CURRENT ISSUES - PERSPECTIVES AND REVIEWS

Testosterone and Partner Compatibility: Evidence and Emerging Questions

Katharina Hirschenhauser

Department of Behavioural Biology, Faculty of Life Sciences, University of Vienna, Vienna, Austria

(Invited Review)

Correspondence
Katharina Hirschenhauser, Department of
Behavioural Biology, Faculty of Life Sciences,
University of Vienna, Althanstraße 14, A-1090
Vienna, Austria.
E-mail: k.hirschenhauser@aon.at

Abstract

In socially monogamous species pair partners often form and maintain long-term pair-bonds. Relationships between pair partners are dynamic and driven by both cooperation and conflicts between the sexes. Successful reproduction depends on behavioural coordination and cooperation, which includes continuing mutual responsiveness between the pair partners, as well as conflicts, for example, over parental investment. Gonadal hormones, such as testosterone, centrally regulate reproduction and are potentially involved in the formation and maintenance of pair-bonds. In greylag geese (*Anser anser*), a positive within-pair testosterone co-variation (TC) among pair partners has been observed at the seasonal level. Goose pairs with a higher TC have a higher reproductive output and long-term success than pairs with lower TC, but it is still not clear whether TC is cause or consequence. In this article, I (i) summarize the evidence for hormonal partner compatibility in geese, (ii) ask whether TC is restricted to monogamous and biparental systems and (iii) synthesize open questions or new aspects of information we may draw by studying hormonal partner compatibility. From longitudinal studies in geese, we know that TC decreases with pair-bond duration. This indicates some form of 'attritional effect' over the years rather than an improved breeding performance with increasing familiarity between the partners (the 'mate familiarity hypothesis'). Under certain circumstances, for example, during ageing, selection may not act in the same direction for males and females. Partner preference increased female androgen levels during laying and social instability may impinge on the pair's TC. Data from other species show that TC is not restricted to monogamous species, but presumably the link between TC and reproductive output may be primarily relevant in species with biparental care. This article surveys the major unanswered questions relating to hormonal partner compatibility and previews potential future work for addressing those open issues.

In socially monogamous birds both partners benefit from being paired. The pair status facilitates access to resources and successful reproduction. However, being paired with a partner *per se* is not a guarantee of reproductive success. Relationships between partners are dynamic and driven by cooperation and conflicts between the sexes. Monogamy in many ways may be seen as a compromise between conflicting evolutionary pressures on the sexes (Westneat & Sargent 1996). In socially monogamous species behavioural coordination and cooperation between pair partners is crucial for successful reproduction, this includes a continuing and mutual responsiveness between the pair partners, as well as conflicts. Sexual conflict over courtship, mating and parental investment is the result of the different costs of reproduction for males and females. As a consequence, each partner can gain by investing less, while their partner invests more

(Arnqvist & Rowe 2005; Chapman 2006). If selection favours pairs with coordinated parental care, then choosing a behaviourally (and/or hormonally) compatible partner is probably advantageous. A pair-bond may serve to synchronize reproductive physiology between the sexes and/or the pair-bond represents a prolonged period of continuous mutual assessment of mate quality (Andersson 1994). Leese (2012) has recently shown that female convict cichlids (*Amatotlania nigrofasciata*) employ the pair-bond for mate assessment, while males do not. Within a greylag goose (*Anser anser*) flock, there are 'good pairs' which successfully raise offspring year after year and other pairs with poor prospects of reproductive success (Hemetsberger 2002). In search for why this is so, we observed that a pair's life-time reproductive output co-varied with the degree of hormonal compatibility between the pair partners; in particular, the positive co-variation of the male and the female partner's seasonal testosterone patterns ('TC'; Hirschenhauser et al. 1999; Weiß et al. 2010). This was an intriguing phenomenon, but it remained open as to whether TC was the cause or effect of successful reproduction. Here, I will focus on the critical role of mate assessment and adjustment to partner and the mechanisms of long-term maintenance of relationships. I will summarize the evidence for hormonal partner compatibility from geese and present new data from the promiscuous and maternal Japanese quail (*Coturnix japonica*). The aim is to highlight novel aspects of hormonal partner compatibility and to develop open questions for future work on the hormonal mechanisms underlying pair-bond formation and maintenance and their functions.

Pair-bonds in Long-term Monogamous Animals

In long-term monogamous mating systems, such as that found in greylag geese, pair-bonds often last for the life of one or both of the individuals. The relationships between individuals are the basic elements of a social group, and this includes the formation and maintenance of pair-bonds (Kotrschal et al. 2010). But, how can we quantify and measure pair-bond quality or the degree of attachment between two individuals? Is a 'good pair' composed of pair partners which cooperate and coordinate their individual interests for coping with sexual conflicts? Pair-bonded individuals are in a dynamic game, in which each is under selection to maximize its own reproductive output (Westneat & Stewart 2003). Sometimes selection acts in the same direction for both males and females, but often it does not. Thus, conflict is a major constituent of the dynamic game. At the level of cooperation, pair partners may be viewed as team players (with variable success). There is no direct measure of the degree of 'team-playing' between two individual partners. For quantifying pair-bond quality ethologists have measured breeding success, the degree of coordination of feeding behaviours between pair partners and the ability to compensate for example, for partner's 'handicap'. Most of these studies have dealt with monogamous and biparental species; this is not surprising because coordination between pair partners is essential for biparental care (Bluhm et al. 1984; Schneider & Lamprecht 1990; Lamprecht 1992; Balshine et al. 2002; Both et al. 2005; Kellam et al. 2006; but see Wright & Cuthill 1989). Many monogamous species are not paired during the non-reproductive season. In contrast, in long-term monogamous animals such as greylag geese, a partner is not only a mate for reproduction but also a social ally throughout the year (Kotrschal et al. 2010). Thus, for long-term monogamous individuals, partner compatibility and within-pair coordination must be especially important. However, measuring the degree of coordination based on behaviour is a challenging task.

Itzkowitz et al. (2002) have shown that in the monogamous convict cichlid (*Amatitlania nigrofasciata*), pair partners coordinate their activities during biparental care, especially in the presence of an intruder. But how do the pairs achieve their coordination? Individuals may adapt their parental behaviour to each other and/or both individuals may initially display greater responsiveness to the external condition, for example, an intruder, from the beginning on. Probably, selection would favour partners which have the ability to compensate for each other's lack of performance. The 'optimal strategy' seems to vary with seasonal duties, such as between parental and non-parental seasons (Nedelcu & Hirschenhauser in press), and probably also with life history states and/or ageing. Moreover, work load during parental care, individual flexibility and responsivity to the partner's performance are probably parts of individual behavioural syndromes. Recent data from Steller's jays (*Cyanocitta stelleri*) suggest that pair partners with similar exploratory and risk-taking behaviour are compatible across different contexts, nest earlier and have better fledging rates than pairs scoring lower in similarity (Gabriel & Black 2012). In great tits (*Parus major*), pairs consisting of a male and a female with similar personalities have the highest long-term reproductive success (Both et al. 2005). In geese, a pair-bond is characterized by its spatial proximity (Frigerio et al. 2001), the directing of the triumph ceremony at the

partner (Fischer 1965), active mutual social support (Scheiber et al. 2005) and, potentially, the continuing preference for breeding with the same partner (Hirschenhauser et al. in press). Analyses of time budgets show that behavioural coordination consists of functionally complementary behaviours, that is, in alternating roles during parental and non-parental phases (Nedelcu & Hirschenhauser in press). Thus, successful goose pairs had a more efficient division of tasks than did non-successful pairs.

Steroid hormone levels, such as glucocorticoids from the adrenal stress axis, are also relevant parameters for measuring pair-bond quality. In geese, excreted glucocorticoid metabolites (from droppings) and remotely recorded individual heart rate patterns revealed that the mere presence of social allies mitigated energy expenditure (Frigerio et al. 2003; Scheiber et al. 2009; Wascher et al. 2012). These studies underline that pair-bonding has direct benefits through passive social support in addition to optimizing biparental care. This contributes to understanding why socially monogamous pair partners continue to cooperate during parental care despite potential conflicts between the sexes for the division of labour (Balshine et al. 2002).

Seasonal Testosterone Patterns and Initial Pair Formation

In general, within populations of a species, every year some males are first in displaying and courting, and some females always start breeding earlier in the season than do others. In birds, individual females may engage in nest building and egg laying for different periods of time and have variable clutch sizes. The optimal timing of courting or breeding early or late in the year is adaptive for a given environment and/or population (Caro et al. 2009). A mistiming between reproduction and food availability, including the seasonal timing of hormone transitions and behaviour, leads to a reduced level of fitness. Hormones, such as the male gonadal steroid testosterone have a distinct seasonal pattern. Seasonal patterns of androgens are related to the individual timing of reproductive events in both sexes. Females also produce seasonally varying levels of androgens in the gonads, for example in growing follicles, as well as in the adrenals (Ketterson et al. 2005; Groothuis & Schwabl 2008). Peak testosterone levels in females mark phases of sexual activity and receptivity (Jawor et al. 2006). In female dark-eyed juncos (*Junco hyemalis*), experimentally elevated testosterone results in a reduced choosiness (McGlothlin et al. 2004), delayed onset of breeding

phases, increased resource defence and mate acquisition behaviours (Clotfelter et al. 2004; Ketterson et al. 2005). The timing of reproductive events is not only related to environment but also to the partner's individual decisions. Thus, selection will favour pair partners that are continuously responsive to each other's pace. In modern human societies, paired men potentially adapt their testosterone to their female partner's cycle (Hirschenhauser et al. 2002). Women and men with low baseline testosterone are more likely to be pair-bonded (Van Anders & Watson 2006), while polygynous married men generally have higher testosterone than monogamous married men (Alvergne et al. 2009). For men during the first 6 mo of a committed relationship, men's testosterone levels were higher than in men who had been with their partner for more than 12 mo (Gray et al. 2004). Men with lower testosterone levels were more responsive to infant cues (Storey et al. 2000) and also vice versa paternal effort has large effects on men's testosterone (Gray et al. 2002; Kuzawa et al. 2009). The expression of sexual (or courtship or territorial) behaviour is often interpreted as an epiphenomenon of transitional changes in reproductive physiology. However, also vice versa hormone levels are powerfully modulated by social interactions and context, for example, individual history or a familiar individual in the audience. This social modulation of testosterone seems to represent a preserved mechanism throughout many vertebrate taxa (Wingfield et al. 1990; Oliveira 2004; Hirschenhauser & Oliveira 2006). More recently, accumulating evidence is showing that from fishes to humans, females also respond with androgen changes to behavioural interactions in courtship, mating and competition contexts (López et al. 2009; Oliveira et al. 2009; Gabor & Grober 2010; Hirschenhauser et al. 2010).

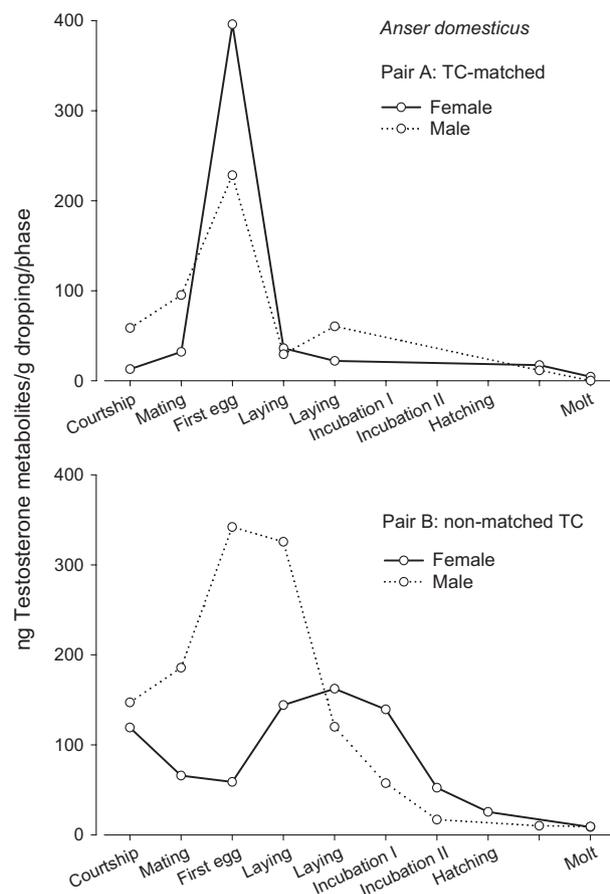## Within-pair Testosterone Co-variation in Goose Pairs

Previously, some authors have suggested that the hormonal state of one partner affects that of the other throughout the year (Moore 1982; Wingfield & Monk 1994). Studying the seasonal transitions of reproductive physiology, for example, hormone patterns and behaviour adds a new perspective to the concept of partner compatibility. Our studies on the within-pair TC in greylag geese and domestic geese (*A. domesticus*) have taken partner compatibility to the level of the seasonal hormonal regulation of behaviour. We measured the individual seasonal testosterone patterns in both sexes and calculated correlation coefficients

between the partners' seasonal testosterone (Hirschenhauser et al. 1999, 2010; Weiß et al. 2010; Fig. 1). These seasonal within-pair TC coefficients ('TC') allowed further tests using the pair as the operational unit of analyses, which goes beyond the individual level. TC includes the individual seasonal timing of life history events including moult. Pairs with high TC have parallel timings of seasonal testosterone peaks and troughs and are highly synchronous, particularly in the phases between courtship and raising offspring/moult. TC also integrates a receptiveness of the partner's reproductive state, as well as a mutual behavioural and hormonal responsiveness to the partner. The dyadic approach may be advantageous particularly because it involves the mutual interaction between pair partners. One of the emerging questions is whether a key feature of a compatible pair is the

Fig. 1: Examples for one pair with co-varying testosterone patterns (Pair A: TC-matched) and one pair with non-matched TC (Pair B) of domestic geese. Lines are the individual seasonal patterns of excreted testosterone metabolite levels (means per seasonal phase) from the female and the male pair partner. Pair A: Kendall's Tau (TC) = 0.7, N = 7 phases, p = 0.039. Pair B: Kendalls' Tau (TC) = 0.2; N = 10 phases; p = 0.458.

mutual interaction between both pair partners' hormones and behaviour. Alternatively, hormonal partner compatibility may be merely a by-product of biparental care, thus, a mirror of the male partner's engagement in care for offspring. Pairs with high TC may benefit from (i) an increased coordination in reproductive physiology, (ii) coordination of hormonally mediated behaviours or (iii) the hormonal and behavioural responsiveness to a mate may itself be the target of selection. However, a number of questions remain open. For example, it is still not fully understood how partners assess each other's behavioural and/or hormonal compatibility during pair formation. And essentially, is TC a cause of reproductive success or its consequence?

Partner Assessment and Adjustment During Pair Formation

A pair-bond is an exclusive social and sexual relationship, which is formed and maintained with an individual of the other sex. In socially monogamous mating systems, the pair-bond may be seasonal or may continue throughout the year and for up to several years hence. Thus, in long-term monogamous species the initial partner choice may be critical for life-time reproductive success. Understanding how selection drives mate choice decisions is still a challenge. Genetic complementarities of the parents, for example, affect offspring fitness (Trivers 1972; Foerster et al. 2003). However, particularly in species with long-term pair-bonds and biparental care, it is unclear whether selection for complementary genes between pair partners contributed to the evolution of mate preferences (Neff & Pitcher 2005; Mays et al. 2008; Hettyey et al. 2010). In barnacle geese (*Branta leucopsis*), age and size assortative mating seems to optimize reproductive output (Choudhury et al. 1996). However, it is still not fully understood as to how partners evaluate and choose one compatible partner (and not another), or why some pair partners stay bonded even in the absence of reproductive success. In fact, the initial pair formation period before the start of breeding may involve crucial within-pair coordination processes ('adjustment phase'; Lamprecht & Rebhahn 1997). For understanding the TC phenomenon in greylag geese, we hypothesized that geese probably engage in some mutual adjustment to the partner (Hirschenhauser et al. 1999). This probably occurs as a rapid process during pair formation, rather than improving over the years of being paired. A recent study on bearded reedlings (*Panurus biarmicus*) put a more detailed focus on the narrow time window prior

to the egg laying phase. In this species, pairs had higher breeding success when they were experimentally allowed longer intervals for within-pair adjustment during the pre-breeding phase (Griggio & Hoi 2011). Allowing more time to adjust to each other may have increased the degree of behavioural coordination between the partners. Thus, the bearded reedling study supports the 'coordination for parental care' hypothesis. However, as with TC, the evidence is correlational and disentangling cause and effect remains a chicken-or-egg-dilemma. Also, using breeding success simultaneously as the definition and the measure of compatibility in pairs is problematic, again we need to learn more about causes and consequences. A similarly detailed study of within-pair adjustment processes specifically during the pre-mating/pair formation phase in greylag geese would be valuable.

Cues for Compatibility

During pair formation, a number of processes remain unclear: how variable is the time between initial courtship and actual pair-bond formation? How do individuals assess each other's value or compatibility during pair formation? Which behavioural features or suites of behaviours could be the cues for identifying a hormonally responsive and cooperative partner? If females indeed choose for these behaviours, the compatibility of a partner is subject to sexual selection. One notable example for assortative mating based on behaviour is that of 'coordinated nest-relief' in Adelie penguin pairs (*Pygoscelis adeliae*): only pair partners with complementary incubation and foraging routines in one season remained together the next season (Davis 1988). To date, few studies have shown that females actually evaluate a male's paternal quality based on a behavioural feature during courtship (grey partridge *Perdix perdix*: Fusani et al. 1997; stickleback *Spinachia spinachia*: Ostlund & Ahnesjo 1998). Testosterone is one possible endocrine mechanism, which could link courtship interactions with future paternal care. Gleason & Marler (2010) tested transitory testosterone changes of male California mice (*Peromyscus californicus*) during courtship and paternal behaviour when the female was experimentally removed during the parental phase. Males with increased testosterone during courtship cared for pups more quickly. Thus, the testosterone response to females seemed to predict the male's paternal quality. However, in mate choice tests female California mice preferred to mate with behaviourally compatible males rather than with a 'universally attractive' male, such as high testosterone responders (Gleason et al. 2012).

Testosterone and Choosiness

In most social systems, males are the advertising and females are the choosing sexes. A female's mating preferences depend on her own quality and current condition (Holveck & Riebel 2010) and individual choosiness is defined as variable 'sampling effort' during mate choice (Real 1991). Variable choosiness represents an adaptive plasticity within populations and is one element of total reproductive investment (Qvarnström et al. 2000). Reproducing with a non-preferred partner may result in fitness deficits of offspring (Bluhm & Gowaty 2004). Differential and compensatory reproductive investment of females because of partner quality has been studied extensively in the zebra finch (*Taeniopygia guttata*; Gil et al. 1999; Bolund et al. 2009). Testosterone may be involved in mate choice as a physiological mediator of the trade-off between sampling effort and limited breeding opportunities. Goymann (2010) has pointed out the neglected role of females in discussing the role of testosterone in mating strategies. Testosterone may increase the males' propensity to seek additional mates – but what regulates the females' propensity to accept these offers or to refuse and avoid mating and/or pair formation with this partner? Female dark-eyed juncos, *Junco hyemalis*, experimentally treated with testosterone were less discriminative in their mate choice (less choosy) than were control females (McGlothlin et al. 2004). Also stress hormones are good candidates for mediating this trade-off, female Gouldian finches (*Erythrura gouldiae*) paired with a non-preferred partner had elevated stress hormone levels over several weeks, which also delayed egg laying (Griffith et al. 2011). Progesterone treatment of female zebra finches increased the expression of 'pairing behaviours' during initial pair formation, but it did not affect partner preference or relationship maintenance (Smiley et al. 2012). In the following, I describe an example for the employment of TC to measure and to further understand an individual's propensity to adjust to a cohabited partner in two polygamous species.

Artificial Monogamy Tests in Japanese Quail

If we regard within-pair TC as a marker of hormonal partner compatibility, we can ask whether the phenomenon is restricted to monogamous species with long-term pair formation and absent in promiscuous and lekking species? We tested the occurrence of TC in male–female pairs of Japanese quail (*Coturnix japonica*), as a representative for a promiscuous bird, and

predicted that we would find only a few (if any) dyads with matched TC. We chose Japanese quail for experimental tests, because they are small galliform birds, domesticated, with a promiscuous mating system and purely maternal (Mills et al. 1997). Pair-bond formation and mate-switching has been reported from the serially polygamous common quail (*C. coturnix*), which is the wild ancestral species of Japanese quail (Rodriguez-Teijeiro et al. 2003). Male and female Japanese quail sensitively respond to social interactions with increased testosterone metabolites (Hirschenhauser et al. 2008) and glucocorticoid levels (Rutkowska et al. 2011). To test the potential for TC and pair-bonding with a partner in Japanese quail, we randomly assorted one male and one female as pair partners and kept them as 'artificially monogamous pairs'.

Fifteen male–female pairs were kept in the same room with no visual or physical contact with adjacent individuals; acoustical communication could not be avoided. Seasonal changes were mimicked by increasing daylight hours over the course of 10 wk (light/dark schedule from 8:16 h to 16:8 h). We regularly sampled individual faecal droppings from male and female 'pair partners' throughout 16 wk (109 d) with the aim of collecting one dropping per individual per phase. From the droppings, we measured excreted testosterone metabolites. We used different enzyme immunoassays for droppings from males and females because prior physiological validation tests based on GnRH revealed the presence of significant amounts of different androgen metabolites in the excreta of male and female quail: 17ß-hydroxy-testosterone in males (Hirschenhauser et al. 2008) and 17-oxo-epiandrosterone (as in Hirschenhauser et al. 2000) in females (K. Hirschenhauser & E. Möstl, unpublished data). To assess the within-pair TC, we calculated a Kendall's Tau correlation coefficient from the male's and the female's individual of each pair (as in the goose studies; Fig. 2). However, here the seasonal changes were 'light-induced' testosterone metabolite patterns.

In contrast to our expectations, the proportion of TC-matched pairs was surprisingly high: we found significant within-pair TC in 60% of all artificial pairs (mean TC ± SEM: 0.6 ± 0.04; Table 1). Given that Japanese quail are promiscuous birds, the large proportion of TC-matched pairs was unexpected. Did some pair-bonding occur in Japanese quail when they were forced to monogamy or was this a random result? One possible explanation for the relatively high degree of TC may be that there was only small variation of individual testosterone metabolite patterns within the sample and in most
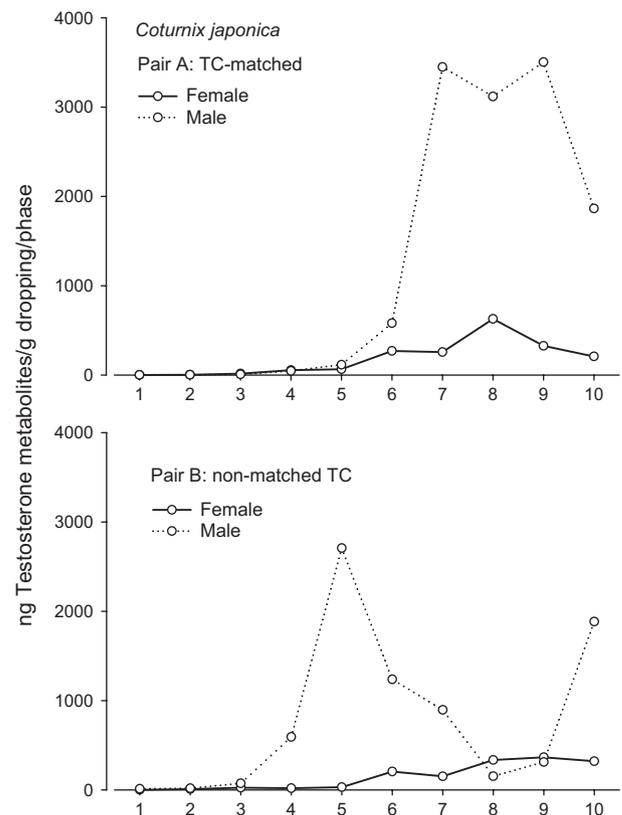

Fig. 2: Individual seasonal (light-induced) patterns of excreted testosterone metabolites from the male and the female of two artificial pairs of Japanese quail. Pair A is shown as one example for a pair with significantly matched testosterone co-variation (TC) (Kendall's Tau = 0.8; N = 10; p = 0.001). Pair B shows the patterns of a pair with non-matched TC (Kendall's Tau = 0.3; N = 10; p = 0.186).

Table 1: Comparison of testosterone co-variation (TC) observed in Japanese quail kept as artificial male–female pairs

	Artificial pairs (15)
Mean TC ± SE	0.6 ± 0.04
TC range (min … max)	0.3 … 0.9
Significant TC	60% of all pairs
Variability of TC (c.v.)	26%
Laying activity (egg/day)	1 ± 0.03
TC with of other males	76.2 ± 5.7%
Range (min … max)	21 … 100%
TC with N other males	10.7 ± 0.8 males
Noise around population average (TC and N other males)	$r_s = 0.5$ (p = 0.042)

of the females (if not both sexes) testosterone patterns may have been close to an 'optimal' (or average) pattern. This may reflect a narrow distribution around the average if the testosterone patterns were simply light induced rather than modulated by social factors.

To test for the discriminative nature of TC, that is, the selective fine-tuning of testosterone metabolite patterns with one specific partner and the general probability of TC occurrence, we additionally calculated 'cross-correlations' with the testosterone metabolite patterns of all other (non-partner) males in the room. We found a high degree of cross-correlations with, on average, 76.4 ± 5.7% of all other males (Table 1). Moreover, the testosterone metabolite patterns of females from high-TC dyads (with their assigned partner) were also correlated with the testosterone metabolite patterns of more (or even most of the) other non-partner males in the room ($r_s = 0.5$, N = 15, p = 0.042; Fig. 3). Thus, most females from high-TC dyads were indeed close to the population average seasonal testosterone metabolite pattern. The TC phenomenon was much less obvious in the Japanese quail than in biparental geese (see below). In particular, the female's preferences were more dispersed and less selective than in biparental species. The artificial monogamy may have produced an artificial pattern of TC, which was probably modulated more by the light regime than socially. These data illustrate that even when 'forced into monogamy' female Japanese quail were not exclusively responsive to the one assigned pair partner. The high proportion of cross-correlations rather marked a low degree of the individual's propensity to adjust to one pair part-
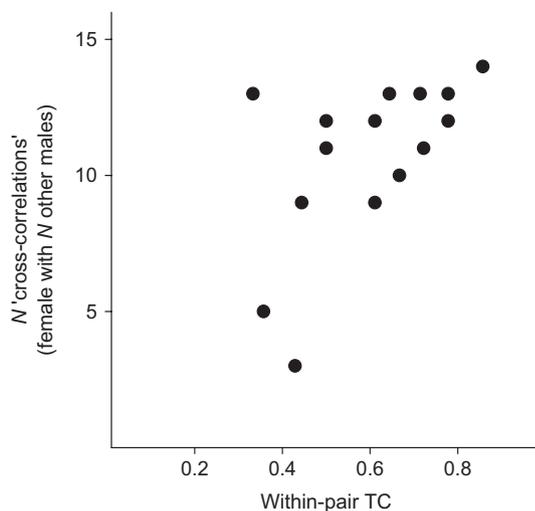
Fig. 3: The relationship between the within-pair testosterone co-variation (TC) of female Japanese quail with a randomly assigned pair partner and the number of 'cross-correlations' with other non-partner males in the room. The testosterone metabolite patterns of females from high-TC scoring dyads were also correlated with more (most of the) other non-partner males in the room ($r_s = 0.5$; N = 15; p = 0.042). Japanese quail were kept as artificial male–female pairs (N = 15 pairs) in the same room.

ner in Japanese quail. Promiscuous and maternal birds, such as Japanese quail, may indeed be choosing their partner for different criteria than do monogamous and biparental birds. In maternal birds, successful reproduction does not require long-term pair formation or biparental-care. Thus, in the Japanese quail social system, in which the female alone provides care and both sexes mate multiply, a male's continuing testosterone responsiveness to one particular female may not be an evolutionary relevant trait. Alternatively, TC could be important also in Japanese quail, but the quail were synchronized with multiple males because of lower variation in seasonal changes of testosterone metabolite patterns.

A different pattern emerged in a similar 'artificial monogamy' test with polygynous and biparental domestic geese (Hirschenhauser et al. 2010). In randomly composed domestic goose pairs, seasonal testosterone profiles were matched between partners in a more exclusive way: TC was *either* focused on the assigned pair partner *or* on the goose housed in the adjacent facility – but then not with the assigned partner as well (Nedelcu & Hirschenhauser in press). As in the quail tests, domestic goose pairs were housed adjacently to each other; however, the geese had visual contact to the adjacent individuals. Furthermore, the goose experiments were conducted in large outdoor facilities, whereas the quail tests took place under artificial light regimes. Is the propensity to discriminate and hormonally adjust to a favoured specific partner (i) linked with biparental care and (ii) is TC subject to mate choice? In experiments, we did not find more TC-matched domestic goose pairs whether they were with their preferred partner or with a randomly assigned partner (Hirschenhauser et al. 2010). Thus, there was no mate choice effect or an effect of being mated with a preferred partner on the pairs' TC in domestic geese; however, females with preferred male partners temporarily had higher androgen levels and thus fertility during the laying phase (Hirschenhauser et al. 2010; Fig. 1). During later breeding phases, TC depends on the male partner's testosterone responsiveness to the female's timing of reproductive events. Thus, both male and female partner seem to have episodic phases in which it is crucial to be responsive to the partner, but in particular, the female's androgen pattern clearly differed due to being mated with a preferred partner.

Pair-bond Duration

In addition to initial coordination processes during pair formation, the pair partners may experience some

continuous mutual (behavioural and physiological) adjustment for long-term pair-bond maintenance. Species, which maintain pair-bonds throughout the year, may have evolved peculiar rituals to maintain the pair-bond year around, including non-breeding phases and the synchronization of breeding activities. For example, during the non-breeding season, monogamous pipefish (*Corythoichthys haematopterus*) engage in daily 'greeting displays' at a fixed site of their overlapping home ranges (Sogabe & Yanagisawa 2008). In kittiwakes (*Rissa tridactyla*), prior residence at nest sites (breeding site fidelity) explained breeding success and divorce probabilities better than did pair-bond duration (partner fidelity) itself (Naves et al. 2007). Pair-bond duration is a rather complex variable, particularly because the co-varying effects of ageing and experience may bias the emerging patterns (Fowler 1995; Ottinger et al. 1995). Moreover, it is often unclear whether a positive association is caused by pairs improving during their pair-bond or by high-quality pairs staying together for longer (Van de Pol et al. 2006). The 'mate familiarity effect' suggests that pair partners increase their within-pair cooperation by re-mating with the same partner every year (Black 1996). This has been confirmed with longitudinal data from the long-lived European oystercatcher (*Haematopus ostralegus*). Reproductive success of oystercatchers in general was correlated with pair-bond duration. However, oystercatcher pairs that stayed together for very long (i.e. more than 12 years) performed badly (Van de Pol et al. 2006). Naves et al. 2007 showed in kittiwakes that breeding experience increased success between the first and second years of the pair-bond, but not with the total pair-bond duration. This was similar with the TC patterns in greylag geese, in which pair-bond durations of up to 18 years were included: TC scores were low in pairs with very long pair-bond duration. Yet, this was not a simple function of ageing because older females were more likely to be part of good TC pairs than older males (Weiß et al. 2010). Thus, if TC may be regarded as a marker for pair quality in greylag geese, then TC did not conform to the 'mate familiarity hypothesis'.

However, we must not overlook the dynamic component of hormonal partner compatibility. Within a social group, social status is a dynamic feature that influences access to resources, including food and opportunities for mating. Testosterone is clearly involved in the search for, and maintenance of, social status (Eisenegger et al. 2011). As a consequence, ongoing challenges affect the stability of seasonal testosterone levels. In geese, during the first years of being paired TC is more or less stable (up to 8 years in

our sample; Nedelcu & Hirschenhauser in press); those pairs, which we have sampled in two consecutive years had similar scores, and TC was either significant in both years or the pair was non-matched in both years (Weiß et al. 2010). However, in greylag goose pairs with longer pair-bond duration, TC of pairs was decreased when they were involved in pair-bond challenges the following year (Weiß et al. 2005) and generally TC decreased over the years of being paired (Weiß et al. 2010). Also in the domestic geese, the pairs' TC was higher the year when they were kept as pairs than when they were kept in one large flock (Hirschenhauser et al. 2010). TC itself was not stable over different contexts but rather continuously responsive to the social environment. Thus, TC may be a fairly dynamic status rather than a fixed trait.

Hormones and Pair-bond Maintenance

It is commonly assumed that testosterone is involved in competition, in sexual and aggressive contexts, whereas oxytocin is the fragrance of 'peace-and-love'. Although it seems paradoxical at first glance, testosterone can be seen as a facilitator of pair-bonding: testosterone increases during courtship and mating, which builds a link to oxytocin and the phenomenon of social bonding, including parent and offspring relationships ('steroid/peptide theory of social bonds'; Van Anders et al. 2011). Oxytocin is of particular interest for studying partner compatibility, as it interacts with sociosexual and parental behaviour, pair-bonding, as well as the adrenal stress axis. It is also part of reward pathways in the brain, involved in social memory and is context-dependent (Gordon et al. 2011). In small mammals, the role of neuropeptides has been subject to detailed studies on the neural mechanisms of social behaviour; in prairie voles (*Microtus ochrogaster*), central oxytocin facilitates partner preference and affiliative behaviour (Insel 1992), whereas vasopressin regulates selective aggression and pair-bonding in the monogamous *M. ochrogaster* but not the polygynous *M. montanus* (Winslow et al. 1993). After 3 d of cohabitation, guinea pigs (*Cavia aperea* f. *porcellus*) increasingly showed side-to-side contact behaviour, which was accompanied by within-pair co-variation of circulating oxytocin levels (Wallner et al. 2006). In birds, the neurons and transmitters involved in social bonding are similar to the mammalian model: Goodson (2005) has identified a steroid sensitive 'social behaviour network' within the forebrain and midbrain of birds and teleosts, that is homologous to the social behaviour network of mammals (Newman 1999). Therefore, these circuits

Divorce and Re-mating

A major unresolved question is that of why some partners remain together even in the absence of hormonal partner compatibility. Is there an 'attritional' effect on mutual responsiveness; does the compatibility between two partners have an expiry date? If the costs of compensating for a non-compatible partner are high, one alternative is that of separation or 'divorce' to re-mate with a higher quality mate. Parrots seem to decide to switch partners when they are paired with a non-compatible partner: highly compatible pairs did not engage in extra-pair copulations, whereas individuals which engaged in extra-pair liaisons subsequently switched partners and dissolved a relationship with poor prospects (Spoon et al. 2007). However, not all pair-bonding species are equally likely to switch partners, this must be related to the costs involved in changing partners. Female oystercatchers more often switch partners than do males; however, this comes at the cost of reduced breeding success with a new mate or at the new nest site (Ens et al. 1993). In many species with long-term pair-bonds, experienced adults in newly formed pairs (because of divorce or loss of mate) have a reduced reproductive success (Fowler 1995; Fig. 4a). The schematic illustration of TC with a new partner gives a different picture, however: if TC with the new partner is equal or higher than the TC with the previous partner was, the total lifespan with high-TC scores is longer

than without mate change (Fig. 4b). Assuming that high TC is correlated with reproductive output, selection might favour as an alternative strategy changing mates at least once in the life of a female goose for optimizing total reproductive success. However, this has not been observed during 30 years of individual records in the Grünau flock of greylag geese (Hemetsberger 2002). One explanation for this may be a lack of available potential new partners in this rather small flock, which lacks the tradition to migrate (Hemetsberger 2002). In the case of re-pairing after the death of one partner, the concept of optimizing the lifespan with a TC-matched partner is conceivable. In contrast, re-pairing after divorce would be adaptive if it was with a new partner that is potentially more compatible than the current/previous partner. However, this assumes that females are capable of recognizing, identifying and evaluating a potential mate's quality.

There are a number of open questions wrapped up in this scheme: Why do some pair partners stay bonded even in the absence of reproductive success and would selection favour divorce under these circumstances? Assuming the 'mate familiarity hypothesis' applies – which factor(-s) would mark the optimal decision between staying paired with a low quality or incompatible mate and long common experience, or divorcing and re-mating with a higher quality mate at the cost of starting it all over again? Is energy expenditure a relevant currency for partner compatibility and can it reliably be measured, for example, with glucocorticoid hormones as indirect measures of energy expenditure (as suggested by Angelier et al. 2007)? Other currencies relevant to partner compatibility could be body mass, immune function, fecundity or longevity (Arnold 1994). In terms of TC,
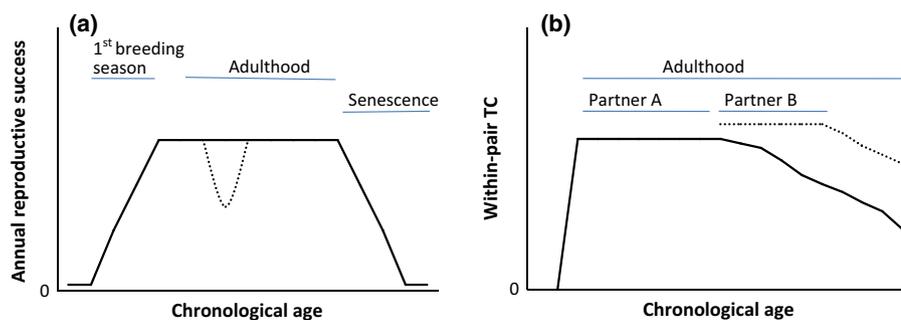
Fig. 4: Scheme of (a) age-related reproductive success in long-term monogamous birds (modified from Fowler 1995). (b) Schematic pattern of within-pair testosterone co-variation (TC) when long-term bonded with the same partner and the modified pattern shape in pairs that have changed mates. Full line: long-term partner; dotted line: new partner. (a) Initially decreased breeding success: after re-mating reproductive success is temporarily decreased. (b) 'Attrition' of TC: the degree of TC decreases after some years of robust high TC (~8 years in greylag geese; Nedelcu & Hirschenhauser in press). The dotted line marks the hypothetical change of TC after separation/re-pairing with a new partner. If TC with the new partner is equal to or higher than the TC with the previous partner the total lifespan with high-TC scores is longer than without mate change.

senescence (Ottinger et al. 1995; Angelier et al. 2007) is another challenging issue: would synchronized hormone patterns of the pair partners during senescence be part of a TC-matched pair? And finally, are there sex-specific differences between reproductive performance, energetic potential and hormonal status during ageing? Research from different species on the cues of initially adjusting to a pair-bond and on separating or maintaining the relationship between pair partners is awaited in this area.

Conclusions – Open Questions – Future Directions

In the future, we need to add evidence of hormonal partner compatibility in new species and taxa. Adding data from new species will improve our understanding of when selection favours a high degree of coordination or conflict between pair partners. Hormonal partner compatibility is more than merely a by-product of biparental care as we have observed TC also in polygynous and promiscuous species, and pair formation is not restricted to biparental species (Leu et al. 2011). The currently most central unanswered question is probably whether TC is cause or consequence of reproductive success. One way this might be addressed is to experimentally regulate both pair partners' seasonal testosterone levels, that is, experimentally 'synchronizing' pairs, which were previously non-TC-matched, and test whether this manipulation changed behavioural responsiveness, coordination and coping with conflict. Alternatively, we could test whether experimental 'de-synchronization' of previously TC-matched pairs would result in interference with breeding success (or vice versa).

We also need to understand how partners assess each other's behavioural and/or hormonal compatibility during pair formation and whether these cues, and hence the hormonal partner compatibility, are subject to sexual selection. Tests with high temporal resolution during the short phase of initial pair formations will be needed to learn more about this. Testing mate choice decisions is probably most meaningful under controlled laboratory conditions. Such tests might be promising with pair-bonding cichlid fish as model species. Last not least, we still do not understand why some pair partners stay together even in the absence of TC and reproductive success. Would selection favour separation under these circumstances? To solve this, modelling the costs and benefits of remaining with the non-TC-matched partner or divorce and re-mate with a new partner, including the risk of choosing just another non-optimal mate, would be a most exciting future step forwards.

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