

# Social and life-history correlates of hormonal partner compatibility in greylag geese (*Anser anser*)

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In long-term monogamous birds reproductive success varies considerably among pairs. Determinants of reproductive success may be individual as well as pair-specific parameters, including the degree of compatibility and coordination among pair partners. However, little is known about the consistency of partner compatibility with regards to social contexts and life-history changes. In the long-term monogamous, biparental greylag geese, reproductive success was previously found to correlate positively with the degree of hormonal compatibility within pairs. In the present study, we analyzed the degree of within-pair testosterone covariation (TC) in relation to individual and pair-specific life history and social instability. We found that greylag goose pairs facing active social challenge had lower degrees of TC than those in unchallenged pair-bonds, whereas the permanent attachment of a third individual to an existing pair or the number of previous partners did not correspond with changed TC. Furthermore, TC decreased with increasing pair-bond duration and increased with female age but was not related with age of the male partner or other life-history parameters. Hence, our data suggest that hormonal partner compatibility in greylag geese is not a stable trait, but rather reflects a pair's status quo, which may be particularly affected by the stability of the social environment. *Key words:* *Anser anser*, greylag geese, partner compatibility, social challenge, testosterone. [*Behav Ecol* 21:138–143 (2010)]

In monogamous birds, reproductive success varies considerably among pairs. Differences in reproductive success have been attributed to a range of individual social and life-history traits, for example, social status (Lamprecht 1986), parental age, or breeding experience (Lamprecht 1990; Nilsson and Persson 1994; Angelier F et al. 2007; Naves et al. 2007). However, reproductive success in long-term monogamous biparental birds is not only determined by individual qualities but may be strongly affected by pair-specific parameters, such as pair-bond duration (Fowler 1995; Black et al. 1996; van de Pol et al. 2006) and compatibility between partners in various morphological, behavioral, hormonal, and life-history traits (Marzluff and Balda 1988a, 1988b; Choudhury et al. 1996; Hirschenhauser et al. 1999; Spoon et al. 2006). For instance, in pinyon jay (*Gymnorhinus cyanocephalus*) pairs similarity of partners in weight, age, and bill length scaled positively with reproductive success (Marzluff and Balda 1988a, 1988b), and a recent study in cockatiels (*Nymphiticus hollandicus*) showed that the number of eggs laid and young reared to fledging increased with behavioral coordination among pair partners (Spoon et al. 2006). Divorce, in turn, often causes physiological costs and reduced reproductive success (Black et al. 1996; Catry et al. 1997; Angelier FH et al. 2007), particularly if the pair breakup is forced (Heg et al. 2003). Angelier FH et al. (2007) suggested that these costs could mirror a lack of coordination among new pair members or could result from the social stress associated with pair breakup.

Social interactions are indeed among the most effective stressors (DeVries et al. 2003), and the social environment, in particular social challenges, are potent modulators of both behavior and physiology (e.g., Mendoza and Mason 1986; Wingfield et al. 1990; Hirschenhauser, Möstl, Wallner, et al. 2000; Wascher et al. 2008, 2009). Androgens, for instance, regulate and are responsive to sociosexual behavior, whereby responsiveness is fine-tuned by the social context and environment (Hirschenhauser and Oliveira 2006; Safran et al. 2008). As a consequence, social challenges may not only cause costs through divorce. Even if challengers are successfully fended off they may substantially affect a pair's compatibility at a behavioral and physiological level. To our knowledge, though, social influences on partner compatibility have not been studied yet.

In the present study, we investigate social influences on hormonal partner compatibility in greylag geese (*Anser anser*). Hirschenhauser et al. (1999) showed that greylag goose pairs, in which male and female testosterone was highly correlated throughout the year, were more likely to nest, had larger clutches, heavier eggs, and higher long-term reproductive success. This within-pair testosterone covariation (TC) did not improve with pair-bond duration, suggesting a rapid adjustment of pair partners during pair formation or choice of partners with similar responsiveness. In addition to male-female pairs, greylag partnerships can be comprised of male-male pairs and occasionally, trios, in which a third party (a secondary partner, usually a female) joins an existing pair (primary partners) for an extended period of time (Black et al. 1996; Weiß et al. 2008). Most of these bonds are stable over years and are typically ended by the death of one of the partners (Black et al. 1996; Weiß BM, personal observations), but challenges by rival males occur, particularly in the mating and breeding season, and may cause the breakup of former

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partners. Social challenges are characterized by a pronounced increase of agonistic interactions between male opponents (from typically less than 5 interactions per day to more than 10 interactions per hour between the opponents, Weiß BM, personal observations) and intense mate guarding behavior (Lorenz 1988; Hirschenhauser, Möstl, Wallner, et al. 2000). Male–male competition, in turn, induces testosterone increases particularly in males of biparental species. As a consequence, the male seasonal testosterone maximum due to gonadal activity may be extended during periods of frequent agonistic interactions (Wingfield et al. 1990). Male testosterone typically decreases to low, baseline levels during breeding but remains facultatively responsive to pair-bond challenges (Wingfield et al. 1990; Goymann et al. 2007). Thus, the interplay between testosterone and continuing high levels of aggression, particularly during the breeding season, may pose a substantial challenge to maintaining the long-term hormonal synchrony between partners.

As a follow-up to Hirschenhauser et al. (1999), we therefore examined the relationship between social environment and TC of greylag pairs, taking into account individual and pair-specific social history, the type of pair-bond (monogamous pair or trio), as well as the stability of the bond, that is, the occurrence of social challenges and divorce. In particular, we expected 1) lower TC in pairs confronted with a competitor than in unchallenged pairs because of the interplay between testosterone and agonistic interactions, 2) lower TC among the secondary partners of a pair than among primary partners because fine-tuning to 2 partners simultaneously may not be feasible, and 3) lower TC in pairs that subsequently broke up than in pairs that remained intact because partner incompatibility may enhance chances of divorce.

## MATERIALS AND METHODS

### Animals and data collection

A free-ranging, nonmigratory flock of greylag geese was introduced into the Upper Austrian valley of the river Alm by Konrad Lorenz and coworkers in 1973 (Lorenz 1988). Birds are individually marked with colored leg bands, and their life histories, including social background and clutch data, have been monitored continuously ever since. In recent years, flock size varied between 130 and 150 individuals. As in other populations, natural predation, mainly by red foxes (*Vulpes vulpes*) is common and may account for losing up to 10% of the adult flock per year (Hemetsberger 2001). The flock is supplemented with pellets and grain twice daily on the meadows around the research station, with low quantities from spring to fall, and with sustaining amounts during winter. In most years, some goslings are carefully hand-raised for various scientific reasons (e.g., Weiß and Kotrschal 2004). Hand-raised geese are fully integrated into the flock and account for ~25% of the flock. Both hand-raised and goose-raised flock members are habituated to the close presence of humans and do not show behavioral or physiological responses if approached by familiar humans (corticosterone: Scheiber et al. 2005, behavior and heart rate: Wascher C, Scheiber I, Braun A, Kotrschal K, unpublished data).

Detailed life history and endocrine data were collected from 23 pairs in 1993 (see Hirschenhauser et al. 1999) and were supplemented by additional data in 2004 and 2005, in which we included pairs with a history of social challenge, as well as trios with an additional male or female permanently joining a pair. This resulted in data from a total of 44 pairs and 7 trios (5 female–female–male, 2 female–male–male). In these trios, we considered 2 dyads per trio: primary partners (the original heterosexual pair) and secondary partners (the primary male

or female and the opposite-sex third party that had joined the pair). In total, we thus analyzed data from 58 female–male dyads. These were 48 dyads sampled once and 5 dyads that were sampled in 2004 and again in 2005 (dyads 24, 25, 27, 30, and 34, Table 1). Six of the 49 females and 8 of the 46 males were sampled repeatedly, that is, in up to 3 (different) pair-bonds or trios (Table 1). Individual age ranged from 2 to 21 years (mean  $\pm$  [standard deviation] SD =  $7.2 \pm 3.8$ ) in females and 2 to 23 years ( $8.4 \pm 4.4$ ) in males. Age difference between partners ranged from 0 to 9 years ( $2.2 \pm 2.2$ ) and pair-bond duration from 0 (newly paired) to 18 years ( $3.2 \pm 3.3$ ) at the onset of the respective sample year.

### Androgen metabolites from goose droppings

Throughout a complete year individual droppings from all involved individuals (49 females, 46 males) were collected every second week and frozen at  $-20^\circ\text{C}$  within 2 h after collection. To avoid the effect of diurnal variation, individual droppings were collected after the morning food provisioning until noon (Hirschenhauser et al. 2005). We aimed at collecting up to 3 droppings per individual per week to cover within-individual variation (Scheiber, Kralj, and Kotrschal 2005).

Immunoreactive androgen metabolites (AM) were assayed from 0.5 g feces extracted in 5 ml methanol using enzyme immunoassay. Assay specifications and sample sizes for the 1993 data are given in Hirschenhauser et al. (1999). A total of 1684 droppings were obtained in 2004 and 2005 and assayed using a group-specific antibody against 17-oxo-androgens (Hirschenhauser, Möstl, Peczely, et al. 2000). The assay-specific standard curve permitted reliable measurements between 2.9 and 410.0 pg/well, which corresponds to the range of 6.5–922.5 ng AM/g dropping. The mean interassay variation was 11.5% and mean intraassay coefficient of variation was 10.9%.

### Data analysis

The sampling period was divided into 13 biologically relevant seasonal phases, starting with the early courtship phase in January to the late winter flock in December (see Hirschenhauser et al. 1999), whereby the number of seasonal phases in which sufficient samples of both pair partners could be obtained varied between pairs (Table 1). In each year data were standardized according to the individual timing of reproductive events, that is, laying of the first egg, start of incubation, hatching of young, and postnuptial molt (Hirschenhauser et al. 1999). Median hormone values per individual per seasonal phase were calculated. Based on these individual seasonal patterns of AM, a Kendall's  $\tau$  correlation coefficient was calculated between the male and the female of a dyad. This coefficient of covariation between the partners was termed the "within-pair TC" (Hirschenhauser et al. 1999).

Kendall's  $\tau$  values were transformed by adding 1 and forming the square to fit a normal distribution (Shapiro–Wilk after transformation: degrees of freedom = 58,  $P = 0.256$ ). We conducted a generalized linear mixed model (GLMM) using the GenStat 10.1 statistical package, applying the restricted maximum likelihood (REML) procedure for repeated sampling with an unbalanced design (GenStat 2007). The GLMM was constructed with transformed TC (Kendall's  $\tau$ ) as the response variable and male and female identity as random terms to account for repeated measurements (from same or different years) in some individuals. Age of the female, age of the male, age difference between partners, the occurrence of social challenges, whether or not the pair-bond lasted for at least one year, pair-bond duration, the type of pair-bond (pair partners, primary and secondary partners in a trio), number of previous partners of the female as well as the male, the raising history

Table 1

Pair-wise TC (Kendall's  $\tau$ ), life history, and pair-bond characteristics of 53 different female–male dyads (44 pairs, 7 trios)

Dyad	Female ID	Male ID	TC	<i>P</i> (TC)	Sample year	<i>n</i> phases	Age female (years)	Age male (years)	Duration (years)	Partner type	Challenge	Hold	p_f	p_m	HR
1	1	1	0.810	<0.01	1993	7	8	8	1	—	No	Yes	3	3	One
2	2	2	1.000	ns	1993	3	21	23	18	m	—	Yes	1	2	None
3	3	3	0.854	<0.01	1993	10	7	9	1	m	No	Yes	2	2	None
4	4	4	0.667	ns	1993	4	5	6	4	m	No	Yes	1	1	None
5	5	5	1.000	<0.01	1993	5	17	12	8	m	—	Yes	3	2	None
6	6	6	0.600	ns	1993	5	8	10	6	m	No	Yes	1	3	None
7	7	7	0.444	ns	1993	9	3	5	1	m	No	Yes	1	2	None
8	8	8	0.636	<0.01	1993	11	7	7	4	m	No	*	1	1	None
9	9	9	−0.333	ns	1993	4	2	11	1	m	No	*	2	3	One
10	10	10	0.429	ns	1993	8	4	5	2	m	No	Yes	1	1	None
11	11	11	0.619	<0.05	1993	7	8	7	5	m	No	Yes	1	1	None
12	12	12	1.000	<0.01	1993	6	3	7	1	m	No	*	1	2	None
13	13	13	0.429	ns	1993	7	8	7	1	m	No	Yes	4	3	None
14	14	14	0.371	ns	1993	8	2	8	1	m	No	Yes	1	2	One
15	15	15	0.390	ns	1993	7	2	3	1	m	No	Yes	1	1	One
16	16	16	−1.000	<0.05	1993	4	4	3	5	m	No	Yes	2	1	None
17	17	17	0.429	ns	1993	7	14	20	11	m	No	No	2	3	None
18	18	18	0.722	<0.01	1993	9	10	7	1	m	No	Yes	2	3	None
19	19	19	0.714	<0.01	1993	8	8	10	1	m	No	Yes	2	5	None
20	20	20	0.000	ns	1993	4	7	10	5	m	No	*	1	3	None
21	21	21	0.333	ns	1993	4	4	10	3	m	No	No	1	4	None
22	22	22	0.643	<0.05	1993	8	3	3	1	m	No	Yes	1	1	None
23	23	23	0.643	<0.05	1993	8	11	9	2	m	No	*	3	5	One
24	24	22	0.333	ns	2004	9	9	14	3	m	Yes	No	9	2	One
25	25	12	0.286	ns	2004	8	11	18	5.5	m	No	Yes	3	4	None
26	26	24	0.357	ns	2004	8	6	6	3	m	No	Yes	1	2	None
27	27	25	0.611	<0.05	2004	9	8	6	4	m	No	Yes	1	1	One
28	28	26	0.357	ns	2004	8	5	5	4	m	No	Yes	1	1	One
29	29	27	−0.06	ns	2004	9	5	5	4	m	No	Yes	1	1	Both
30	30	28	0.556	<0.05	2004	9	11	12	8	p	No	Yes	1	2	One
31	31	29	0.429	ns	2004	7	9	8	6	m	No	Yes	1	1	One
32	32	30	0.571	<0.05	2004	8	4	5	3	m	No	Yes	1	1	None
33	33	31	0.444	ns	2004	9	5	5	3	m	No	Yes	2	1	One
34	34	32	0.786	<0.01	2004	8	6	8	1	m	No	Yes	2	2	Both
35	35	33	0.683	<0.05	2004	7	5	5	4	m	No	Yes	1	1	Both
36	36	34	0.527	<0.05	2004	11	4	4	3	m	No	Yes	1	1	Both
37	37	35	0.714	<0.05	2004	8	5	4	1	m	No	*	2	2	One
38	38	36	0.643	<0.05	2004	8	5	5	3.5	m	No	*	1	1	Both
39	39	37	0.524	ns	2004	7	3	3	1	m	No	Yes	1	1	Both
40	40	38	0.571	<0.05	2004	8	9	6	4	m	No	Yes	4	1	One
41	41	39	0.714	<0.05	2004	8	4	4	2	m	No	Yes	1	1	Both
42	42	40	0.611	<0.05	2004	9	8	11	0	m	No	*	3	4	Both
43	43	30	0.389	ns	2004	9	12	12	10	s	No	*	1	1	One
24	24	22	0.467	ns	2005	10	10	15	4	s	Yes	No	9	2	One
25	25	12	0.143	ns	2005	8	12	19	6.5	p	Yes	Yes	3	4	None
27	27	25	0.556	<0.05	2005	9	9	7	5	p	No	Yes	1	1	One
30	30	28	0.200	ns	2005	9	12	13	9	m	Yes	Yes	1	2	One
34	34	32	0.556	<0.05	2005	8	7	9	2	p	Yes	Yes	2	2	Both
44	44	32	0.643	<0.05	2005	6	5	9	0	s	Yes	Yes	1	3	One
45	25	41	0.214	ns	2005	8	12	13	0.5	s	Yes	No	4	4	None
46	42	25	0.500	ns	2005	8	9	7	0	s	No	Yes	4	2	One
47	24	42	0.524	ns	2005	7	10	9	0	p	Yes	Yes	10	3	One
48	45	43	0.418	ns	2005	10	6	2	0.5	m	Yes	Yes	3	1	One
49	46	44	0.786	<0.01	2005	8	10	12	0.5	s	No	Yes	3	8	Both
50	47	44	0.600	ns	2005	5	6	12	1	p	—	*	2	7	One
51	38	45	0.600	ns	2005	5	6	6	0	p	—	No	2	3	Both
52	48	45	0.200	ns	2005	5	2	6	0	s	—	No	1	3	One
53	49	46	0.800	<0.05	2005	5	2	5	0	m	—	No	1	3	One

m, monogamous; p, primary partner; s, secondary partner; asterisks, partnership ended through death; p\_f, total number of partners of the female; p\_m, total number of partners of the male; HR, hand-raised; ns, not significant. Empty cells indicate missing or ambiguous information.

(both, one or none of the pair partners hand-raised), and the sample year were entered into the model as fixed terms.

We present Wald statistics for REML because the change in deviance when dropping a term from the model approximates

a  $\chi^2$ -distribution (Foerster and Kempenaers 2005; Galwey 2006). We sequentially deleted fixed terms in order of decreasing significance. As error estimates for single terms are influenced by the other terms present in the model, the removal of

a term usually changes the error estimates of the remaining terms. Therefore, the least significant term was determined after each step (i.e., removal of a term, according to standard stepwise model reduction procedures). In this manner, deletion of fixed terms was continued until only terms with a  $P$  value below 0.1 remained in what was considered the final model. However, only terms with  $P < 0.05$  were considered as having a significant influence on the response variable. Excluded terms were reentered one by one into the final model.  $P$  values of reentered terms remained above 0.1 after reentry, which confirmed that these terms did not explain a significant part of the variation (Galwey 2006; Poesel et al. 2006).

## RESULTS

The degree of TC ranged from  $-1$  to  $1$  (mean  $\pm$  SD =  $0.494 \pm 0.318$ ). TC was significantly lower in partners that faced a social challenge, that is, continuous competition over a pair partner or nest site from a rival male or a competing pair (Figure 1, Table 2). This was also obvious in the 3 dyads sampled in a year without social challenge, as well as in a year with challenge (dyads 25, 30, and 34, Table 1). In contrast, the type of pair-bond (monogamous pair, primary or secondary partners in a trio) had no significant influence on TC (Table 2).

Pairs that split up in the year after data collection had lower TC values than those whose pair-bond lasted, but this difference was not significant (Table 2). At a longer time scale, TC decreased slightly with increasing pair-bond duration (Table 2) but increased with female age: Older females showed a higher degree of hormonal synchrony with their partners than younger ones (Table 2, Figure 2). In contrast, male age as well as the age difference between pair partners had no significant influence on TC (Table 2).

Finally, TC was not influenced by the raising history of the pair partners and neither the number of previous partners of the female nor the male had a significant influence on TC with the current partner (Table 2).

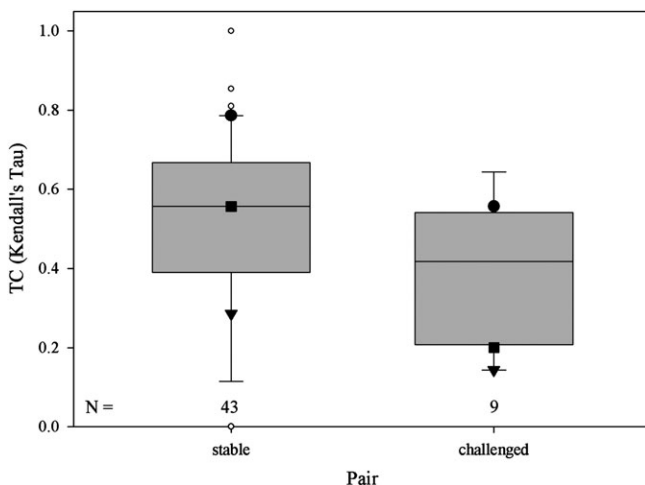
## DISCUSSION

Testosterone compatibility between pair partners was suggested as a physiological correlate of pair-bond quality in grey-

lag geese (Hirschenhauser et al. 1999). The current study shows that TC varies with certain life-history traits and that it may be particularly vulnerable to social instability. This suggests that TC is not a stable, pair-specific trait, but rather the reflection of a pair's status quo. As TC is a predictor of several fitness components (Hirschenhauser et al. 1999), this may also be indicative of variation in pair-specific reproductive success relative to the social environment.

In our study, low degrees of TC corresponded with the occurrence of active challenges, that is, with intense agonistic and mate guarding behavior that continued for weeks or even months, suggesting that social challenges may not only alter individual behavior and physiology (e.g., Mendoza and Mason 1986; Wingfield et al. 1990; Hirschenhauser and Oliveira 2006) but may indeed disrupt (hormonal) fine-tuning between pair partners. Behavioral synchrony and compatibility between partners, in turn, have been shown to influence reproductive success (Marzluff and Balda 1988a, 1988b; Barlow 1992; Choudhury et al. 1996; Spoon et al. 2006); hence, social challenges may affect reproductive success of pair partners by reducing their behavioral or physiological coordination. In contrast, the mere presence or absence of a third party in the social bond did not relate to the degree of TC as trio partners did not show different synchrony than socially monogamous partners. A permanently attached third party is a likely competitor over paternity or parental effort, but a larger social unit may also provide certain benefits, such as increased social support and better access to resources (Weiß and Kotschal 2004; Scheiber, Weiß, et al. 2005). Thus, in contrast to continuous active challenge, the attachment of a potential competitor may have no negative impact on reproductive success, which may provide an explanation for the existence and persistence of trios in the monogamous greylag geese.

Compatibility of pair partners may not only influence reproductive success but also the likelihood of remating or divorce (Spoon et al. 2007), which may again have negative effects on reproductive success (Black et al. 1996; Catry et al. 1997; Heg et al. 2003). Adélie penguins (*Pygoscelis adeliae*), for instance, were more likely to remate with the same partner in the following breeding season, if their incubation routines were well coordinated (Davis 1988). In barnacle geese, probability of



**Figure 1**

TC (Kendall's  $\tau$ ) of socially stable and instable greylag pairs. Boxplots show median and first and third quartiles, whiskers indicate 10th and 90th percentile. Dyads 25 ( $\blacktriangledown$ ), 30 ( $\blacksquare$ ) and 34 ( $\bullet$ ) were measured both in a year with stable pair-bond and challenged pair-bond.

**Table 2**

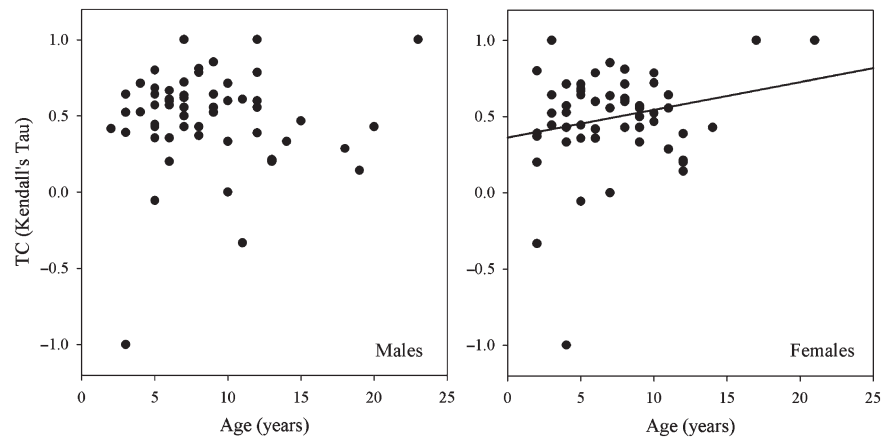
Statistical results of the GLMM with TC as the response variable

Fixed term	Full model			Final model		
	Wald statistic	n.d.f.	$P$	Wald statistic	n.d.f.	$P$
Age female	3.28	1	0.082	<b>5.71</b>	<b>1</b>	<b>0.021</b>
Age male	1.38	1	0.250	<i>0.04</i>	2	<i>0.849</i>
Age difference	0.03	1	0.856	<i>1.63</i>	2	<i>0.210</i>
Pair challenged	2.34	1	0.241	<b>17.08</b>	<b>1</b>	<b>0.004</b>
Pair-bond holds	4.05	1	0.090	<i>1.17</i>	2	<i>0.319</i>
Pair-bond duration	8.07	1	0.008	<b>12.28</b>	<b>1</b>	<b>0.004</b>
Type of pair-bond	2.82	2	0.539	<i>0.69</i>	2	<i>0.728</i>
Number of partners female	1.82	1	0.189	<i>2.70</i>	2	<i>0.109</i>
Number of partners male	1.87	1	0.183	<i>0.45</i>	2	<i>0.508</i>
Raising history	1.33	2	0.522	<i>2.54</i>	2	<i>0.316</i>
Sampleyear	1.37	2	0.579	<i>0.38</i>	2	<i>0.837</i>

n.d.f., degrees of freedom.

For the full model, results of all tested fixed terms are given. For the final model, results of terms that remained in the final model are given in bold and results of excluded terms when individually reentered into the final model are given in italics.





**Figure 2**  
TC (Kendall's  $\tau$ ) and individual age for males (left) and females (right).

divorce decreased with increasing pair-bond duration (Black et al. 1996) and also in our study, half of the divorces occurred within the first year of a pair-bond, even if pairs had not experienced a breeding season together and no challenge had occurred (see Table 1). Such short pair-bonds may represent some sort of trial liaisons (Black et al. 2007), which are ended if partners do not seem to be compatible, whereas bonds maintained beyond a trial stage may be less prone to be broken voluntarily. This may explain why we did not find a general trend that hormonally mismatched pairs were more likely to divorce and also why less well-matched pairs indeed may stay together for years despite their low reproductive success (Hirschenhauser et al. 1999). Possible reasons for this include partners failing to detect their incompatibility, a lack of more suitable alternatives or social constraints on mate preference and choice (see Gowaty 2008).

The majority of studies addressing pair quality or reproductive success in birds with respect to individual or pair-specific life history found reproductive success to increase with pair-bond duration (Fowler 1995; Black et al. 1996; van de Pol et al. 2006), even though this was not always the case (Naves et al. 2007). In the present study, TC as an indicator of pair quality did not increase with pair-bond duration; rather, it slightly decreased over time. These results may be the effect of TC actually decreasing within a pair, or of life-history differences between the observed pairs. For instance, Black (2001) described that barnacle geese producing the most offspring did so early in life, whereas those that postponed reproduction lived longer. This suggests that pairs that coordinate and fine-tune their behaviors may successfully reproduce but at the expense of a long life. Hence, the negative relationship we observed between TC and pair-bond duration could result from shorter life-spans of well-coordinated, successful pairs in comparison to unsuccessful pairs. On the other hand, lower TC in challenged pairs likely did not result from pair-specific differences in quality/success but from within-pair changes because TC decreased with social instability in those pairs that were sampled during both, stable and instable years.

In contrast to the negative relationship between TC and pair-bond duration, TC increased with female age and did not show a significant relationship with male age. Age-specific increases and decreases in reproductive success of birds have been attributed to a variety of factors relating to improvement of competence, progressive appearance or disappearance of phenotypes, and optimization of access to resources and reproductive effort (see Forslund and Pärt 1995; Pärt 2001; Reid et al. 2003; Low et al. 2007). Our data indicate that also compatibility among partners may be age-related and may represent one of the mechanisms leading to variation in reproductive success. In our study, age-related differences in partner com-

patibility were only apparent in female geese, suggesting a certain influence of breeding on the observed changes in TC. For instance, females may develop breeding routines as they grow older, which may facilitate adjustment by the male. Alternatively, females may become more attractive to males as their experience grows, which in turn may promote physiological and behavioral responsiveness by their partners.

Hirschenhauser et al. (1999) argued that synchrony between pair partners is likely achieved by the male adjusting to the energetically more constrained female. However, the majority of trios in geese consist of 2 females and a male (Black et al. 1996; Weiß et al. 2008), who cannot adjust to 2 females simultaneously. Therefore, we expected primary partners of a trio to be better matched in testosterone than secondary partners, but our assumption was not confirmed. Alternatively, primary as well as secondary partners may initially match or also females may adjust to their partners to some extent. The latter is supported by a recent study in domestic geese (*A. domesticus*), which provides evidence for female androgen responsiveness to preferred partners (Hirschenhauser et al. 2009).

Finally, the number of previous partners had no influence on TC with the current partner. Similarly, life-time reproductive success in barnacle geese was not affected by the number of partners (Black 2001). Thus, experience with different partners neither improved the ability of fine-tuning to one's mate nor did individuals who changed mate more frequently appear to show lower responsivity or be more difficult to adjust to.

In line with previous work on TC in geese, in this study, we showed that greylag goose pairs did not fine-tune and improve their hormonal compatibility over the years, suggesting that partners that do not match from early on likely never will. However, TC does not have to be a lasting, stable trait, as the coordination and compatibility of well-matched pairs may be substantially reduced by social instability, which may have long-term, deleterious effects on reproduction.

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