentration limits for reliable measurement ranged from 0.1 to 60 ng/g faeces. Cross-reactions of the testosterone assay are given in Table 1. Faecal samples (0.5 g) were extracted with 1 ml water plus 1.5 ml methanol by vortexing (30 min). Thereafter, an aliquot of each sample was evaporated to dryness, redissolved in acetate buffer (pH 4.8) and hydrolysed using a mixture of β -glucuronidase/arylsulfatase (Merck 4114). Intra- and interassay variations were determined using homogenized pool samples. Mean intra-assay coefficient of variation was 9.5%, mean inter-assay coefficient of variation was 19.6%.

Data processing

The annual cycle was divided into 13 biologically relevant seasonal phases (Wingfield & Farner 1980): (1) courtship in February; (2) peak copulation, two to four weeks before the first egg; (3) end of copulation, two weeks before the first egg; (4) egg-laying; (5) first two weeks of incubation; (6) second two weeks of incubation; (7) hatching mid-April to beginning of May and the first two weeks thereafter; (8) moult in

Table 1. Specification of the cross-reactions of the rabbit antitestosterone antibody in the biotin–streptavidine enzyme immunoassay.

Steroid	Proportion (%) at 50% binding
4-Androsten-17 β -ol-3-one (testosterone)	100.0
5 α -Androstan-17 β -ol-3-one (5 α -DHT)	23.7
5-Androstan-17 β -ol-3-one (5-DHT)	12.3
4-Androsten-3 β ,17 β -diol	7.6
5 α -Androstan-3 α ,17 β -diol	5.5
5 α -Androstan-3,17 β -diol	1.3
5-Androstan-3 α ,17 β -diol	1.1
4-Androsten-17 α -ol-3-one (epitestosterone)	<0.1
5 α -Androstan-3 α -ol-17-one (androsterone)	<0.1
5 α -Androstan-17 α -ol-3-one	<0.1

June/July; (9) summer flock, August, September; (10) October; (11) November; (12) winter-flock, December; (13) precourtship, January. Individual data were aligned along the time axis according to the timing of reproductive events (Dittami 1981, Wingfield & Farner 1977). Where possible, mean hormone values per phase per individual were calculated.

Based on these individual phase means of faecal testosterone, Kendall's τ was calculated for the course of two individual years within pairs. We term this coefficient for the parallel nature of seasonal patterns the 'pair-wise annual testosterone covariation' (TC). Kendall's τ was preferred for the correlation of phase-wise steroid levels between pair partners, because it is suitable for the relatively small number of phases and it is relatively robust with respect to extreme values (Zöfel 1992).

Then, Spearman's r_s between the pairs' Kendall's τ and reproductive parameters were calculated. Spearman's r_s also served to correlate these pairwise parameters (TC) with parental age and pair-bond duration. For correlating parameters of reproductive success, we preferred Spearman's r_s because of its insensitivity to ties. Where necessary, results were controlled for the intercorrelation with a third variable using partial correlation. All statistics are given as means \pm sd and all probabilities are given two-tailed.

Results

Individual and pair-wise testosterone patterns

Throughout the year, testosterone equivalents in individual droppings varied between 0.02 and 79 ng/g faeces in the males and between 0.01 and 45 ng/g faeces in the females. In both sexes, testosterone showed a distinct seasonality (Figs 1 & 2) with peaks during the two weeks ahead of laying the first egg (one-way ANOVA with post-hoc Bonferroni, males: $F_{12,180} = 17.63$; $P < 0.000$; females: $F_{12,172} = 9.74$; $P < 0.000$).

Kendall's τ values obtained by correlating the phase-means of male and female testosterone over the annual cycle in 23 pairs spanned the entire range between -1 and $+1$. In 11 of 23 pairs, we found a significant correlation between individual annual testosterone profiles of birds in a pair (Table 2). On a weekly scale, correlating male and female faecal testosterone revealed no significant covariation within the pairs sampled. This indicates that within-pair testosterone covaries over intermediate timescales rather than on a daily base.

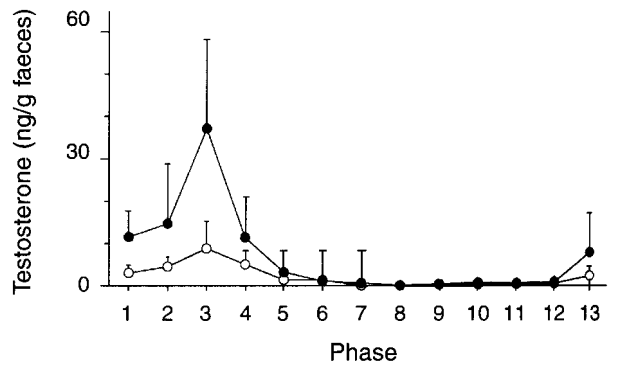


Figure 1. Annual testosterone levels as determined by enzyme immunoassay from the faeces of male and female Greylag Geese. ●, Males; ○, females. The amount of steroid (testosterone) per g faeces is plotted for 13 biologically relevant phases along the Greylag annual cycle. Vertical bars are standard error. Phases (number of individuals sampled per phase) were: 1, courtship period in February (19 males/20 females); 2, two to four weeks before the first egg (14/19); 3, two weeks before the first egg (14/12); 4, egg-laying (13/12); 5, first two weeks of incubation (11/7); 6, second two weeks of incubation (14/7); 7, hatching in April and the first two weeks thereafter (17/14); 8, moult (15/14); 9, summer flock (17/19); 10, October (10/14); 11, November (9/16); 12, winter flock, December (15/14); 13, precourtship phase, January (13/17).

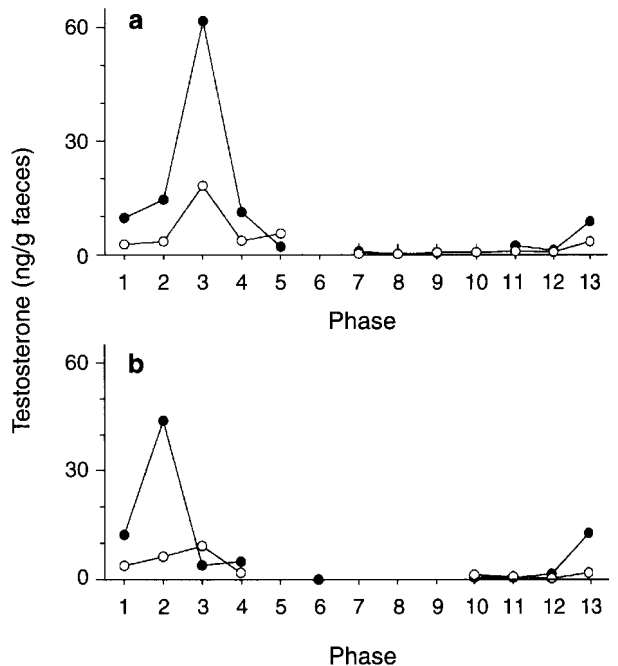


Figure 2. Examples of the annual testosterone fluctuations of the male (○) and the female partner (●) from (a) one pair with significant correlation of seasonal testosterone levels between the male and the female pair partner (pair 8; Kendall's $\tau_{11} = 0.64$; $P < 0.01$) and (b) one pair with no significant correlation of seasonal testosterone levels between the male and the female partner (pair 10; Kendall's $\tau_8 = 0.43$; ns).

Table 2. Pair-wise TC coefficients of correlation, sample sizes (number of phases) and probabilities of significance, pair-bond duration, clutch sizes, mean egg weights and the pairs' reproductive output.

Pair No.	Testosterone covariation TC (Kendall's τ)	<i>n</i>	<i>P</i>	Pair-bond duration (years)	Clutch size 1993 (eggs / clutch)	Egg weight 1993 mean \pm sd (g)	Pair productivity (<i>n</i> offspring/year of pair-bond)
1	0.810	7	<0.01	1	5	179.2 \pm 3.6	1.0
2	1.000	3	ns	18	0	—	1.6
3	0.854	10	<0.001	1	7	176.1 \pm 4.9	7.0
4	0.667	4	ns	4	3	181.3 \pm 10.2	0.0
5	1.000	5	<0.01	8	—	—	1.4
6	0.600	5	ns	6	6	170.8 \pm 4.2	0.2
7	0.444	9	ns	1	0	—	0.0
8	0.636	11	<0.01	4	6	167.8 \pm 3.1	0.0
9	-0.333	4	ns	1	0	—	0.0
10	0.429	8	ns	2	6	167.1 \pm 6.1	0.0
11	0.619	7	<0.05	5	5	172.4 \pm 6.5	0.0
12	1.000	6	<0.01	1	6	174.3 \pm 4.9	3.0
13	0.429	7	ns	1	4	152.8 \pm 2.1	0.0
14	0.371	8	ns	1	0	—	0.0
15	0.390	7	ns	1	0	—	0.0
16	-1.000	4	<0.05	5	4	171.5 \pm 3.2	0.0
17	0.429	7	ns	11	6	163.0 \pm 8.8	0.7
18	0.722	9	<0.01	1	4	—	0.0
19	0.714	8	<0.01	1	3	165.3 \pm 4.8	0.0
20	0.000	4	ns	5	0	—	0.0
21	0.333	4	ns	3	6	163.6 \pm 5.2	0.0
22	0.643	8	<0.02	1	6	167.9 \pm 4.1	5.0
23	0.643	8	<0.02	2	6	173.6 \pm 3.1	2.5

Pair-wise testosterone patterns and reproduction in the year sampled

Clutch sizes ranged from three to seven eggs (5.2 \pm 1.2). Visiting nests every second day throughout the laying period and measuring egg size allowed us to exclude eggs dumped by other females. Mean egg weights per female and clutch were between 152.8 and 181.3 g (169.8 \pm 6.9).

The mean TC of those 16 pairs that had a nest in the year sampled was significantly higher than the mean TC of the seven pairs that failed to nest, despite sufficient nesting sites being available (Mann-Whitney *U*: $Z_{16,7} = -3.35$; $P < 0.001$; Fig. 3). The pair's TC was positively correlated with clutch size ($r_{22} = 0.49$; $P < 0.02$; Fig. 4). Clutch size was not significantly correlated with life-history parameters, such as age (females: $r_{22} = 0.24$; ns; males: $r_{22} = -0.01$; ns), age difference from partner ($r_{22} = 0.17$; ns) or pair-bond duration ($r_{22} = 0.11$; ns).

TC and egg weight were significantly correlated ($r_{15} = 0.65$; $P < 0.01$; Fig. 5). In short, the better a pair's testosterone covariation, the heavier were the eggs produced by the female. Clutch size and egg weight were not correlated ($r_{15} = -0.01$; ns).

Clutch size is a measure of the female's fecundity. To translate fecundity into reproductive success, the goslings need to hatch and the hatchlings must fledge. Because these events are not independent (the more eggs are laid, the more goslings may potentially hatch), percentages are given in the following. Hatching success ranged from 0 to 100% (49.4 \pm 41.1), as did fledging success (43.9 \pm 38.5). Thus, on average only every fifth egg resulted in a fledged goose.

In contrast to its correlation with female fecundity, TC was not significantly correlated with percentage of

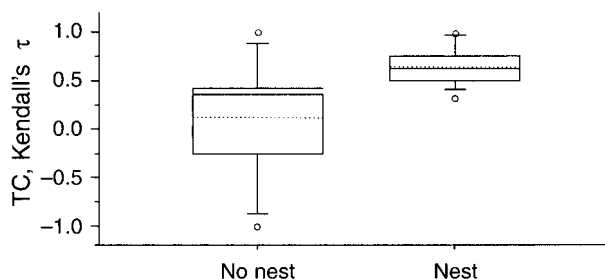


Figure 3. Mean degree of correlation between male and female seasonal testosterone levels (TC) of all pairs that failed to nest ($n = 7$) and of pairs nesting ($n = 16$) in the year sampled. Mann-Whitney *U* test: $Z_{16,7} = -3.35$; $P < 0.001$.

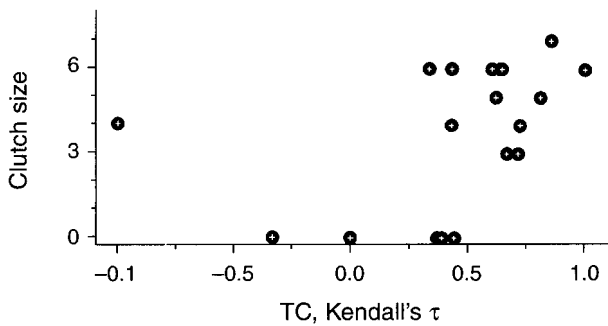


Figure 4. The relationship between the degree of correlation of seasonal testosterone levels between male and female pair partners (TC) and the pairs' clutch sizes in the year sampled. Spearman's rank correlation: $r_{22} = 0.49$; $P < 0.02$ but not all points are visible as some coincide.

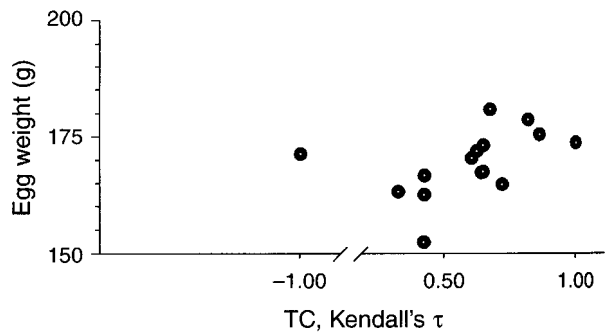


Figure 5. The relationship between the degree of correlation of seasonal testosterone levels between male and female pair partners (TC) and the mean egg weight per female in the year sampled. Spearman's rank correlation: $r_{15} = 0.65$; $P < 0.01$.

eggs hatched ($r_{15} = 0.27$; ns) nor with the percentage of hatched goslings fledged ($r_{11} = 0.43$; ns; Table 3). Hatching and fledging percentages were independent ($r_{11} = 0.34$; ns) so that after controlling for hatching success, a partial correlation between TC and fledging success was also non-significant ($r_8 = 0.21$; ns).

Pair-wise testosterone patterns and long-term reproductive output

Annual reproductive performance in long-lived animals such as geese contributes only a fraction to lifetime performance. Therefore, we searched for relationships between hormonal patterns in the year investigated and lifetime reproductive parameters. To compare pairs with different pair-bond duration, we considered the average annual numbers of fledged offspring. On average, pairs produced between zero and seven fledged offspring per year (1.2 ± 1.9).

Testosterone covariation (TC) was significantly correlated with the pair's long-term productivity, that is the mean number of fledged young per year of the pair-bond ($r_{23} = 0.47$; $P < 0.02$; Fig. 6). In contrast, life-history parameters, such as age in both sexes (females:

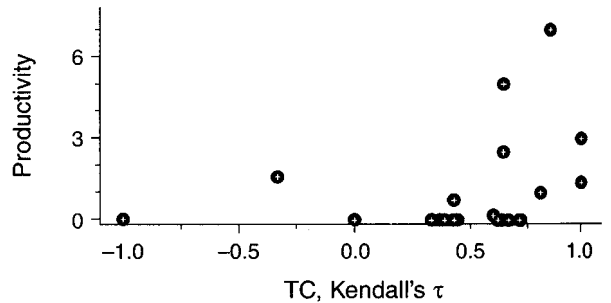


Figure 6. The relationship between the degree of correlation of seasonal testosterone levels between male and female pair partners (TC) and the pairs' long-term reproductive output expressed as mean number of offspring raised to fledging divided by pair-bond duration. Spearman's rank correlation: $r_{23} = 0.47$; $P < 0.02$ but not all points are visible as some coincide.

$r_{23} = 0.32$; ns; males: $r_{23} = 0.27$; ns), age difference to pair partner ($r_{23} = 0.06$; ns) and the duration of the pair-bond ($r_{23} = 0.07$; ns) were not significantly correlated with the average number of fledged young. Reproductive success in the year sampled was not correlated with the long-term reproductive output of the pair (hatching success: $r_{16} = 0.45$; ns; fledging success: $r_{11} = 0.31$; ns).

Table 3. Summary of results: correlation (r_s) of testosterone covariation (TC) with parameters of immediate and long-term reproductive output in the 16 nesting pairs and in all 23 pairs.

	Reproductive parameter	Spearman's correlation with TC	
		16 nesting pairs	All 23 pairs
Year sampled	Clutch size	ns	$r_{22} = 0.49$; $P < 0.02$
	Mean egg weight	$r_{15} = 0.65$; $P < 0.01$	
	Hatching success (%)	ns	
	Fledging success (%)	ns	
Long-term	Pair productivity	$r_{16} = 0.61$; $P < 0.01$	$r_{23} = 0.47$; $P < 0.02$

DISCUSSION

In monogamous animals, reproductive success may vary considerably among pairs (Black 1996). The free-roaming flock of Greylag Geese studied is no exception. Despite subsidiary food supply, on average only six of approximately 32 pairs per year successfully raise young to fledging. Thus, energy supply alone may be insufficient to explain the success or failure of this flock of geese. Previously, in searching for possible determinants of the differences in success between pairs, mainly life-history parameters have been considered (Black & Owen 1995, Choudhury *et al.* 1996, Cooke & Rockwell 1988, Lamprecht 1986, Nilsson & Persson 1994, Raveling 1981). Life-history data from more than 200 female Greylag Geese of the Grünau flock indicate that reproductive success is positively related to age, and thus experience of the female, and to pair-bond duration (own unpubl. data). It seems that some geese lose fewer goslings to predators or parasites than others.

Raveling (1978) considered that synchronization of pair activities during the breeding season may be an important determinant of reproductive success in geese. Akesson and Raveling (1981) suggested that, within a successful pair, male testosterone and female oestrogen may covary. We assayed oestrogen from the same set of faecal samples and with similar procedures as described for testosterone. In contrast to testosterone, correlations between male and female oestrogen and cross-wise correlation of oestrogen and testosterone of pair partners were not significant (Hirschenhauser *et al.* unpubl.). O'Connell *et al.* (1981) showed that in Ring Doves the female's gonadal condition affects the male's endocrine response. However, none of these studies considered androgen fluctuations in the female.

Despite the fact that in small mammals rapid, but long-lasting increases in oxytocin levels were found in both partners during pair formation (Barth *et al.* 1997, Carter 1992), it is still surprising that annual inter-individual covariation of a steroid hormone should be linked with reproductive success. For the first time, our results indicate that this may be the case with intermediate or long-term rather than the event-related hourly, daily or even weekly testosterone patterns in Greylag Geese. This highlights the importance of parallel changes between members of the pair, in seasonal testosterone maxima and minima rather than at synchronous short-term responses to the pair's variable environment.

Because of the feedback between steroid hormones

and behaviour, the causality of TC is not easily resolved. Behaviour is not only affected by hormones. Indeed, circulating steroid hormones are profoundly modulated by behaviour (Balthazart 1983, Silver 1992, Nelson 1995). Thus, TC may either be a cause or a consequence of reproductive output. We base speculation about causality on the two major results of this study: (1) the degree of seasonal correlation in testosterone between members of the pair (TC) is significantly correlated with the pair's reproductive effort in the year of the investigation and (2) TC during the year investigated correlated positively with the pair's long-term reproductive output.

Even though the argument necessarily remains speculative, we suggest that the male adjusts to the female rather than vice versa. Egg size is correlated with survival of the hatchlings (Nisbet 1978, Slagsvold *et al.* 1984), and egg weight correlated positively with TC. Egg weight over the years remains a relatively stable trait within individual females (Snow Geese *Chen caerulescens caerulescens*: Cooke *et al.* 1995, Greylag Geese: Hemetsberger unpubl. data) and may therefore be regarded as a trait of female quality. Since female birds are energetically more constrained over the reproductive cycle than males, the quality of a male may be in his responsiveness to the female's energetic needs, in particular to adjust to the female's timing of reproductive events such as the decision to nest, egg production and incubation.

Hormones may respond to social circumstances. Testosterone-motivated social interactions, for example, may cause a range of individual stress levels in male geese (Frigerio *et al.* 1997). This, in turn, may depend on the position of the individual or pair within the rank hierarchy of the flock (Kotrschal *et al.* 1998) or on individual personalities shaped during ontogeny in relationship to their social positions (Sapolsky 1992, Virgin & Sapolsky 1997). The potential for hormonal responsiveness may be an individual personality trait (Sapolsky 1992, Schwabl 1995) and to a certain extent may be flexibly negotiable between pair members. Thus, the male's potential to adjust may vary within trait-determined limits, his motivation to adjust may depend on his perception of her quality.

Two different mechanisms may account for the degree of within-pair covariation in testosterone: individuals could increasingly synchronize their testosterone fluctuations over the years of the pair-bond. However, the lack of a positive correlation between TC and pair-bond duration does not support this long-term mutual adjustment hypothesis. Alternatively,

achieving hormonal compatibility within the pair may be a rapid process during courtship or may even be a matter of mate choice itself (for example, based on male performance). The capacity to assess a potentially compatible partner may depend on mutual behavioural interactions between the pair partners, or may depend on both partners' individual styles of coping with social or environmental conditions. Thus, a highly synchronized pair either consists of two individuals that adjust well to each other (especially the male to the female) or is composed of two individuals with similar responsiveness that they have acquired independently during early life-history (Koolhaas *et al.* 1997). We therefore suggest that, via courtship behaviour (Choudhury *et al.* 1996, O'Connell *et al.* 1981), pair partners display and receive information about the female's reproductive condition, the male's potential responsiveness and both individuals' ability to cope with the social and physical environments. In this way, particularly females may (indirectly) assess the ability of a prospective partner for hormonal synchrony.

It remains to be seen why less well synchronized pairs stay together over years despite their low reproductive output (Table 2). They are probably constrained by a shortage of potential alternative partners. It seems that pair partners either match in their parameters, including TC, from the outset or they never will.

We acknowledge funding by the FWF, project no. P10483-BIO and permanent support from the Herzog von Cumberland-Stiftung. J. Hemetsberger kindly provided the egg and flock demography data. We thank W. Kawinek for performing the hormone analyses and J. Dittami, D. Frigerio, A. Ros, B. Wallner and J. Wingfield for critical comments on early drafts of the manuscript.

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Received 31 December 1997; revision accepted
12 August 1998