Female androgen patterns and within-pair testosterone compatibility in domestic geese (*Anser domesticus*)

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ABSTRACT

For successfully raising offspring, long-term monogamous pair partners need to be behaviorally and hormonally coordinated. In the monogamous, biparental greylag geese (*Anser anser*) a dyadic pairbond-specific measure, 'within-pair testosterone compatibility' (TC) indicated how closely synchronized are seasonal androgen levels, which co-varied with reproductive output. Males, in particular, were assumed to respond to their females' hormonal and fecundity phases. We now present experiments with biparental domestic geese (*Anser domesticus*) kept as pairs to ask whether TC occurs also in these generally polygynous animals. We further ask how different conditions of mate choice affect TC and whether established TC is maintained during a polygynous flock situation. We measured androgen metabolites (AM) non-invasively from individual droppings. In females, AM was related with gonadal activity as it increased after GnRH but not ACTH challenge. Females with preferred partners had higher maximum AM during egg laying and higher rates of initiating incubation than randomly paired females. Domestic ganders had seasonal AM patterns typical for polygynous males. Within-pair TC ranged from almost perfectly positive to non-correlated in domestic geese but mate choice did not explain TC variation. TC of previous pairs was generally reduced in the flock situation, probably confounded by factors of the social environment, i.e. mating opportunity and availability of multiple partners. On top of the underlying reproductive physiology our results suggest two episodic components of TC: a female androgen responsiveness to the preferred partner at least during egg formation, and the male's facultative potential to respond to her readiness to breed.

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1. Introduction

Long-term monogamy is generally characterized by spatial proximity and exclusive social relationships between pair partners. Pair partners are mutually dependent with regards to resource procurement and reproductive output (Wickler and Seibt, 1983; Lamprecht and Rebhan, 1997). Thus, the initial mate choice and pair formation, as well as the maintenance of the pairbond are critical for lifetime reproductive success, especially as pair dissolution may have negative fitness consequences (Angelier et al., 2007; Black et al., 1996).

The major function of monogamous pair bonding is biparental care, which probably necessitates at least some behavioral (Lamprecht and Rebhan, 1997; Spoon et al., 2004) and physiological coordination and synchronization between pair partners

(Hirschenhauser et al., 1999a; Weiß et al., in press). Particularly in long-lived species, pairs seem to improve their coordination over time, for example, with respect to incubation routines (Davis, 1988; Cézilly et al., 2000). However, pair formation and long-term pair bonds are not restricted to monogamy but may also occur in polygynous systems with biparental care. In greylag geese as well as domestic geese (*Anser anser*; *A. domesticus*) a male may be associated with one primary and one or more secondary female partners, which are not recruited by the male but attach on their own initiative (Lamprecht and Buhrow, 1987; Weiß et al., 2008a). We defined the mating system of wild geese as monogamous, both socially and sexually. Social monogamy is appropriate as rates of extra-pair fertilizations are typically <5% in wild geese (Larsson et al., 1995; Dunn et al., 1999) and in the studied flock of Greylag geese mate fidelity based on microsatellite analyses was particularly high (Weiß et al., 2008b; Weiß and Hirschenhauser, unpublished data). On the other hand, domestic ganders were frequently associated with a group of females and vigorously defended all of these females, their preferred nest sites and offspring against competitors or predators. Therefore, on a continuum scale

of more or less flexible mating tactics, we would set domestic geese at the polygamous end of the scale, while the greylag geese are clearly clustered towards the monogamous side.

Reproducing with non-preferred partners may be costly to the breeder with regard to offspring number and quality (Gowaty, 1996; Bluhm and Gowaty, 2004). Both, mate choice and partner compatibility may affect the probability of pair separation and thus, the common success of a pair. Correlates of pair bond quality have been suggested based on tests for individual divorce tendency (Lamprecht and Rebhan, 1997; Cézilly et al., 2000) or for glucocorticoid responses to mate separation (Mendoza and Mason, 1986; Remage-Healey et al., 2003). In cichlid fish (Cichlasoma citrinellus) partner compatibility was predicted by complementary individual fighting potential, as well as similar size and color of partners (Barlow, 1992). Assortative mating according to age and size scaled positively with pairbond duration and lifetime reproductive success in barnacle geese (Branta leucopsis; Choudhury et al., 1992, 1996) and in dark-eyed juncos (Junco hyemalis carolinensis; Reed et al., 2006). Recently, the effects of behavioral synchrony and responsiveness to the partner on reproductive success were shown in juncos (Clotfelter et al., 2007), cockatiels (Nymphicus hollandicus; Spoon et al., 2006) and in greylag geese (Nedelcu, Weiß, Scheiber, Wascher, Chiu-Werner, Kotrschal, unpublished). The mammalian literature provides further examples from a wide array of species (Carter et al., 1995; Barth et al., 1997; von Holst, 1998; Young et al., 1998) including humans (Persky et al., 1978; Storey et al., 2000; Hirschenhauser et al., 2002). Thus, these principles obviously are not limited to particular vertebrate taxa, indicating their systemic nature. Theoretically, a simple ability to observe and react to a change in the partner's behavior is sufficient for synchronization (Rands et al., 2003) but in fact, the social bond as well as physiological arousal may add a motivational component to the phenomenon (Blascovich et al., 1999).

Throughout the vertebrates, male testosterone (T) responds to and regulates courtship, sexual and agonistic interactions between conspecifics (Hirschenhauser and Oliveira, 2006). Domesticated animals typically show more courtship and sexual behavior and more activity of the pituitary–gonadal axis than their wild ancestors (Haase and Donham, 1980). In general, prolonged high T is incompatible with paternal behavior and can have adverse effects on survival (Dufty, 1989; Wingfield et al., 2001). Bird studies, in particular, indicate that social interactions and behavior act as short-term modulators of male T and thus, individual T patterns may be viewed as a function of intrinsic motivational and extrinsic social factors. In temperate-zone birds, the duration of mating periods with seasonally maximum T is typically longer in males from polygynous, non-paternal species than in males from monogamous species with biparental care ('challenge hypothesis'; Wingfield et al., 1990). Here we argue that the interaction between mating and breeding with T may be explained insufficiently, if the focus is only on one member of the pair, i.e. the male. Especially mating behavior and biparental care clearly involve the interaction between pair partners, as well as between the pair and its social environment. If the degree of behavioral responsiveness to the partner is part of the pairbond quality, some hormonal fine-tuning between pair partners at least in the functionally crucial sex steroids (Carter et al., 1995; Storey et al., 2000; Hirschenhauser et al., 2002) may be expected.

Seasonal androgen profiles of female birds generally resemble those of males. Seasonal maxima of female androgens are associated with egg production and fecundity, and are highest in socially monogamous species (Ketterson et al., 2005). Our study is based on measures of excreted androgen metabolites from individual fecal droppings of male and female geese. We have shown previously that measuring androgen metabolites (AM) from droppings of male domestic geese resulted in meaningful androgen

patterns in response to gonadotropin-releasing hormone (GnRH) during spring, summer and fall (Hirschenhauser et al., 2000). In females, so far, we had assumed the validity of AM from the seasonal patterns of AM in greylag goose droppings, which were well compatible with the annual patterns of circulating testosterone based on plasma samples in barheaded geese (A. indicus; Dittami, 1981; Hirschenhauser et al., 1999b). However, the 17-oxo-group-specific antibody used for androgen determination from goose droppings does not discriminate between androgens of different origin, gonads or adrenals (Möhle et al., 2002), which could be relevant particularly in females (Longcope, 1986; Goymann, 2005). For example, preovulatory chicken follicles produce androgens such as androstenedione and dehydroepiandrosterone (DHEA) within the ovaries (Velasquez et al., 1996). The adrenal glands and/or gonads may secrete DHEA in male songbirds (Soma et al., 2000). In domestic geese the seasonal timing of peak DHEA levels coincided with reproductive phases in both sexes (Xuan et al., 2005) but no specific test of its origin has been published so far. The first goal of this study was to experimentally test for the origin of the androgen metabolites measured in the droppings from female geese. In contrast to testosterone in males, the major androgen circulating in the blood of female gulls was androstenedione (Groothuis and Schwabl, 2002) and hence, although we cannot exclude species-dependent differences the androgens circulating in the blood (as precursors of excreted metabolites) potentially differ between males and females. Thus, presumably, the androgen metabolites we measure in the droppings of females reflect androstenedione levels. However, for simplicity we will term both, male and female measures as 'androgen metabolites'.

The second goal of this study was to experimentally test a dyadic and pairbond-specific measure in domestic geese, the 'within-pair testosterone compatibility' (TC) based on the co-variation of the seasonal androgen patterns of both, the male and the female of a pair. In greylag geese, pairs with a higher degree of TC produce larger clutches, heavier eggs and have higher lifetime reproductive output than less T-synchronized pairs (Hirschenhauser et al., 1999a). Thus, TC seems to be a physiological correlate, if not a causal agent, of pair bond quality both in the year sampled and over longer periods of time. Recent TC analyses have replicated and expanded our previous results in greylag geese (Weiß et al., in press). The mechanisms underlying TC, however, remained unresolved so far. We performed a series of experiments with domestic geese to test the robustness of TC to limited versus unlimited mating opportunities and social interactions.

Specifically, our experiments with domestic geese during two complete breeding seasons focused on three questions: (i) whether TC could be detected among males and females from a polygynous and domesticated species kept in pairs. If TC is a consequence of biparental care, we expect to find high degrees of TC in domestic goose pairs, i.e. if they have only one partner. (ii) Whether TC is based on an initial choice process; if TC is based on mate choice we predicted to find more pairs with higher degrees of TC in pairs with preferred partners than in randomly assigned pairs. (iii) Whether previously established hormonal partner compatibilities are maintained in a polygynous group situation; in other words, whether and to what degree TC is robust to disturbances by the social environment.

2. Methods

2.1. Animals and data collection

In spring 2004 (group A) and spring 2005 (group B) one-day-old A. domesticus Danish white goslings were purchased from a com-

mercial breeder and raised as a group in an outdoor pen until their first winter. In both groups, pairs were formed before their first mating season, with partners randomly assigned in group A and with self-chosen partners in group B (see below). The pairs were separated from other pairs by wire-mesh fences to prevent physical access to adjacent individuals, but visual and acoustical contact remained. This made available compartments of approximately 40 m^2 per pair. At all times the geese had *ad libitum* access to standard pellet food and had access to ponds for drinking and bathing. Throughout the entire sampling period each female was offered a $100 \times 100 \times 100$ cm wooden breeding shelter for egg laying and incubation. From February on we checked the nests daily and recorded individual laying performance. Domestic geese produce large quantities of eggs (Table 3) over elongated laying periods when compared with non-domesticated geese, but females do not necessarily initiate incubation. In addition, prolonged exposure of eggs to suboptimal conditions including warm temperatures and dirt, may reduce hatchability (Ozbey and Esen, 2007). Therefore, to facilitate breeding attempts, we manipulated the clutches to keep the number of eggs per clutch functional in terms of time since deposition, to avoid rolling out of nest, and to enable constant thermoregulation. We kept the clutch size constant at four eggs by removing the 'oldest' egg as soon as the female had laid a new egg. Nests were checked daily, eggs were weighed to the nearest of 0.5 g using a UWE Handi-Weigh spring balance, and marked to track the laying sequence and time since deposition. From these records we calculated egg productivity (number of eggs laid per female) and laying activity throughout the individual laying period (mean number of eggs per day).

Group A was sampled in 2005 in the 'random partner situation'. One female was predated by a red fox (*Vulpes vulpes*) in April, thus, complete seasonal hormone profiles were available from only nine 'random partner' pairs. The widowed male was left in its original compartment until the end of the sampling period. In December 2005 the individuals of group A were moved to a larger outdoor pen (400 m^2) and were kept as one large flock ('flock situation'). Two males died within the first two weeks in the flock for unknown reasons. Thus, throughout the breeding season 2006 we collected weekly fecal samples from nine females and eight males in the 'flock situation'. Egg data are missing from the flock situation, as most breeding shelters were frequently used for laying by multiple females and thus, egg measures could not be assigned to individuals.

Group B was sampled in 2006 ('preferred partner situation'). Preferred partners were determined by continuously monitoring the target individual(-s) of triumph ceremonies within the group during their first fall. The triumph ceremony is a pairbond-related display: after an attack the male vocalizes loudly and returns to its female partner. Just before reaching the female the gander starts a cackling sound accompanied by 'greeting' movements with its neck. In response the female usually joins the male's cackling (Fischer, 1965; Lorenz, 1966). Triumph ceremonies were monitored for ten subsequent days in October 2005, repeated once in November and then for three subsequent days in December 2005. From each scan sample period we determined the top three preferred males for each female by relating the individual counts per male to the total number of triumph events observed for each female (28.8 ± 3.2, 22.7 ± 3.7 and 42.4 ± 2.7, average total numbers of triumph ceremonies observed per female during October, November and December, respectively). Only males top ranking three times with the same female were considered as preferred partners. Following this rule we recruited six pairs for the 'preferred partner group B', which were then kept in the pair-wise outdoor pens until the end of the data collection in July 2006.

2.2. Androgen metabolites from goose droppings

The geese were habituated to the presence of observers, which allowed us to be present within a distance of approximately 5 m and to collect individual droppings directly after defecation. Throughout a breeding cycle, that was from the 'courtship' phase in January to the summer photo-refractory, post-nuptial molt phase in July (Table 1), we collected droppings from all individuals every second week and kept it frozen at $-20\ ^\circ$C within two hours after collection (Hirschenhauser et al., 2005). To standardize daytime, droppings were always taken in the mornings between 9:00 and 11:00 a.m. We aimed at collecting three droppings from three different days per individual per week to cover within-individual variation (Scheiber et al., 2005). Sample sizes vary (Table 1) as we did not always succeed in collecting sufficient samples within the preset time window from all individuals, which was particularly difficult during incubation when collection was limited to breeding pauses and both, geese and ganders were usually more sensitive to the presence of an observing person.

Immunoreactive androgen metabolites (AM) were assayed from 0.5 g dropping extracted in 5 ml 60% methanol using an enzyme immunoassay (EIA; Möstl et al., 2005) designed and optimized at the Institute for Biochemistry, Veterinary University of Vienna. This assay is based on a group-specific antibody against 17-oxo-androgens immunized in rabbits, which does not require enzymatic deconjugation during extraction (Hirschenhauser et al., 2000). Previous studies have shown that the EIA measuring 17-oxo-androgen metabolites resulted in meaningful patterns of natural seasonal variation in both sexes, as well as increased excretion patterns of male geese in response to GnRH, after injection of ^{14}C-labeled steroid, and due to social challenges (Hirschenhauser et al.,

Table 1
Overview of all seasonal phases and sample sizes in the three test situations.

Seasonal phase number	Month	Reproductive event	N individuals (f/m) per seasonal phase		
			Group A (random partners)	Group B (preferred partners)	Group A (flock situation)
1	Jan	Courtship	10/10	6/6	9/9
2	Feb	Mating	10/10	6/6	9/8
3	Mar/Apr	First egg and the two weeks thereafter	10/10	6/6	9/7
4		2–4 weeks after first egg	10/10	6/6	9/7
5		4–6 weeks after first egg	10/10	6/6	9/7
6	Apr/May	Incubation I, first two weeks of incubation	3/4	6/6	8/7
7		Incubation II, last two weeks of incubation	4/5	5/5	4/2
8	May	Hatching, first two weeks after the female had left the nest	1/1	4/2	3/5
9	June	Molt	7/8	3/4	8/7
10	June/July	Peak of post-nuptial molt	8/10	4/5	8/7

1999a,b; Hirschenhauser et al., 2000; Kotrschal et al., 2000). A total of 2278 fecal samples were analyzed for AM. The inter-assay variation was 11.5% (based on 61 microtiter plates), mean intra-assay coefficient of variation was 16.8%.

2.3. Androgen metabolites in female geese

To investigate the origin, gonads or adrenals, of excreted AM in the droppings of female geese we compared the effects of gonadotropin-releasing hormone (GnRH) and adrenocorticotropic hormone (ACTH) treatments on AM. We injected seven female geese with 4 µg GnRH (Receptal, Hoechst-Roussel Vet. Wiesbaden; Hargitai et al., 1993; Hirschenhauser et al., 2000) per kg body mass into the pectoral muscle (November 2004 between 10:05 and 10:45 a.m.). After that, all droppings were collected for the subsequent 6 h (13.7 ± 0.7 droppings per female). In addition to individual pre-experimental baseline samples, the same seven females received two control treatments: one control was a treatment with 0.25 ml saline Ringer solution; the other treatment was with 0.25 mg ACTH (Synacthen, Ciba-Geigy, Basel) per goose to control whether the AM excreted in droppings from females were related with activity of the hypothalamo–pituitary–adrenal axis (BMBWK 66.006/0014). The dose of ACTH was effectively increasing glucocorticoid metabolites in droppings of domestic ganders within 2–4 h (Kotrschal et al., 2000; Möstl et al., 2005). Both control treatments were followed by the same sampling routine as after the GnRH treatment (12.0 ± 1.6 and 16.4 ± 1.0 droppings per female, Ringer and ACTH, respectively). Treatment with saline solution took place one day before the GnRH experiment, the ACTH treatment was done two days after the GnRH.

2.4. Data processing

We compared mean AM levels in droppings from all females before and after GnRH injection with control treatments. Because GnRH is expected to elicit short and pulsatile secretions of luteinizing hormone in the pituitary and steroids in the gonads (Negro-Vilar et al., 1986), the effect on excreted levels of AM may be averaged by calculating means. Consequently, it is useful to also depict the peak levels of excreted AM (Hirschenhauser et al., 2000, 2008). Based on gut passage time we know that steroid levels obtained from goose feces reflect cumulative secretion over the 2 h preceding defecation (Mattocks, 1971; Hirschenhauser et al., 2005). Therefore, we calculated 'baseline AM levels' from all droppings

within 0 and 2 h from treatment and compared those with mean and peak 'response AM levels' between 2 and 6 h from treatment with either GnRH, ACTH or Ringer solution (control). Data met normal distribution assumptions after logarithmic transformation (Kolmogorov–Smirnov test, mean AM responses: $Z = 0.55$; $N = 35$; $P = 0.93$; peak AM responses: $Z = 0.91$; $N = 35$; $P = 0.37$). We used two-way repeated measures ANOVA with post hoc Holm–Sidak adjustments for multiple pair-wise comparisons.

For the seasonal AM patterns the sampling period was divided into 10 seasonal phases between the early courtship phase in January and late molt in July (Table 1). In each sampling year individual data were standardized according to the individual timing of reproductive events, such as laying of the first egg, start of incubation, hatching of young, and peak post-nuptial molt (Kotrschal et al., 1998; Hirschenhauser et al., 1999b). Median hormone values per individual per phase were calculated. Seasonal patterns of AM and M/F ratios (male partner's AM per phase divided by female partner's AM in the same phase) did not differ from normal distribution ($N = 10$ phases; random partner: $Z = 0.60$; $P = 0.86$; preferred partner: $Z = 0.97$; $P = 0.30$; flock situation: $Z = 0.54$; $P = 0.93$).

The degree of within-pair testosterone compatibility (TC) was calculated using Kendall's Tau correlation coefficients as in Hirschenhauser et al. (1999a). Kendall's Tau computes the excess of concordant (n_c) over discordant (n_d) pairs $[(n_c - n_d)/\frac{1}{2}n(n - 1)]$ and was preferred because it is suitable for the relatively small number of phases and is robust to extreme values (such as seasonal peaks) as it uses ranks of the data (Conover, 1980). Pairs with a significant Kendall's Tau correlation coefficient were termed 'TC-matched pairs'.

Data on within-pair TC did not satisfy the assumptions of normal distribution ($Z = 0.18$; $N = 23$; $P = 0.050$). Thus, TC patterns are analyzed using non-parametric Mann–Whitney U-tests for independent pairs (group A versus B: random versus preferred partner pairs) and Wilcoxon signed rank tests for dependent data (group A during two years: random partner pairs versus flock situation). Statistical analyses were conducted using the statistical packages SPSS for Windows 15.0.1 and SigmaStat 3.5.

3. Results

3.1. Androgen metabolites in female geese

In female geese the mean AM response levels 2–6 h after treatment with GnRH were higher than baseline AM levels, but AM lev-

Table 2
Results of two-way repeated measures ANOVA to show the effects of treatments with either GnRH, saline Ringer solution or ACTH on mean and peak levels of excreted androgen metabolites (AM) in the droppings of female geese ($N = 7$; see also Fig. 1).

	Mean AM response to GnRH	Peak AM responses
Repeated factor (within-subjects effect)	Daytime/baseline vs. response level	
	$F(1, 6) = 4.2$	$F(1, 6) = 9.3$
	$P = 0.087$	$P = 0.023$
Independent factor (between-subjects effect)	Treatment GnRH, Ringer or ACTH	
	$F(2, 6) = 0.3$	$F(2,6) = 0.8$
	$P = 0.734$	$P = 0.471$
Interaction of the two factors	$F(2, 6) = 7.2$	$F(2, 6) = 10.7$
	$P = 0.009$	$P = 0.002$
Pairwise comparisons (Holm-Sidak)	Response to control treatment	
	$t(7) = 1.1$	$t(7) = 2.02$
	$P = 0.276$	$P = 0.064$
	Response to GnRH treatment	
	$t(7) = 3.9$	$t(7) = 5.03$
	$P = 0.001$	$P < 0.0001$
	Response to ACTH treatment	
	$t(7) = 1.1$	$t(7) = 0.1$
	$P = 0.287$	$P = 0.948$

Significant effects ($P < 0.05$) are depicted in bold.

els were not changed after ACTH or saline control treatment (Table 2). Yet, based on individual means only the interaction between effects of daytime and treatments was significant, but neither the effect of daytime nor treatments alone (Table 2). In contrast, the effect of GnRH treatment was clearly reflected by using individual peak AM levels during the 2–6 h after treatment: peak AM responses after GnRH treatment were significantly higher than baseline AM levels, as well as compared with peak AM levels after saline control and ACTH treatment (Fig. 1 and Table 2).

3.2. Seasonal AM patterns

In general, the seasonal AM patterns of male and female domestic geese were similar to those known from the monogamous *A. anser*, with peak AM levels around laying of the first egg and decreased AM during the ongoing laying and incubation phases (Hirschenhauser et al., 1999a,b). Towards the end of the laying phase AM levels were low in both sexes and in either test situation, i.e. when kept as pairs or as one large group (Fig. 2).

In males, the range between seasonal AM maxima and minima was similar between test groups. However, in female geese seasonal AM patterns co-varied with being with a preferred partner or not. Particularly in the early laying phase, females paired with a randomly assigned male (group A, 'random partner situation) had lower seasonal AM peaks than when kept in a polygynous group (group A, 'flock situation') or when females were with a preferred partner (group B; Fig. 2). Also, males from 'random pairs' of group A had on average 3-fold higher peak AM than their female partners, while male and female AM peaks were almost overlapping in 'preferred partner pairs' of group B (M/F ratio 0.9, group B) and intermediate (1.6) in the 'flock situation' of group A. Throughout all seasonal phases, AM differences between the male and female pair partner were greater among randomly assigned pairs than among preferred partners (oneway ANOVA, group A (random) versus B (preferred): $F = 9.88$; df = 1;18; $P = 0.006$), or between pairs of group A when kept as 'random partners' or as a 'flock' (paired t-test, group A random versus flock: $t = 3.62$; df = 9; $P = 0.006$).

3.3. Within-pair testosterone compatibility in domestic geese

We observed variable degrees of TC in domestic goose pairs, from non-correlated to high degree of TC (Table 3). However, TC may have been random as it did not vary significantly with the test conditions. The degree of TC did not differ between goose pairs
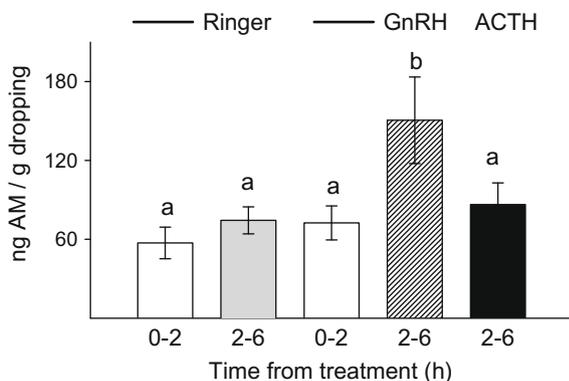

Fig. 1. Excreted androgen metabolites (AM) in droppings of female domestic geese (mean ± SE; $N = 7$). Bars show baseline (0–2 h) and peak levels of AM after treatment (2–6 h) with saline Ringer solution (gray bars), baseline (open bar) and response AM levels after treatment with GnRH (hatched bar), or after ACTH (filled bar). Different letters indicate significant differences between treatments.
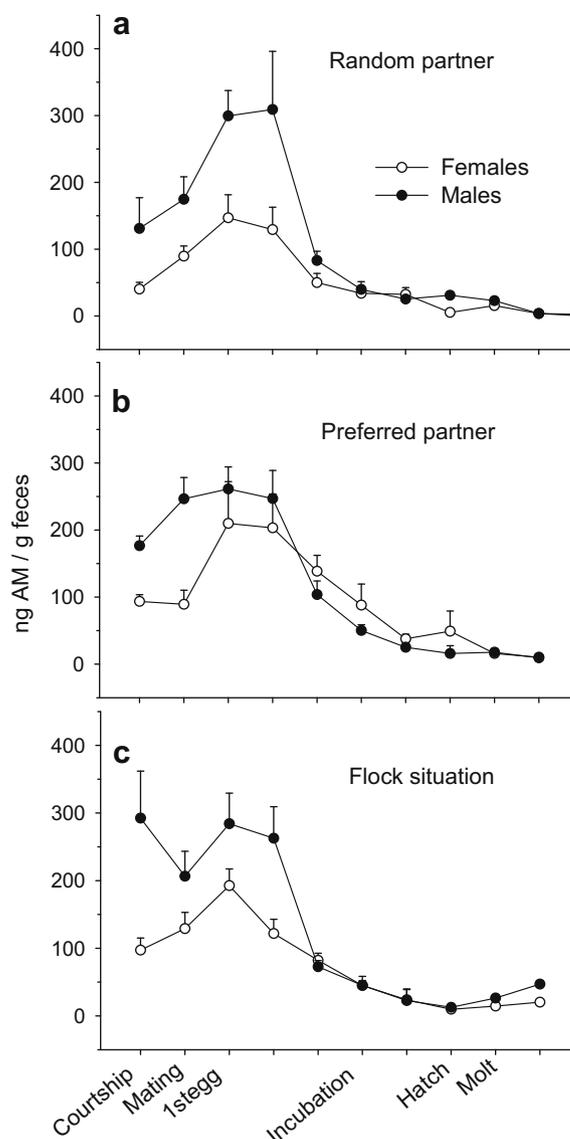

Fig. 2. Seasonal patterns of AM in male (filled dots) and female (open dots) domestic geese during the different test situations: (a) 'random partner pairs' (group A); (b) 'preferred partner pairs' (group B); (c) group A (the previous random partner pairs) when kept in the flock situation. Plotted are means ± SE per phase.

with a random or a preferred partner (Mann–Whitney U-test: $Z < 0.01$; $W = 51.0$; $N = 6/10$; $P = 1.0$; Table 3). Thus, mate choice did not explain variation of TC in domestic geese. Also, when the random partner pairs were kept as a flock in the second year, the median degree of TC did not change significantly (Table 3; Wilcoxon matched pairs, group A random versus flock: $Z = -1.18$; $N = 7$; $P = 0.237$) although the proportion of TC-matched pairs was to some extent reduced (example in Figs. 3 and 4). Notably, despite the smaller sample size, in the 'preferred partner' group variability of TC was higher than in the random pairs (group B and A: 42.5% and 24.4%) as both the minimum and maximum TC coefficient of the entire sample occurred in the preferred partner group (Kendall's Tau = 0.2 and 0.9, respectively; Table 3).

3.4. Within-pair TC and reproductive output

Dates of laying the first egg ranged over three weeks in group A when kept as randomly assigned pairs and over two weeks when kept as preferred partners (group B). Individual females produced

Table 3
List of results for each pair's TC, reproductive output and performance.

Pair No.	TC	Kendall's τ N phases	P	Egg productivity (eggs per female)	Laying activity (eggs per day)	Egg weight (mean ± SE)	Incubated Y[a]/N
Random partners (group A 2005)							
1	0.7	9	0.007	13	0.4	189.1 ± 6.8	Y
2	0.7	6	0.039	49	0.5	158.6 ± 1.3	N
3	0.8	7	0.011	32	0.5	142.8 ± 1.3	N
4	0.5	9	0.061	21	0.5	149.5 ± 3.5	Y
5	0.7	7	0.024	46	0.4	147.3 ± 1.5	N
6	0.6	9	0.022	18	0.5	128.5 ± 5.9	Y
7	0.8	5	0.050	54	0.5	154.1 ± 5.4	N
8	0.4	7	0.176	35	0.6	154.2 ± 4.1	N*
9	0.3	9	0.211	21	0.5	135.7 ± 2.8	Y*
10	0.6	7	0.051	33	0.4	161.2 ± 1.4	N
Median	0.7		60%	33	0.5	151.8	40%
Preferred partners (group B 2006)							
11	0.3	8	0.322	39	0.5	152.5 + 0.8	Y
12	0.7	6	0.039	47	0.4	141.7 + 1.1	Y*
13	0.9	10	<0.001	27	0.5	173.3 + 5.5	Y*
14	0.8	9	0.004	32	0.4	141.9 + 1.4	Y
15	0.2	8	0.458	53	0.5	149.3 + 1.0	N
16	0.6	7	0.051	32	0.3	144.9 + 0.9	N
Median	0.7		50%	35	0.4	147.1	67%
Flock situation (group A 2006)							
1	0.6	9	0.022				Y
2	Male died						N
3	0.3	8	0.322				N
4	0.4	8	0.138				N
5	0.4	8	0.138				N
6	0.6	8	0.026				N
7	Male died						N
8	Female died						
9	0.6	8	0.026				Y
10	0.5	6	0.188				Y/N
Median	0.5		43%				25%

[a] Asterisks indicate the two pairs which hatched young in the sampling year.

between 13 and 54 eggs, over a laying period of up to 122 days. Among the 'preferred partner pairs' of group B 67% of the females initiated incubation, as compared with just 40% of the group A females with random partners. In the flock situation, only 25% of all females attempted to incubate. As expected, females, who initiated incubation, laid fewer eggs during a shorter period of time than females, that continued to lay and never initiated incubation (sum of eggs: $Z = -1.95$; $W = 49.5$; $N = 8/8$; $P = 0.05$; duration of laying period: $Z = -2.10$; $W = 48.0$; $N = 8/8$; $P = 0.038$). However, the date of first egg laid ($Z = -1.70$; $W = 52.0$; $N = 8/8$; $P = 0.105$), as well as individual laying activity (eggs per day: $Z = -0.05$; $W = 67.5$; $N = 8/8$; $P = 0.959$) were unrelated with incubation.

Females in pairs with a higher degree of TC tended to lay fewer eggs per day and at least in the random pairs (group A), ceased egg
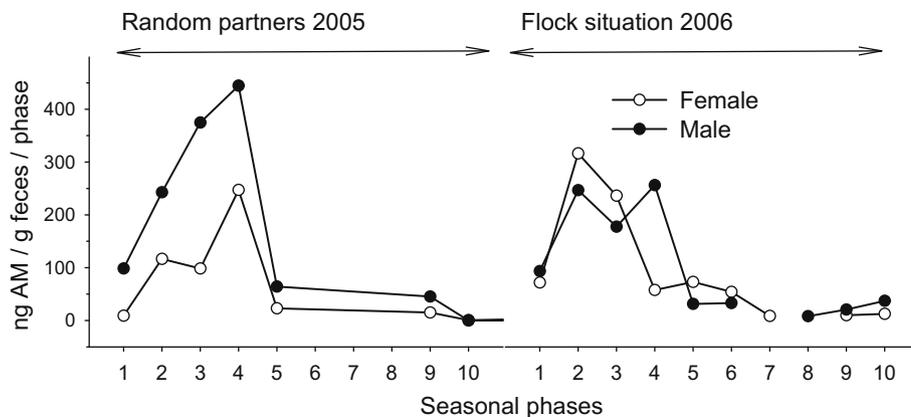

Fig. 3. Example of individual seasonal AM profiles in the female and the male partner of one pair (No. 5 in Table 3), AM profiles matched when kept as a (random partner) pair in 2005. In the following year, when kept in the flock, the pair was non-matched; the partners mingled with a second pair (No. 4 in Table 3) and mostly were seen as a four-member group. Also the TC of the second pair in this group was non-matched in the flock situation.
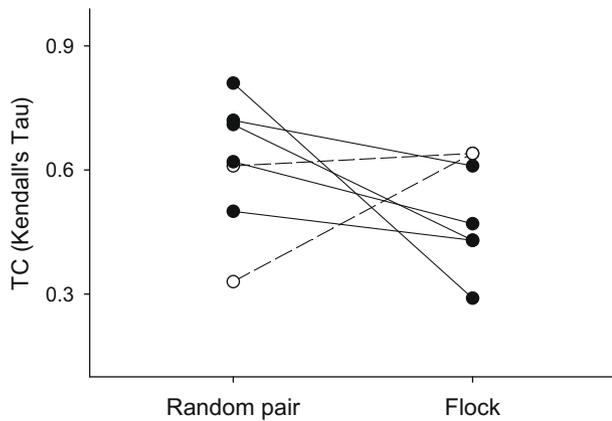
Fig. 4. Within-pair testosterone compatibility (TC) of random pairs (2005) and when kept in one flock in the following year (2006). Dependent data (from same individuals in a pair) are connected. $N = 7$ pairs; in 5 of the 7 pairs TC was reduced when kept as a flock (filled dots, full lines), one pair's TC was stable, one pair increased after reunion of the flock (open dots, dashed lines).

laying earlier in the season (date of last egg; Table 4). The duration of egg laying was not correlated with TC (Table 4) but it was also not independent from date of last egg ($r_s = 0.97$; $N = 10$; $P < 0.0001$). When we used partial correlation to control for the interfering effect of date of last egg, there was a significant relationship between TC and duration of laying ($r = -0.8$; df = 7; $P = 0.012$). Thus, females from pairs with higher TC laid eggs over a shorter period of time. Egg weight was not correlated with TC ($r_s = 0.01$; $N = 16$; $P = 0.99$) and there was no difference between the degree of TC of breeding pairs and pairs that never initiated incubation (Mann–Whitney U-test $Z = -0.89$; $W = 59.5$; $N = 8/8$; $P = 0.382$).

4. Discussion

Based on excreted androgen metabolites (AM) we tested the effects of partner preference and mating opportunity on individual and dyadic (within-pair) seasonal androgen patterns in domestic geese. Our experiments revealed (i) a mate choice effect on seasonal AM patterns of female, but not male geese; (ii) that within-pair testosterone co-variation (TC) may occur in domestic geese; (iii) that TC was not explained by partner preference and (iv) established TC was to some degree vulnerable to disturbances related with the social environment, such as mating opportunity and availability of multiple partners. Altogether, our results point at two episodic components of the TC phenomenon: during the egg formation phase, the female's androgen responsiveness to a preferred partner, and the male partner's facultative androgen responsiveness to her readiness to breed. Thus, TC as a dyadic physiological measure of partner compatibility may be viewed as marker for a mutual responsiveness between the pair partners.

4.1. Androgen metabolites in females and mate choice

In female vertebrates, androgens may be synthesized in the gonadal follicles and in the adrenals (Longcope, 1986; Velasquez

et al., 1996; Boonstra et al., 2008; Soma et al., 2000). Our GnRH and ACTH challenge experiments indicated that the AM in droppings of female geese were neither of adrenal origin nor was there much cross-reactivity with fecal glucocorticoid metabolites. Levels of excreted AM were responsive to GnRH in female geese and reached a seasonal peak during the early laying phase. Therefore, we are confident that our measures of AM from individual droppings (i.e. 17-oxo-androgen metabolites; Hirschenhauser et al., 2000) reflected gonadal activity in both, male and female geese. This confirms the reproductive context for studying the biological mechanisms underlying the within-pair testosterone compatibility (TC) phenomenon.

Although the seasonal androgen patterns of female birds usually resemble those of males, androgens seem to have different functions in the two sexes. In female birds seasonal androgen peaks are linked with egg production and fecundity (Hirschenhauser et al., 1999b; Jawor et al., 2007), yet high testosterone levels will impair female fecundity (Rutkowska et al., 2005). So far, we had assumed that the male is adapting to the female's pace of life (i.e. laying of first egg, initiation of incubation; Hirschenhauser et al., 1999a). On the other hand, the seasonal AM patterns of ganders were similar over the three test situations. Thus, our current results point at a potential androgen responsivity of females to the availability of compatible partners. Particularly during the early egg laying phase, female geese were responsive hormonally to a preferred partner. Also in other species females were shown to fine-tune their investment to male quality in specific breeding phases: for example, female canaries hearing songs with 'sexy syllables' during laying had higher androgen levels than control females hearing less complex songs (Marshall et al., 2005). However, although during the mating phase goose partners may have become more mutual, during later breeding phases presumably the male will have to respond to the female's timing of reproductive events in order to be TC-matched.

4.2. Within-pair TC and mate choice

We observed matched and unmatched pairs whether the geese were kept as pairs or as a flock. This probably reflects the flexible mating tactics along a monogamy–polygyny continuum in domestic geese. The fact that high degrees of TC actually occurred in pairs of polygynous domestic geese points at a key role for biparental care in the TC phenomenon. The duration of high androgen levels (characteristic for mating phases) and the timing of the seasonal androgen decrease (facilitating paternal care) typically vary with mating strategy (Wingfield et al., 1990) and possibly are the essential part of the dyadic TC phenomenon, as well. In the domestic goose example, the seasonal timing of reproductive and of AM peaks varied considerably among females. In pairs with preferred partners, females had higher AM during egg laying, shorter periods of egg laying and later on were seemingly more motivated to initiate incubation (Table 3). Some males seemed to be capable of responding to the female's pace of breeding, as reflected in a high score of within-pair TC. These males may have been more focused and responsive to their female partner (hormonally, as well as behaviorally) than others. Male geese seem to have individually different tendencies to either focus on one specific partner or en-

Table 4
Correlation coefficients (r_s) of TC with various egg laying variables in the three experimental groups, probabilities in parentheses, significant results in bold.

Variable	Random partner ($N = 10$)	Preferred partner ($N = 6$)	All pairs ($N = 16$)
Date of first egg	0.4 (0.243)	−0.03 (0.956)	0.1 (0.694)
Date of last egg	**0.7 (0.025)**	−0.7 (0.111)	0.15 (0.583)
Duration of egg laying	0.5 (0.133)	−0.7 (0.111)	0.1 (0.856)
Egg productivity (eggs per female)	0.4 (0.291)	−0.8 (0.066)	0.03 (0.926)
Laying activity (eggs per day)	−0.6 (0.092)	−0.4 (0.397)	−0.5 (0.069)

gage in a polygynous tactic with two or more females. Although it remains unclear why males would invest in either tactic, TC may be a marker for the male's readiness for paternal investment with one female rather than continuing mating at the expenses of reproductive success. In line with this, TC may be viewed as a physiological indicator for a pair bonding tendency and maybe a monogamous mating tactic. Moreover, the occurrence of TC suggests that during domestication, geese seem to have maintained the facultative readiness to invest hormonally into one exclusive pair partner, which probably represents the robust remains of social mechanisms from their mainly monogamous ancestors. However, this was not simply explained by the initial partner preference in domestic geese.

4.3. Within-pair TC and reproductive output

Domestic geese were artificially bred for body mass and prolonged laying periods resulting in large quantities of eggs. In this study, TC was related directly with only one of the laying or breeding parameters, i.e. females from pairs with higher TC laid eggs over a shorter period of time. However, this did not affect breeding success. Effective incubation of these large clutches is physically unfeasible. In order to enable observations beyond the laying phase, we experimentally reduced clutch sizes. Although all females had nests with eggs, not every female initiated incubation of that clutch. In our experiments, particularly females with preferred partners seemed motivated to initiate incubation, whereas 'random partner pairs' and the flock situation had only few incubating females (Table 3). Unexpectedly and for unresolved reason, breeding success was extremely low: only two pairs successfully hatched young during the two years sampled. Thus, domestic geese may not have been the optimal model for parameters beyond the clutch phase (in addition to the effects of domestication).

In conclusion, high degrees of within-pair TC occurred in polygynous domestic geese but none of the experimental situations explained the observed variation. Our study with domestic geese suggests that, at least during the egg formation phase, the female's androgen responsiveness to the partner was an episodic component of TC. Yet, a number of questions require to be solved in the future. For instance, we do not yet know whether TC applies particularly to long-lived species with long-term bonds such as geese, whether social monogamy or sexual exclusivity are key components, or whether it is merely an epiphenomenon of decreased androgen levels during paternal phases. It requires more than hormones to be a successful pair, but the continuous flexibility of androgen patterns of both, males and females in response to their pair partner seems an essential prerequisite for partner compatibility. Therefore, TC should be viewed as a condition, which remains a function of the physical and social environment rather than a stable trait.

Acknowledgments

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