

Sexual selection and animal personality

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ABSTRACT

Consistent individual behavioural tendencies, termed “personalities”, have been identified in a wide range of animals. Functional explanations for personality have been proposed, but as yet, very little consideration has been given to a possible role for sexual selection in maintaining differences in personality and its stability within individuals. We provide an overview of the available literature on the role of personality traits in intrasexual competition and mate choice in both human and non-human animals and integrate this into a framework for considering how sexual selection can generate and maintain personality. For this, we consider the evolution and maintenance of both main aspects of animal personality: inter-individual variation and intra-individual consistency.

Key words: sexual selection, behavioural syndrome, sex differences, individual differences, consistency, repeatability, behavioural synchronization, mate choice, competition.

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I. INTRODUCTION

(1) Background

In behavioural ecology, individual behaviour is normally presumed to be plastic, so that an organism can adapt its behaviour in every situation in order to behave in the best way possible in a given set of circumstances (e.g. Sih, Bell & Johnson, 2004a; Sih *et al.*, 2004b). Nevertheless, individuals often show very limited behavioural plasticity which can be manifest in consistent individual differences in behaviour (e.g. Benus *et al.*, 1991; Boissy, 1995; Gosling & John, 1999; Koolhaas *et al.*, 1999; Gosling, 2001; Groothuis & Carere, 2005; Réale *et al.*, 2007), also known as personality differences (Eysenck & Eysenck, 1985; Gosling, 2001; Dall, Houston & McNamara, 2004), behavioural syndromes (e.g. Sih *et al.*, 2004a, b), coping styles (Benus *et al.*, 1991; Koolhaas *et al.*, 1999) or temperaments (Boissy, 1995). These behavioural differences among individuals are still sometimes considered to be non-adaptive variation around a potentially adaptive population mean (Wilson, 1998; Buss & Greiling, 1999; Dall *et al.*, 2004). However, they (1) often occur in a non-random fashion, in that individuals differ consistently in suites of correlated traits and along a subset of potential axes of behavioural variation (Sih *et al.*, 2004a) and (2) have fitness consequences (Dingemanse & Réale, 2005; Smith & Blumstein, 2008).

If an individual is consistent in its behaviour over time, over different functional behavioural categories (contexts) and/or situations (*sensu* Sih *et al.*, 2004a), it will appear to behave “maladaptively” in many situations. Consequently, the question arises why these personality differences exist; i.e. what is their evolutionary origin, and how are they maintained? More specifically: (1) why do individuals in the same population differ in their behavioural responses, even under the same environmental conditions, and (2) why are individuals consistent in their behaviour over time or space, even when ecologically significant factors change (Stamps, 2007)? The first question focuses on the reasons for the evolution of different levels of expression of a behavioural trait, i.e. inter-individual variation, whereas the second concentrates on reasons for the evolution of behavioural consistency, i.e. intra-individual stability (Stamps, 2007). As discussed further by Stamps (2007), one would either expect a combination of both low inter- and intra-individual variation in a population (if one behavioural pattern results in highest fitness) or a combination of both high inter- and intra-individual variation (if more than one behavioural pattern results in equal fitness); but instead high inter- and low intra-individual variation are often observed (e.g. Dall *et al.*, 2004; Sih *et al.*, 2004b; Dingemanse & Réale, 2005).

A number of hypotheses, which are not necessarily mutually exclusive, have been postulated recently to explain the observed patterns from a functional perspective (Mangel, 1991; Dall *et al.*, 2004; Sih *et al.*, 2004b; McElreath & Strimling, 2006; Nettle, 2006; McElreath *et al.*, 2007; Stamps, 2007; Wolf *et al.*, 2007; Biro & Stamps, 2008; Sih & Bell, 2008; Wolf, van Doorn & Weissing, 2008; McNamara *et al.*, 2009).

Inter-individual variation in behaviour has been hypothesised to occur due to life-history trade-offs (McElreath & Strimling, 2006; Stamps, 2007; Wolf *et al.*, 2007), a balance between mutation and weak selection (Penke, Denissen & Miller, 2007b) or condition-dependent selection (e.g. Gross, 1996). Furthermore, fluctuating selection as a result of temporal and/or spatial variation in environmental conditions, possibly in combination with dispersal between habitats, has been suggested as a cause for inter-individual variation (Mangel, 1991; Réale & Festa-Bianchet, 2003; Dingemanse *et al.*, 2004; Dingemanse & Réale, 2005; Smith & Blumstein, 2008). Finally, negative frequency-dependent selection has been proposed to create variation in the level of behavioural expression (e.g. Wilson *et al.*, 1994; Dall *et al.*, 2004): game-theoretical approaches predict that fitness-payoffs of different behavioural strategies depend on the frequencies with which the competing strategies are played, resulting in a stable mix of coexisting strategies with equal fitness-payoffs (Maynard Smith, 1982; Gross, 1996; Dall *et al.*, 2004). Nevertheless, such variation-driving processes on their own are not sufficient to explain behavioural consistency. Indeed, for personality differences to exist, mechanisms creating inter-individual behavioural variation need to act together with mechanisms generating and maintaining intra-individual behavioural consistency. Explanations for the existence of intra-individual behavioural consistency include benefits of predictability (Dall *et al.*, 2004; McNamara *et al.*, 2009), constraints (costs or limits of flexibility, Sih *et al.*, 2004b; noisy information, McElreath & Strimling, 2006) and positive feedback loops between state and behaviour (Dall *et al.*, 2004; Sih *et al.*, 2004b; Wolf *et al.*, 2008). Another possibility, which has not received much attention, is a role of sexual selection in the evolution and maintenance of personality differences (both of inter-individual variation and intra-individual consistency), potentially acting together with some of the other evolutionary processes that have been hypothesised.

(2) Objectives

Our aims are to draw attention to the potential role of sexual selection in the evolution and maintenance of personality differences, to review the existing studies and finally to develop a conceptual framework to study such a role (see Fig. 1). It seems important to raise awareness of the potential role of sexual selection in this context because (a) sex is ubiquitous in multicellular organisms (e.g. Barton & Charlesworth, 1998), and (b) it is highly under-represented by researchers studying personality (Dingemanse & Réale, 2005; Sih & Bell, 2008). This under-representation of the topic is also clear from a search of the ISI Web of Knowledge v.4.2 conducted for “sexual selection” in combination with “personality” or “behavio(u)ral syndrome”. Only 35 publications matched these search terms (in October 2008). Just five of these studies were based on non-human animals, while the rest were on humans. We provide an overview of how sexual selection could generate and maintain personality traits, how this theory has been tested in the literature, and

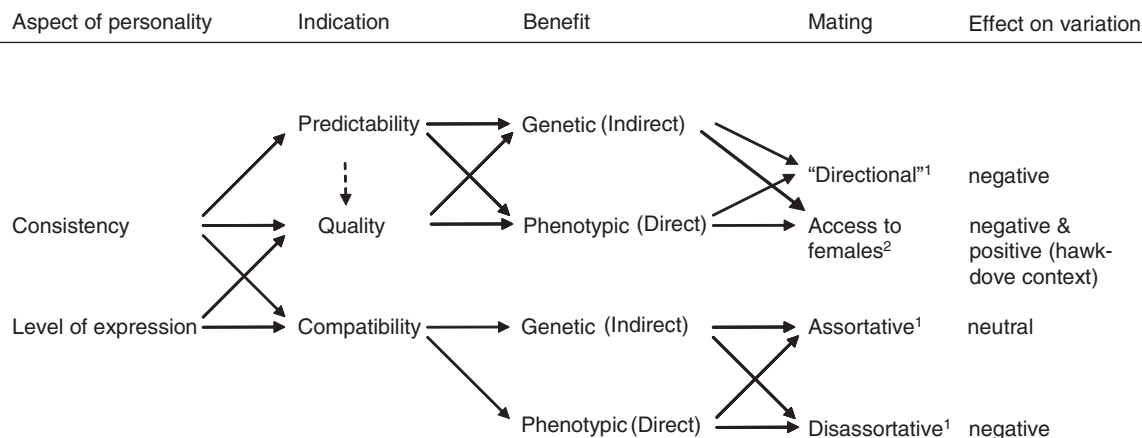


Fig. 1. Suggested framework for understanding sexual selection on personality, both behavioural consistency and variation in the level of behaviour. ¹ = selection *via* mate choice; ² = selection *via* male-male competition. For further details see text.

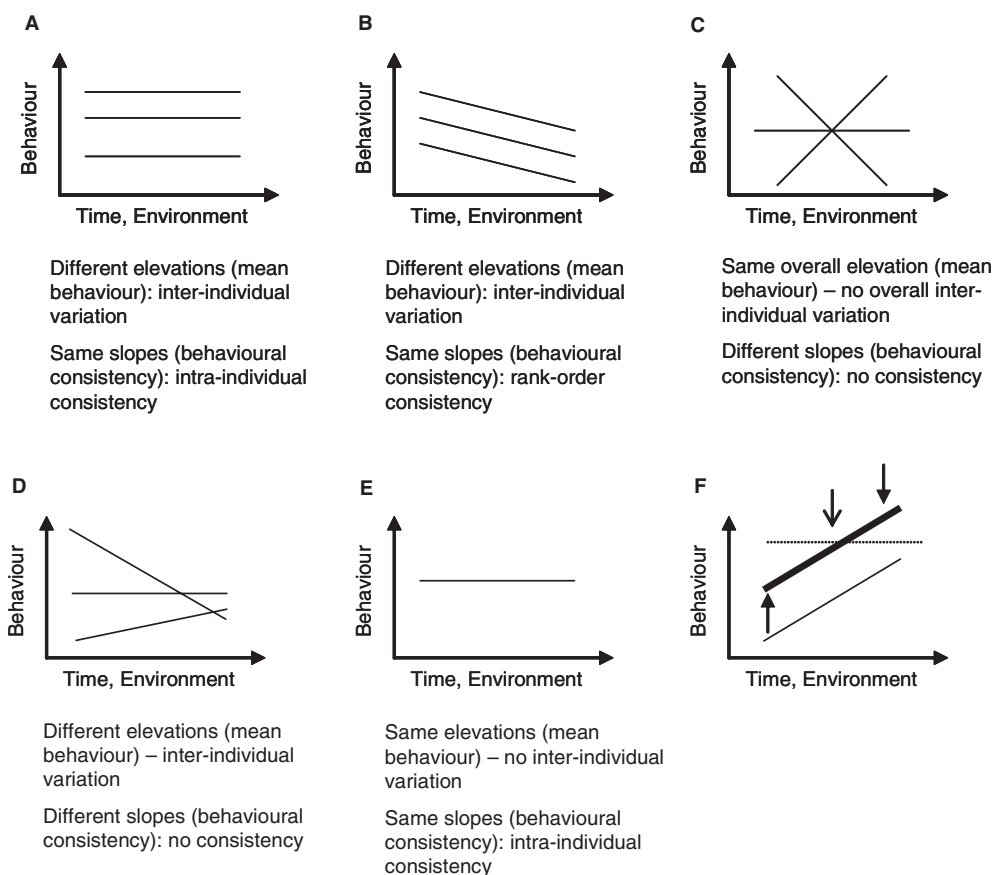


Fig. 2. Examples of phenotypic reaction norms across time or different environmental conditions (adapted from Pigliucci, 2001). Each line represents the behavioural phenotype expressed by one individual in one context at different times or across different contexts or situations. Each line is characterised by an elevation (mean behaviour) and a slope (behavioural consistency). Under scenarios A and B individuals differ consistently from each other in their behaviour, i.e. intra-individual and/or rank-order (at a population level) consistency is high *and* inter-individual variation is high: personality differences exist. C-E indicate either individual consistency and/or inter-individual variation is low: no personality differences are present. In F sexual selection could act on intra-individual consistency and/or inter-individual variation [selection pressures on the bold reaction norm line shown as arrows (filled arrow, pressure on slope; open arrow, pressure on mean level); resulting reaction norms: dotted line, from pressure on slope; thin line, from pressure on mean]. Note that the shape of selection pressures could be manifold, here we just present one possibility.

we critically evaluate how sexual selection has been used in psychology to explain sex differences in human behaviour. We begin with a short introduction to sexual selection and further details on the components of animal personality.

(3) Sexual selection

Sexual selection is caused by variation in reproductive success amongst individuals (Darwin, 1871; Andersson, 1994). Females typically produce far fewer gametes but invest more in each gamete than males. The greater is the investment of one sex into gametes and post-fertilization care (parental investment, see Trivers, 1972), the more selective such individuals should be in whom they mate with, and hence the greater the competition for matings in the less-investing sex (nearly always males: Darwin, 1871; Trivers, 1972; Andersson, 1994). The resulting competition for access to females leads usually to greater variance in reproductive success of males than of females.

(4) Personality, selection and reaction norms

Recently (but see Wilson *et al.*, 1994), empirical personality studies have started to use reaction norm approaches to quantify aspects of personality and selection pressures acting on personality (Sih *et al.*, 2004b; van Oers *et al.*, 2005; Penke *et al.*, 2007b; Réale *et al.*, 2007; Martin & Réale, 2008; Dingemanse *et al.*, 2009; Réale & Dingemanse, 2009). Reaction norms are used by evolutionary ecologists and quantitative geneticists to study phenotypic plasticity (e.g. in life-history traits) and underlying genetic mechanisms (e.g. Falconer & Mackay, 1996; Roff, 1997; Lynch & Walsh, 1998; Pigliucci, 2001; Brommer *et al.*, 2005; Nussey *et al.*, 2005a, b; Brommer, Rattiste & Wilson, 2008). A reaction norm is “the function that relates the environments to which a particular genotype is exposed and the phenotypes that can be produced by that genotype” (Pigliucci, 2001, p. 5). This function is characterised by an intercept and a slope but can have many shapes, although it is often simplified to a straight line (Pigliucci, 2001). “Genotype” in the definition of reaction norms would refer to “individual” in a personality approach and “environments” to either different environments (e.g. different contexts or situations) or a temporal scale (e.g. repeated tests of the same individuals in the same situation). The mean elevation of a reaction norm then shows the mean behaviour of an individual across environments and times and the slope indicates an individual’s degree of behavioural consistency (Fig. 2). Flat lines (Fig. 2A, E) and/or consistencies of the rank order of individuals across environments/time (Fig. 2B) indicate behavioural consistency (other shapes/types of consistency are possible, *cf.* signature of personality; Mischel, 2004). Consequently, a difference in the intercept of behavioural reaction norms of different individuals suggests inter-individual variation in the level of behaviour (Fig. 2A, B, D), a difference in the slopes suggests inter-individual variation in the degree of behavioural consistency (Fig. 2 C, D). Inter-individual differences in intercepts and/or slopes can be

statistically tested with general linear mixed-effects models (e.g. Martin & Réale, 2008, see below).

Roberts & DeVecchio (2000) identify different forms of consistency, two of which are relevant here. Intra-individual measures of consistency ask if an organism behaves in a stable manner over time or across different environments, whereas rank-order consistency refers to the relative placement of an individual within a group across behavioural tests. By analogy, consistency can be assessed either on a population level, often measured as repeatability (e.g. Sinn, While & Wapstra, 2008b, see Table 1) or as a rank correlation (rank-order consistency, e.g. Briffa, Rundle & Fryer, 2008; Sinn, Gosling & Moltschanivskyj, 2008a); or it can be evaluated on an individual level, for instance measured as a coefficient of variation (Cummings & Mollaghan, 2006; Schuett, 2008; W. Schuett, S.R.X. Dall & N.J. Royle, in preparation). While repeatability is a population characteristic estimating how much of the behavioural variation is due to intra- and inter-individual variation, other individual-based consistency indices and statistical approaches can be used to test specifically for inter-individual variation in consistency or inversely for the degree of intra-individual consistency (see above, and also Asendorpf, 1990; Dochtermann & Jenkins, 2007; Sinn *et al.*, 2008a; Réale & Dingemanse, 2009).

We leave it to the reader to think either in terms of reaction norm characteristics, i.e. elevation and slope, or in terms of intra-individual consistency and inter-individual variation in behaviour as characteristics of personality. For the purpose of this review we will not distinguish in detail between the different types of consistency, but collectively label them intra-individual consistency. However, we suggest that future empirical studies consider the appropriate measure of consistency and associated statistical approaches according to the specific research question. We suggest the reaction norm approach is valuable from an empirical perspective as it forces the researcher to quantify both key elements of animal personality, inter-individual variation and intra-individual consistency in behaviour over time/environments, simultaneously. Most of the examples we give below relate to consistency over time but the underlying rationale could similarly apply to consistency over contexts or across situations (i.e. environments).

The two main components of animal personality differences: behavioural consistency over time and/or different contexts (slope in a reaction norm approach) and variation in the level of behavioural expression (elevation in a reaction norm approach), are both likely to have heritable components. Consequently, sexual selection acting on these aspects is expected to result in evolution (see Fig. 1, Fig. 2F).

We hypothesize that (I) sexual selection has the potential both to generate and to maintain individual consistency in behaviour arising from non-random mate choice and/or male-male competition. On the other hand, we propose that (II) inter-individual variation in the level of behaviour will not be generated by sexual selection but only be maintained by the same, once variation is created by one or more of the other evolutionary processes detailed above.

Table 1. Selected studies investigating (a) sex differences, (b) inter-individual agreement, (c) inter-individual variation in mate choice, (d) influences of partners' personality and (e) assortative mate choice in/on the level (I) and consistency (II, only a & b) of behaviour

Species	Behavioural trait	Direction	N	Notes	Analyt. ^a	Effect on ^b	Study
I. Level of behaviour							
(a) Sex differences							
Midas cichlid (<i>Cichlasoma citrinellum</i>)	aggression	m > f	130f, 132m		KW		Holder <i>et al.</i> (1991)
Convict cichlid (<i>Cichlasoma nigrofasciatum</i>)	aggression	f > m	23f, 23m		Rep-AOV		Budaev <i>et al.</i> (1999)
Three-spined stickleback (<i>Gasterosteus aculeatus</i>)	aggression (median per group)	m > f	24 groups (8 groups each: 12f, 12m; 6f + 6m)		KW		Whoriskey (1991)
Prairie vole (<i>Microtus ochrogaster</i>)	aggression (proportion of individuals)	m > f	20f, 22m	^c	FET		Bales & Carter (2003)
Hooded Lister rat (<i>Rattus norvegicus</i>)	fearfulness	m > f	16f, 16m		AOV		Johnston & File (1991)
Roman rat (<i>Rattus norvegicus</i>)	fearfulness (41 variables in different tests)	m > f (for 14 variables) f > m (for 19 variables)	394–455f, 390–459m	for 33 variables $P < 0.05$; (for 8 variables m = f, $P > 0.05$)	AOV		Aguilar <i>et al.</i> (2003)
Convict cichlid (<i>Cichlasoma nigrofasciatum</i>)	risk-taking	m > f	10f, 10m		WT		Rangeley & Godin (1992)
Hooded Lister rat (<i>Rattus norvegicus</i>)	social behaviour (duration)	m > f	16f, 16m		Sp-AOV		Johnston & File (1991)
Prairie vole (<i>Microtus ochrogaster</i>)	social behaviour (proportion of individuals)	f > m	20f, 22m	^c	FET		Bales & Carter (2003)
Rodent species	parental responsiveness			review			Lonstein & De Vries (2000)
Human (<i>Homo sapiens</i>)	aggression (relational)	girls > boys	235f, 256m (4 age classes)		AOV		Crick & Grotpeter (1995)
Human (<i>Homo sapiens</i>)	aggression (overt)	boys > girls	235f, 256m (4 age classes)		AOV		Crick & Grotpeter (1995)
Human (<i>Homo sapiens</i>)	choosiness	f > m	334f, 134m		ACOV		Woodward & Richards (2005)

Table 1. (Cont.)

Species	Behavioural trait	Direction	<i>N</i>	Notes	Analyt. ^a	Effect on ^b	Study
Human (<i>Homo sapiens</i>)	emotional stability	m > f	59f, 59m? (dat); 106f, 105m (mar)		TT		Botwin <i>et al.</i> (1997)
Human (<i>Homo sapiens</i>)	exacting & choosiness	f > m	57f, 53m (dat); 104f, 103m (mar)		TT		Botwin <i>et al.</i> (1997)
Human (<i>Homo sapiens</i>)	humour (rate)	m > f	29 groups (each 6 persons, mixed & single sexcd)		GWM		Robinson & Smith-Lovin (2001)
Human (<i>Homo sapiens</i>)	humour successful (rate)	m > f	29 groups (each 6 persons, mixed & single sexcd)		GWM		Robinson & Smith-Lovin (2001)
Human (<i>Homo sapiens</i>)	intellect-openness	m > f	106f, 105m (mar)		TT		Botwin <i>et al.</i> (1997)
Human (<i>Homo sapiens</i>)	orientation (short-term)	m > f	133f, 131m		TT		Fetchenhauer & Rohde (2002)
Human (<i>Homo sapiens</i>)	preference for dominance	f > m	57f, 53m (dat); 104f, 103m (mar)		TT		Botwin <i>et al.</i> (1997)
Human (<i>Homo sapiens</i>)	preference for humour	f > m	74f, 55m (mar)		TT		Bressler <i>et al.</i> (2006)
Human (<i>Homo sapiens</i>)	production preference for humour	f > m	61f, 59m		TT		Bressler & Balshine (2006)
Human (<i>Homo sapiens</i>)	production preference for intellect-openness	f > m	57f, 53m (dat); 104f, 103m (mar)		TT		Botwin <i>et al.</i> (1997)
Human (<i>Homo sapiens</i>)	preference for surgency	f > m	57f, 53m (dat); 104f, 103m (mar)		TT		Botwin <i>et al.</i> (1997)

Table 1. (Cont.)

Species	Behavioural trait	Direction	<i>N</i>	Notes	Analyt. ^a	Effect on ^b	Study
Human (<i>Homo sapiens</i>)	preference for sense of humour	f > m	74f, 55m		T [†] T		Bressler <i>et al.</i> (2006)
Human (<i>Homo sapiens</i>)	response to partner's infidelity (sexual or emotional) risk-taking ToM (usage of affective state terms)	m more responsive to sexual, f more to emotional infidelity m > f girls > boys	128f, 128m		χ ² T		Shackelford <i>et al.</i> (2002)
Human (<i>Homo sapiens</i>)			133f, 131m		T [†] T		Fetchenhauer & Rohde (2002)
Human (<i>Homo sapiens</i>)			14f, 25m		T [†] T		Knickmeyer <i>et al.</i> (2006)
Human (<i>Homo sapiens</i>)	ToM (usage of neutral propositions) anxiety, assertiveness	boys > girls anxiety: f > m assertive.: m > f	14f, 25m 17729	meta-analyses; data from 68 studies, 105 samples; varying <i>N</i> for different behavioural traits	T [†] T		Knickmeyer <i>et al.</i> (2006) Feingold (1994)
Human (<i>Homo sapiens</i>)	aspects of FFM	anxiety: f > m assertive.: m > f gregarious: f > m trust: f > m tenderminded: f > m	105742	meta-analyses; varying <i>N</i> for different behavioural traits			Feingold (1994)

Table 1. (Cont.)

Species	Behavioural trait	Direction	<i>N</i>	Notes	Analyt. ^a	Effect on ^b	Study
Human (<i>Homo sapiens</i>)	aspects of FFM (30 facets)	m > f (for 3 facets) f > m (for 16 facets)	22642	meta-analyses; data from 29 human studies of 26 cultures; for 19 of 30 facets $P < 0.05$ cross-cultural & cross-age review			Costa <i>et al.</i> (2001)
Human (<i>Homo sapiens</i>)	aggression (overt)	m > f					Campbell (1999)
Human (<i>Homo sapiens</i>)	aggression (relational)	f > m		review			Campbell (1999)
Human (<i>Homo sapiens</i>)	different behaviours			review			Buss (1995)
Human (<i>Homo sapiens</i>)	humour (appreciation)	f > m		review			Kaufman <i>et al.</i> (2008)
Human (<i>Homo sapiens</i>)	social cognition			review			Geary (2002)
Human (<i>Homo sapiens</i>)	vulnerability to social stress	f > m		review			Troisi (2001)
(b) Inter-individual agreement in mate choice							
Midas cichlid (<i>Cichlasoma citrinellum</i>)	aggression	h > l		review		f-MC, not m-MC	Barlow (1986)
Fighting fish (<i>Betta splendens</i>)	aggression (winner/loser)	h > l (winner > loser)	20f		WT	f-MC	Doutrelant & McGregor (2000)
Japanese quail (<i>Coturnix japonica</i>)	aggression ^c	l > h	37f, 34m		TT	f-MC	Ophir & Galef (2003)
Japanese quail (<i>Coturnix japonica</i>)	aggression ^c	l = unknown > h	20f, 25m	f could choose b/w known aggressive/unaggressive & unknown m	TT	f-MC	Ophir <i>et al.</i> (2005)
Prairie vole (<i>Microtus ochragaster</i>)	aggression (towards f)	h = l	15 trials		TT	not f-MC	Ophir <i>et al.</i> (2008)

Table 1. (Cont.)

Species	Behavioural trait	Direction	N	Notes	Analyt. ^a	Effect on ^b	Study
Trinidadian guppy (<i>Poecilia reticulata</i>)	boldness towards predator (courtship inhibited)	h > l	20f		BT	f-MC	Godin & Dugatkin (1996)
Trinidadian guppy (<i>Poecilia reticulata</i>)	boldness towards predator (courtship possible)	h > l	20f		BT	f-MC	Godin & Dugatkin (1996)
Collared flycatcher (<i>Ficedula albicollis</i>)	song post distance (relative to source of risk)	h > l ^d	16m		PP-COR	time to pair bond	Garamszegi <i>et al.</i> (2008)
Human (<i>Homo sapiens</i>)	humour appreciation (receptivity to humour)	h > l	74f, 55m		TT	f-MC, m-MC	Bressler <i>et al.</i> (2006)
Human (<i>Homo sapiens</i>)	humour (production)	h > l	74f, 55m		TT	f-MC, not m-MC	Bressler <i>et al.</i> (2006)
Human (<i>Homo sapiens</i>)	humour	h > l	61f, 59m		TT	f-MC, not m-MC	Bressler & Balshine (2006)
Human (<i>Homo sapiens</i>)	humour (sense of)	h > l	74f, 55m		TT	f-MC, m-MC	Bressler <i>et al.</i> (2006)
Human (<i>Homo sapiens</i>)	moral virtues			review			Miller (2007)
(c) Inter-individual variation in mate choice	aggression		102f		REP1	f-MC	Forstmeier & Birkhead (2004)
Zebra finch (<i>Taeniopygia guttata</i>)	exploration		18m (10FE, 8 SE)		WT	m-MC	Groothuis & Carere (2005)
Zebra finch (<i>Taeniopygia guttata</i>)	song rate		83f		REP1	f-MC1	Forstmeier & Birkhead (2004)

Table 1. (Cont.)

Species	Behavioural trait	Direction	<i>N</i>	Notes	Analyt. ^a	Effect on ^b	Study
(d) Partners' personality and reproductive success							
Convict cichlid (<i>Cichlasoma nigrofasciatum</i>)	aggression (latency to approach mirror)	ass > nona**	23 pairs (sp: 13, n-sp: 10)	sp: $r = 0.52$, $P = 0.044$; n-sp: $r = ?$, $P > 0.05$	S-COR	RS (spawning: y/n)	Budaev <i>et al.</i> (1999)
Cockatiel (<i>Nymphicus hollandicus</i>)	behavioural compatibility b/w partners	h > l	21 pairs (5 w/o, 16 w eggs)		MWU	RS (egg laying: y/n)	Spoon <i>et al.</i> (2006)
Cockatiel (<i>Nymphicus hollandicus</i>)	behavioural compatibility b/w partners	h > l	21 pairs		S-COR	RS (no. chicks reared to independence)	Spoon <i>et al.</i> (2006)
Cockatiel (<i>Nymphicus hollandicus</i>)	behavioural compatibility b/w partners	h > l	14 pairs		S-COR	RS (hatching success of fertile eggs)	Spoon <i>et al.</i> (2006)
Cockatiel (<i>Nymphicus hollandicus</i>)	behavioural compatibility b/w partners	l > h	21 pairs		MWU	EPC (y/n)	Spoon <i>et al.</i> (2007)
Dumpling squid (<i>Euprymna tasmanica</i>)	boldness (foraging test)	ass > nona (for intermediate & bold f)	92 mating attempts		S-COR	RS (proportion successful reproduction)	Sinn <i>et al.</i> (2006)
Great tit (<i>Parus major</i>)	exploration	ass > nona	69 pairs		GLM, GLMM	EPP	van Oers <i>et al.</i> (2008)
Great tit (<i>Parus major</i>)	exploration	ass > nona	141 pairs?		GLM	RS (fledgling condition)	Both <i>et al.</i> (2005)
Great tit (<i>Parus major</i>)	exploration	ass > nona	44 pairs		GLM	RS (no. of recruits)	Dingemans <i>et al.</i> (2004)
Convict cichlid (<i>Cichlasoma nigrofasciatum</i>)	exploration (latency to enter novel area)	ass > nona**	23 pairs (sp: 13, n-sp: 10)	sp: $W = 456$, $P = 0.044$; n-sp: $W = ?$, $P > 0.05$	KT	RS (spawning: y/n)	Budaev <i>et al.</i> (1999)
Convict cichlid (<i>Cichlasoma nigrofasciatum</i>)	exploration (activity in novel area; PCA comp.)	ass > nona**	23 pairs (sp: 13 n-sp: 10)	sp: $r = 0.57$, $P = 0.029$; n-sp: $r = 0.03$, $P = 0.473$	S-COR	RS (spawning: y/n)	Budaev <i>et al.</i> (1999)

Table 1. (Cont.)

Species	Behavioural trait	Direction	N	Notes	Analyt. ^a	Effect on ^b	Study
Convict cichlid (<i>Cichlasoma nigrofasciatum</i>)	general (activity in novel area, response to novel fish; PCA comp.)	ass > nona**	23 pairs (sp); 13 n-sp: 10)	sp: $r = 0.49$, $P = 0.047$; n-sp: $r = -0.31$, $P = 0.193$	S-COR	RS (spawning: y/n)	Budaev <i>et al.</i> (1999)
(e) Behaviourally assortative partnerships Great tit (<i>Parus major</i>)	exploration	negative	100 pairs?	if m older than 1 year	ACOV		Dingemans <i>et al.</i> (2004)
Human (<i>Homo sapiens</i>)	agreeableness	positive	59 pairs? (dat); 107 pairs? (mar)		COR		Botwin <i>et al.</i> (1997)
Human (<i>Homo sapiens</i>)	broad interests (openness)	positive	85 pairs (mar)	analyses w/o & w controlling for age & attractiveness	P-COR		Little <i>et al.</i> (2006)
Human (<i>Homo sapiens</i>)	conscientiousness	positive	65 pairs (mar)		P-COR		Little <i>et al.</i> (2006)
Human (<i>Homo sapiens</i>)	conscientiousness	positive	59 pairs? (dat); 107 pairs? (mar)		COR		Botwin <i>et al.</i> (1997)
Human (<i>Homo sapiens</i>)	extraversion	positive	65 pairs (mar)		P-COR		Little <i>et al.</i> (2006)
Human (<i>Homo sapiens</i>)	(intellect)- openness	positive	59 pairs? (dat); 107 pairs? (mar)		COR		Botwin <i>et al.</i> (1997)
Human (<i>Homo sapiens</i>)	multiple personality measures	positive, (negative)	93 pairs (mar)	32 out of 93 correlations $P < 0.05$ (30 positive, 2 negative)	COR		Buss (1984)
Human (<i>Homo sapiens</i>)	personality (measured using BFI)	positive	66 pairs (dat)		TT, COR		Gonzaga <i>et al.</i> (2007)

Table 1. (Cont.)

Species	Behavioural trait	Direction	N	Notes	Analyt. ^a	Effect on ^b	Study
Human (<i>Homo sapiens</i>)	personality (measured using NEO)	positive	172 pairs (mar)	in 14 out of 16 studies assessed: all analyses supported	TT, COR		Gonzaga <i>et al.</i> (2007)
Human (<i>Homo sapiens</i>)	behaviour (agreeableness)	positive		assortative mating b/w partners for measured problem behaviours (1 found support for social homogamy, 1 no analyses revealed significant ass mating) review			Rhule-Louie & McMahon (2007)
Human (<i>Homo sapiens</i>)	different behaviours						Vandenberg (1972)
II. Consistency of behaviour							
(a) Sex differences							
Three-spined stickleback (<i>Gasterosteus aculeatus</i>)	aggression	f > m**	20 juvenile f, 18 juvenile m	f: $r = 0.65$, $P < 0.01$; m: $r = 0.37$, $P < 0.01$;	REP		Bakker (1986)
Three-spined stickleback (<i>Gasterosteus aculeatus</i>)	aggression	f > m**	19 f, 19(20) m	f: $r = 0.77$, $P < 0.01$; m(territorial aggr.): $r = 0.62$, $P < 0.01$; m(courtship aggr.): $r = 0.54$, $P < 0.01$	REP		Bakker (1986)

Table 1. (Cont.)

Species	Behavioural trait	Direction	<i>N</i>	Notes	Analyt. ^a	Effect on ^b	Study
Midas cichlid (<i>Cichlasoma citrinellum</i>)	aggression (y/n)	m > f**	14f, 14m	f: $P < 0.05$ m: $P > 0.05$ ($P < 0.05$ indicates instability) data from 2 sites	CQJ		Holder <i>et al.</i> (1991)
Great tit (<i>Parus major</i>)	exploration	f = m	74f, 111m; 11f, 22m 12f, 12m		REP2		Dingemans <i>et al.</i> (2002)
Zebra finch (<i>Taeniopygia guttata</i>)	exploration	m > f			REP3		Schuett & Dall (2009)
Zebra finch (<i>Taeniopygia guttata</i>)	foraging (time spent)	f > m*	9f, 9m	$P = 0.067$	REP3		Schuett & Dall (2009)
Zebra finch (<i>Taeniopygia guttata</i>)	foraging w partner (relative time)	m > f*	9f, 9m	$P = 0.057$	REP3		Schuett & Dall (2009)
Zebra finch (<i>Taeniopygia guttata</i>)	leadings (no. of)	f = m	9f, 9m		REP3		Schuett & Dall (2009)
Zebra finch (<i>Taeniopygia guttata</i>)	latency to approach feeder	f = m	9f, 9m		REP3		Schuett & Dall (2009)
Convict cichlid (<i>Cichlasoma nigrofasciatum</i>)	parental care (activity)	m = f**	13f, 13m	f: $\alpha = 0.78$; m: $\alpha = 0.77$	α		Budaev <i>et al.</i> (1999) ^f
Convict cichlid (<i>Cichlasoma nigrofasciatum</i>)	parental care (brood provisioning)	f > m**	13f, 13m	f: $\alpha = 0.90$; m: $\alpha = 0.83$	α		Budaev <i>et al.</i> (1999) ^f
Long-tailed tit (<i>Aegithalos caedatus</i>)	parental care (brood provisioning)	m > f**	10f, 16m	f: $r = 0.37$, $P = ?$; m: $r =$ 0.7 , $P = ?$,	REP		MacColl & Hatchwell (2003) ^f
House sparrow (<i>Passer domesticus</i>)	parental care (feeding rate per chick)	m > f	10-37f, 17-37m (different years, time span, adjust- ments)		REP4		Nakagawa <i>et al.</i> (2007a) ^f

Table 1. (Cont.)

Species	Behavioural trait	Direction	<i>N</i>	Notes	Analyt. ^a	Effect on ^b	Study
House sparrow (<i>Passer domesticus</i>)	parental care (incubation time)	m = f	18-60f, 24-61m (different years, time span, adjust- ments)		REP4		Nakagawa <i>et al.</i> (2007a) ^f
House sparrow (<i>Passer domesticus</i>)	parental care (delivery rate)	m > f**	23f, 30m	f: $r \pm$ S.E.M. = -0.057 \pm 0.2, $P = 0.605$; m: $r \pm$ S.E.M. = 0.375 \pm 0.16, $P = 0.018$	REP		Schwagmeyer & Mock (2003) ^f
House sparrow (<i>Passer domesticus</i>)	parental care (delivery rate, adjusted for brood size & date)	m > f**	23f, 30m	f: $r \pm$ S.E.M. = 0.076 \pm 0.2, $P = 0.64$; m: $r \pm$ S.E.M. = 0.436 \pm 0.15, $P = 0.008$	REP		Schwagmeyer & Mock (2003)
Savannah sparrow (<i>Passerculus sandwichensis</i>)	parental care (feeding rate)	m > f**	19f, 14m	f: $r = 0.20$, $P = 0.083$; m: $r = 0.60$, $P = 0.012$	REP		Freeman-Gallant & Rothstein (1999) ^f
Montandon's newt (<i>Triturus montandoni</i>)	sexual behaviour (duration pre-mating)		15f, 7m	neither f nor m consistent	REP		Michalak (1996)
Montandon's newt (<i>Triturus montandoni</i>)	sexual behaviour (timing 1 st sper- matophore transfer)		14f, 4m	neither f nor m consistent	REP		Michalak (1996)

Table 1. (Cont.)

Species	Behavioural trait	Direction	N	Notes	Analyt. ^a	Effect on ^b	Study
Montandon's newt (<i>Triturus montandoni</i>)	sexual behaviour (no. spermatozoa deposited/picked up)		15f, 7m	neither f nor m consistent	REP		Michalak (1996)
(b) Consistency as indicator of quality							
Chestnut-sided warblers (<i>Dendroica pensylvanica</i>)	5 song variables (coefficients of variation)	h > l	20 cases of extrapair offspring		TT	extra-pair success (paternity winner vs loser)	Byers (2007)
Banded wren (<i>Thryothorus pleurostictus</i>)	song variable (trill)	h = l (playback)	22m		GLM	time spent close to (high/low-consistent playback) m song rate towards (high/low-consistent) playback	de Kort <i>et al.</i> (2009)
Banded wren (<i>Thryothorus pleurostictus</i>)	song variable (trill)	l > h (playback)	22m		GLM		de Kort <i>et al.</i> (2009)
Mockingbird (<i>Mimus gilvus</i>)	song variable (syllable)	h > l	32m		Log-R ^g	RS	Botero <i>et al.</i> (2009)

For sex differences in the level of behaviour and behaviourally assortative partnerships: only significant results and only a selection of studies are reported due to the vast number of studies published with these aspects. Aggr.: aggression; ass: assertive; assertive.: assertiveness; BFI: Big Five Inventory; b/w: between; dat: dating couple; f: female; FE: fast explorers; FFM: Five Factor Model; gregarious.: gregariousness; h: high; l: low; m: male; mar: married couple; NEO: Neuroticism-Extraversion-Openness Personality Inventory; no.: number of; nona: nonassertive; n-sp: non-spawning; PCA comp.: Principle Component Analysis component; SE: slow explorers; sp: spawning; tendermind: tender-mindedness; ToM: theory of mind; w: with; w/o: without; y/n: yes/no, binary variable; *: trend; **: not statistically tested.

^a**Analyt.:** analytical methods; ANCOV: ANCOVA; α : Cronbach alpha; AOV: ANOVA; BT: binomial test; χ T: χ^2 -test; COR: correlation; CQT: Cochran Q test; FET: Fisher's exact test; GLM: generalized linear model; GLMM: generalized linear mixed model; GWM: generalized Weibull model; KT: Krauth test; KW: Kruskal-Wallis test; Log-R: logistic regression; MWU: Mann-Whitney U test; P-COR: Pearson's product moment coefficients; PP-COR: partial correlation; Rep-AOV: repeated ANOVA; REP: repeatability; REP1: repeatability of female preference function; REP2: repeatabilities for sexes compared using *F*-statistics; REP3: repeatabilities for the sexes *z*-transformed and compared; REP4: repeatabilities compared with a type of paired *t*-test using linear mixed models; S-COR: Spearman rank correlation; Sp-AOV: split-plot ANOVA; TT: *t*-test; WT: Wilcoxon test.

^b**Effect on:** EPC: extra-pair copulation; EPP: extra-pair paternity rate; f-MC: female mate choice; f-MC1: female mate choice, dependent on females' activity tendency; m-MC: male mate choice; RS: reproductive success.

^cThe percentage of individuals displaying the behaviour of interest at least once was tested for sex differences, not the mean values.

^dIndividuals that were exploratory and/or risk-takers sung from lower posts when a human was around. These individuals bonded faster with a partner than individuals singing from higher posts.

^eAggression in Japanese quail is a predictor of winning fights (see Ophir & Galef, 2003; Ophir *et al.*, 2005 and literature therein).

^fStudies whose data was used in the meta-analysis carried out on sex differences in behavioural consistency of parental care.

^gIndirect support: alpha males were more consistent than beta males (logistic regression) and all (but one) offspring were produced by alpha males.

In the following we outline how sexual selection can generate and maintain animal personality, starting with inter-individual variation in the level of behavioural expression (elevation) as this is the component of personality differences to which nearly all attention from a sexual selection perspective has been paid. An overview of the studies discussed is provided in Table 1. In this review, we will not consider further alternative mating tactics of individuals within one sex (i.e. discrete differences in mating behaviour, e.g. sneaker *versus* fighter males) and how they are influenced by sexual selection. This is for several reasons. Firstly, several excellent reviews on these alternative reproductive strategies exist already (e.g. Andersson, 1994; Gross, 1996; Brockmann, 2001), highlighting that different tactics are often associated with certain behavioural features (e.g. for sneaker males it is not adaptive to be aggressive, whereas for territorial males it can be). Secondly, alternative reproductive tactics are often also associated with different morphological, physiological and/or life-history traits. These phenotypic constraints in themselves frequently explain why males following varying tactics differ consistently in their behaviour (e.g. sneaker males are often much smaller than territorial males and would therefore be unlikely to be successful in an escalating fight over access to a mate and hence are expected to be consistently less aggressive). Finally, we refer readers interested in the link between personality and discrete alternative mating strategies to recent publications by Réale & Dingemans (2009) and Sih & Bell (2008).

II. SELECTION FOR LEVEL OF BEHAVIOURAL EXPRESSION

(1) Sex differences in the level of behaviour in animals and humans

Because sexual selection results in different selection pressures acting on males and females that manifest in sex differences for those traits under selection, for instance in body size or visual ornaments (Andersson, 1994), a first indication of a role of sexual selection on behavioural traits could be sex differences in behavioural expression (for other processes generating sex differences see Blanckenhorn, 2005; Fairbairn, Blanckenhorn & Székely, 2007).

As summarised in Table 1, there is evidence from numerous studies that males and females, both in humans and other animals, can differ in the mean level of their behavioural expression (the mean elevation of each sex). These sex differences occur in a variety of behaviours, ranging from aggression to fearfulness (see Table 1), and along different axes of human personality which is categorised into five dimensions (Five-Factor Model: Openness, Conscientiousness, Extraversion, Agreeableness, Neuroticism, see McCrae & Costa, 1999). Several frameworks based on sexual selection have been suggested in the human literature to explain why men and women differ in their mean behaviour (e.g. Buss, 1995; Troisi, 2001; Geary, 2002; Miller, 2007). These

frameworks, along with the empirical studies from which they are derived, have often been criticised as “just-so-stories” because interpretations are made *post-hoc* and are not based on results obtained from experiments with clear theory-driven predictions (Geary, 2002). Also, the frequent use of self-reported questionnaires has been criticised where self-assessment may not reflect actual personality traits (see Penke, Denissen & Miller, 2007a) or where self-assessment ability may differ among people of varying personalities (see, for similar potential biases in animal studies, Biro & Dingemans, 2009). Finally, there is one general problem with studies exclusively investigating differences between the mean behaviour levels of males and females: these mean differences do not necessarily imply that males and females differ in their personalities. Only when there are sex differences in behavioural consistency and/or inter-individual variation in the level of behaviour can we really talk about sex differences in personality.

We suggest, therefore, for future studies more rigorous prediction testing (e.g. derived from the existing frameworks). Some recent human studies have applied experimental approaches, avoiding the potential problems of questionnaires (e.g. Bressler & Balshine, 2006; Knickmeyer *et al.*, 2006). Further approaches could involve assigning people to behavioural tasks (e.g. play-acting, participation in a manipulated quiz-show or a Prisoner’s dilemma game, *cf.* Wedekind & Milinski, 1996) and then measuring their behavioural responses (e.g. risk-taking or degree of cooperation) in an objective way. Subsequent analyses should not only involve testing for sex differences in the mean behaviour *per se* but also in inter-individual variation in the level of behaviour and in their levels of behavioural consistency. The latter could involve consistency over time and/or different contexts, such as sex differences across personality dimensions in humans.

(2) Mate choice and personality traits

A number of mechanisms that could drive the evolution of mate choice have been discussed (e.g. Andersson, 1994; Kokko *et al.*, 2003; Andersson & Simmons, 2006). Proposed mechanisms of mate choice involve either direct benefits (females prefer male traits reflecting his ability to supply material benefits, like food or paternal care, e.g. Møller & Jennions, 2001), or indirect benefits (females prefer males that have genes that increase fitness of offspring). Indirect benefits may occur because sons are more attractive (Fisher, 1930) or because offspring are more viable in general (Zahavi, 1975). Higher offspring fitness may occur either because some males have genes that code for intrinsically superior phenotype offspring, or because some male genomes are more compatible with particular female genomes (genetic compatibility, e.g. Tregenza & Wedell, 2000). Hence, sexual selection can generate similar mate preferences across females or preferences that differ among females according to their compatibility with particular males. For the purpose of this review we will refer to male (behavioural) traits that lead to direct or indirect benefits for females collectively as indicators of quality and will consider them separately from

traits that are beneficial for just particular females (due to some sort of compatibility).

(3) Female preference for male behavioural traits: inter-individual agreement

If some male behavioural traits signal their quality—for instance their parental abilities or genetic quality—we expect consistent female preferences for these traits (assuming that all females have the same ability to assess benefits gained by choosing a certain male), resulting in inter-individual agreement in choice, and selection for these behaviours, or levels of behavioural expression. If these behavioural expressions are costly to produce (which is normally assumed if a trait signals quality reliably; Zahavi & Zahavi, 1997), then we also expect variation in males' expression of these behavioural traits, as not all males can afford to display the signal due to quality differences.

Miller (2007) expands previous researchers' ideas (e.g. Darwin, 1871) that many human moral virtues have been sexually selected as costly signals. According to this argument, moral virtues are predicted to signal either genetic quality in that genes that are associated with generally higher fitness might be required for showing moral virtues like a “sophisticated, empathetic social intelligence”; or to signal good parental abilities (which may have genetic and environmental components) which are predicted to be indicated by empathic personality traits as they could help during caring for offspring; or signal good partner skills, which lead to mutual benefits and effective coordination in long-lasting partnerships (Miller, 2007).

Miller's idea is supported by empirical studies demonstrating that many moral traits are sexually attractive and could be indicators of mental fitness as well as genetic quality and parental quality (reviewed in Miller, 2007). As a number of studies have been published with regard to humour and mate choice in humans and humour has been shown to be correlated to health (Thorson *et al.*, 1997; Celso, Ebener & Burkhead, 2003; Boyle & Joss-Reid, 2004), we can use their findings to apply Miller's (2007) ideas. If humour indicates quality, and women are the choosier sex, we not only expect males to invest more into showing humour but also females to respond more to humour, for instance with laughter (Kaufman *et al.*, 2008). Furthermore, females should prefer males showing a higher level of humour as partners. As predicted, males use humour more often than females (McGhee, 1979; Myers, Ropog & Rodgers, 1997; Robinson & Smith-Lovin, 2001), and females appreciate humour more by laughing more than men do (Kaufman *et al.*, 2008). Also, males prefer females who are receptive to their own humour, whereas females prefer a partner that produces humour (Bressler, Martin & Balshine, 2006). Similarly, in a study, in which humour of persons was experimentally manipulated, Bressler & Balshine (2006) demonstrated that only females preferred humorous-appearing persons as partners for relationships.

For future research, it would be desirable to show experimentally that humour is indeed a quality indicator, e.g.

that its correlation to health is not just a neutral by-product of an adaptation or a confounding factor (see general discussion in e.g. Buss & Greiling, 1999). This could be done for instance by quantifying costs related to humour production or by showing that humour has reproductive consequences. Also, consistent behavioural differences in humour traits need to be demonstrated for classification as personality traits (see above). It may be also worth considering in more detail that for instance social intelligence may not only be important for parental abilities and parental cooperation but could also be used in deceptive and manipulative ways, leading to a trade-off during mate choice with respect to that trait.

From animal studies there is indirect support for the hypothesis that personality traits can signal male quality to a female from a study of collared flycatchers, *Ficedula albicollis*, (Garamszegi, Eens & Torok, 2008; Table 1). Risk-taking and exploratory male collared flycatchers consistently sang from a lower song post when an observer was nearby than risk-averse or less exploratory males. These bold males singing from lower posts bonded relatively faster with a partner than individuals singing from higher posts. This could indicate (among other possibilities) that males on the lower posts were of superior quality or likely to commit more to raising offspring as risk-takers are likely to have lower prospects for future reproduction (Wolf *et al.*, 2007; but see e.g. Nettle, 2005 for potential for reduced parental care by extraverts).

More evidence for mate choice based on non-sexual personality traits is provided in an elegant study by Godin & Dugatkin (1996). After showing that female Trinidadian guppies, *Poecilia reticulata*, prefer males that have conspicuous colour patterns and that behave boldly towards a predator (both traits were positively correlated), the authors demonstrated that when appearance and behavioural effects are disentangled experimentally, females show preferences for males behaving boldly towards a predator, regardless of their colour patterns. These results support the hypothesis that behaviour (here: boldness) can be an honest signal of quality - which is used in mate choice by females - particularly when considering that bold males feed at a higher rate (Murphy & Pitcher, 1991; Godin & Crossman, 1994) and are more likely to survive an approach by a predator than shy individuals (Godin & Davis, 1995). Thus, it seems that only high-quality males can pay the costs of approaching predators (e.g. costs related to the risk and energy demands, predator inspection is reviewed in Dugatkin & Godin, 1992) and therefore advertise their quality to their mates by being bold (for further discussion see Dugatkin & Godin, 1992; Godin & Davis, 1995). This is underpinned by the fact that the level of risky predator inspection shows significant inter-individual variability in guppies (Dugatkin & Alfieri, 1991).

Further support for female mate choice on the basis of male behaviour comes from studies on the biparental and socially monogamous Midas cichlids, *Cichlasoma citrinellum* (see Table 1): male Midas cichlids show a higher level of among-individual variation in aggressiveness than females (Holder,

Barlow & Francis, 1991). This could indicate that the level of male aggressiveness is under sexual selection, particularly as females prefer aggressive over non-aggressive males (Barlow, 1986). Males on the other hand do not discriminate among females based on their aggression (Barlow, 1986). Furthermore, partnerships with aggressive males are more successful in establishing and maintaining a breeding territory and better in guarding their young (Rogers, 1985). Contrary to males, females are all similarly aggressive when caring for young and are all effective parents (discussed in Barlow, 1986). Similarly, female fighting fish, *Betta splendens*, prefer males they have seen winning an aggressive interaction over losers (Doutrelant & McGregor, 2000). Males in this species provide parental care, such as aggressive defence of their broods against intruders (Jaroensutasinee & Jaroensutasinee, 2003). Thus, female fighting fish are likely to use information on a male's aggression during male-male encounters as a predictor of male's aggression in a parental context: defence of offspring. Indeed, male prairie voles, *Microtus ochrogaster*, that behave more aggressively towards females during mate choice show more parental care and less aggression towards offspring than males that are less aggressive towards potential female mates (Ophir *et al.*, 2008). The mate choice of female prairie voles, however, is independent of the degree of female-directed aggression (Ophir *et al.*, 2008). In contrast to female Midas cichlids and fighting fish, female Japanese quails, *Coturnix japonica*, prefer less aggressive males (Ophir & Galef, 2003). Ophir & Galef (2003) allowed females to observe aggressive interactions between dyads of males, before they could choose between the previously presented males. Females spent a significantly higher proportion of time (a measurement of sexual preference, White & Galef, 1999) next to the males which had been the less aggressive ones (the losers) in male dyads. This effect was only evident if females actually observed the aggressive encounters, not if they only chose between losers and winners whose interactions they had not watched. In further experiments the authors (Ophir & Galef, 2003) showed that mate choice results were not confounded by males reacting to the choosing female during the aggressive encounters. Therefore, female preferences reported were a result of a choice based on aggression *per se* rather than a choice based on any behavioural changes of the males due to the outcome (i.e. win or loss). Finally, male aggressive behaviour during male encounters was a predictor of the extent to which males expressed (potentially) harmful behaviours (e.g. aggressive pecking) towards the female in a mate-choice context (Ophir & Galef, 2003). These findings suggest that female quail (a) use information from aggressive male interactions about which males are likely to sexually harass and harm them (dominant ones) and avoid these males; therefore, (b) basing their choice on male context-consistency in aggression. Further investigations have confirmed that female quail do not choose less aggressive males (they are indifferent to known less aggressive males and unfamiliar males) but rather avoid more aggressive males (Ophir, Persaud & Galef, 2005), which fits with the notion that the female quail avoid sexual coercion by males.

In contrast to Midas cichlids and fighting fish, Japanese quail have a promiscuous breeding system, in which females have been reported to perform all parental care themselves (Mills *et al.*, 1997). Consequently, reproductive payoffs - i.e. the relationship between costs (e.g. risk of injury or disease transmission from mating) and benefits (e.g. paternal care, good genes) of mating with a male - in relation to the level of male aggression (or other behaviours) may differ (a) for females of different species with contrasting life histories (Qvarnström & Forsgren, 1998), (b) for females of different personalities (see below), or (c) depending on the frequencies of different male personalities in the population (e.g. Gross, 1996; Dennenmoser & Thiel, 2008). More research is needed to test these ideas directly.

(4) Female preference for male behavioural traits: inter-individual variation

Individual female guppies are consistent in their choice of male colouration but differ from one another in their preference, despite an overall preference for more conspicuous males (Godin & Dugatkin, 1995). Similarly, Forstmeier & Birkhead (2004) demonstrate that captive female zebra finches, *Taeniopygia guttata*, are consistent in their preference for male behavioural traits, namely song rate and aggression. However, some females consistently prefer males with high song rates, others prefer males with low song rates, some prefer highly aggressive and others less aggressive males. Why do females differ consistently in their choice? If song rate or level of aggression is a sign of quality, then we would expect all females to prefer the same expression of the trait, i.e. the quality reflecting trait expression. Only if females had different abilities to assess and identify the high quality signal or if they differed in their choosiness, would we predict individual females to differ in their preference. Indeed, there is some evidence that females vary consistently in their choosiness: individual females are consistent in their inclination to copulate with a male (Forstmeier, 2004, 2007) as well as in their time allocation to the preferred male during mate-choice trials (Forstmeier & Birkhead, 2004). If some females are less accurate in their assessment abilities or if some females are less choosy, such females should not be consistent in their choice. Rather, what seems likely is that a female's personality plays a role in choosing a mate. Indeed, Forstmeier & Birkhead (2004) found evidence that females that spent more time approaching available males during mate-choice trials preferred males that sung at higher rates. It should be noted that both the female tendency to approach males (Forstmeier & Birkhead, 2004) and male song rate (as well as male aggression, Forstmeier, 2004, 2007; Forstmeier, Coltman & Birkhead, 2004) can be considered personality traits in zebra finches as individuals differ consistently from one another in these behaviours.

To our knowledge, there are only two other studies published on non-human animals that have considered the personality of not only the chosen but also the choosing individuals during mate choice (Groothuis & Carere, 2005; Schuett, 2008). In the first, male great tits, *Parus major*, from

bi-directional selected lines for fast *versus* slow exploration (Drent, van Oers & van Noordwijk, 2003) were assayed for their preference for females (also originating from these two selection lines). Males of the fast line expressed preference for similar females, whereas males of the slow line did not display preferences for females of either line (Groothuis & Carere, 2005). Similarly, moderately or highly exploratory female zebra finches prefer males that appear to be exploratory (male exploration manipulated); less exploratory females on the other hand show no preference for males manipulated to appear either exploratory or non-exploratory (Schuett, 2008; W. Schuett, J-G.J. Godin & S.R.X. Dall, in preparation). These studies (and the studies outlined below, indicating similar consequences for patterns of reproductive success) raise two questions: why do some individuals mate assortatively, and why do all individuals not mate assortatively? High exploration levels could signal high quality in general (as discussed above for male risk-taking behaviour) or high-quality parental care (due to context consistency), therefore all individuals should prefer fast explorers as mates. At the same time mating with the same personality type may have advantages (see below), resulting in a trade-off in choice for slow-exploring individuals. Also, slow-exploring individuals might need longer to assess a prospective mate's behavioural type accurately, or may have a smaller time horizon for making a mate-choice decision for instance due to being more easily distracted. This could be the case if slow-exploring individuals, which have been shown also to be risk averse (in great tits: van Oers *et al.*, 2004a; in zebra finches: Schuett & Dall, 2009), invest more time in information-gathering to decrease the risk (see also Dall & Johnstone, 2002), leaving less time to invest in mate choice. Finally, underlying genetic mechanisms may drive these patterns. For instance there is substantial additive genetic variation for exploration and boldness in great tits but also considerable genetic dominance, with low boldness and exploration being dominant over high boldness and exploration, respectively (van Oers *et al.*, 2004b). Clearly, more work is needed to shed further light on preference patterns and their underlying genetic mechanisms. However, what is clear from these studies on great tits and zebra finches is that behavioural traits both of the choosy and the chosen sex have an impact on mate choice, and so sexual selection is likely to influence the maintenance of personality traits.

(5) Combination of behavioural levels in a pair and reproductive success: advantages of choosing a mate who behaves similarly or dissimilarly

(a) General rationale: genetic and behavioural compatibility

One proposed function of mate choice is that it allows females to choose genetically compatible males (e.g. Tregenza & Wedell, 2000), which can either lead to assortative mating (genetic similarity hypothesis, e.g. Rushton, 1989) or disassortative mating (overdominance and heterozygote advantage). In support of this, male monogamous oldfield

mice, *Peromyscus polionotus rhoadsi*, have higher lifetime reproductive success if paired with their preferred female than males paired with an unpreferred female or males paired with a female which has been preferred by another male (Ryan & Altmann, 2001) and female field crickets, *Gryllus bimaculatus*, preferentially fertilise eggs with sperm from unrelated males (Tregenza & Wedell, 2002; Bretman, Wedell & Tregenza, 2004). Similarly, behavioural compatibility or “complementarity”/“similarity” between partners could have an important role in mate choice (Trivers, 1972; Burley, 1983; Barlow, 1992). That behavioural coordination can result in higher reproductive success is supported by a study by Spoon, Millam & Owings (2006): in cockatiels, *Nymphicus hollandicus*, highly behaviourally compatible partners exhibit more coordinated incubation and have higher reproductive success than individuals with lower behavioural compatibility. Compatibility in this study was measured as a composite of proximity, behavioural synchrony, allopreening, copulation frequency and aggression between partners. Also, individuals in a partnership with low behavioural compatibility are more likely to perform extra-pair copulations than highly compatible pairs (Spoon, Millam & Owings, 2007).

(b) Disassortative mate choice for behaviour

Some authors (Dingemanse *et al.*, 2004; Both *et al.*, 2005; van Oers *et al.*, 2008) have argued that disassortative mating by personality could be adaptive, in that (a) partners of similarly extreme personalities could be behaviourally or genetically incompatible or (b) females produce offspring with intermediate personality that could be viable. Although in different years great tits at the different extremes of the exploratory trait distributions had highest survival rates - correlated to environmental conditions-, moderately exploratory individuals showed the lowest variance in adult survival in the long term and therefore the highest life expectancy (Dingemanse *et al.*, 2004). However, if disassortative mating by behavioural type is favoured by sexual selection, and personality effects are additive in expression, this is likely to erode personality differences over time, at least if personality traits are controlled by multiple loci, which is supported by the literature (e.g. Reif & Lesch, 2003), and if we consider disassortative mating as the only selection pressure acting in this context.

In accordance with the disassortative mating hypothesis, great tits have an increased likelihood of being in a disassortative partnership (for exploration) if the male is older than one year (Dingemanse *et al.*, 2004). Furthermore, van Oers *et al.* (2008) showed in a study of wild great tits that assortatively exploratory pairs (at both extremes of the trait distribution) have the highest extra-pair-paternity rates in their broods. However, the extra-pair males were not more dissimilar in their personality to the female than their within-pair males, which would be expected if females in assortative partnerships seek extra-pair matings to produce behaviourally intermediate offspring. Also, contrary to expectation, within-pair offspring

had a higher probability of surviving to the next year than extra-pair offspring. On the other hand, males in assortative partnerships can be expected to have a fitness disadvantage from an increased likelihood of having extra-pair offspring in their nest (unless they offset this disadvantage by engaging in an increased number of extra-pair matings themselves).

(c) *Positive assortative mate choice for behaviour*

Alternatively, choosing a partner assortatively from a behavioural perspective could be adaptive and result in higher reproductive success than choosing a partner disassortatively or at random. This assortative mating scenario might tend to maintain existing variation in the level of behavioural expressions. Females choosing males that behave similarly to themselves could be at an advantage if similar individuals are able to coordinate their behaviour to a greater extent than nonassortative pairs. Improved cooperation and coordination within a pair during parental care could increase reproductive success (see studies on cockatiels above). For instance, synchronised behaviour may be important in a foraging context if predation risk decreases when partners are feeding closely together (e.g. *via* risk dilution; Krause & Ruxton, 2002). Moreover, assortative pairs may provision their young more efficiently because, for instance, they can stagger their nest visits more reliably.

Assortative pairs of extreme personalities (i.e. at the ends of the exploratory spectrum) in great tits have been shown to raise fledglings in better condition (measured as residual fledging mass) than disassortative pairs (Both *et al.*, 2005). Furthermore, we have found evidence in a cross-fostering breeding experiment on zebra finches that foster parents in which both adults were highly exploratory raised offspring in the best condition compared to any other behavioural combination (Schuett, 2008; W. Schuett, S.R.X. Dall & N.J. Royle, in preparation). However, less-exploratory females always reproduced chicks of intermediate condition, independent of the males' exploratory or aggressive tendencies (Schuett, 2008; W. Schuett, S.R.X. Dall & N.J. Royle, in preparation). Similarly, reproducing pairs in dumpling squid, *Euprymna tasmanica*, showed similar boldness levels in feeding tests: intermediate and bold females were more likely to reproduce successfully if paired with a similar male than if paired with a dissimilar male (Sinn, Apiolaza & Moltschanivskyj, 2006). Shy females, on the other hand, tended to reproduce regardless of the boldness of the partner. Also, convict cichlid pairs, *Cichlasoma (Archocentrus) nigrofasciatum*, that reproduce successfully have been shown to have similar behavioural types (e.g. in terms of latency to explore a novel environment and interact with a mirror), whereas no interaction between male and female personality could be detected in non-spawning pairs (Budaev, Zworykin & Mochev, 1999).

There is also some evidence from humans for assortative partnerships in terms of personality as summarised in Table 1; most of these are positive but sometimes negative

assortments are reported (Vandenberg, 1972; Thiessen & Gregg, 1980; Buss, 1984; but see discussion in Penke *et al.*, 2007a). Negative correlations between personality traits of partners are not only rarer in human partnerships, but they are also more distinctive in unstable partnerships than in stable ones (Vandenberg, 1972). Human partners have been shown to be behaviourally similar in numerous aspects of the five personality axes categorised for humans (i.e. Openness, Conscientiousness, Extraversion, Agreeableness, Neuroticism, see McCrae & Costa, 1999). Assortative human partnerships have been identified in antisocial behaviour [e.g. crime and any behaviour that is linked to negative results for the individual and the society (Rhule-Louie & McMahan, 2007), factor Agreeableness], broad interests (Little, Burt & Perrett, 2006, factor Openness), Extraversion (e.g. Little *et al.*, 2006), Conscientiousness (e.g. Botwin, Buss & Shackelford, 1997; Little *et al.*, 2006), Intellect-openness, Agreeableness (e.g. Botwin *et al.*, 1997) and overall personality (Gonzaga, Campos & Bradbury, 2007). Both Gonzaga *et al.*'s (2007) and Botwin *et al.*'s (1997) study also illustrate that humans actually prefer partners with personality traits that resemble themselves, instead of ending up with a similar partner just as a result of similar environmental and demographic backgrounds.

Unfortunately, most studies (both in humans and non-human animals) have not considered the personality of the focal individuals before mating [but see e.g. Buss (1984) and Little *et al.* (2006) controlling for length of relationship], making it difficult to investigate whether individuals pair up assortatively in the first place or if they become more similar after pairing (Rhule-Louie & McMahan, 2007). Only the first scenario would indicate a role of sexual selection on personality traits. Furthermore, it is unfortunate that human studies investigating the link between personality traits and fitness are rare (Dingemanse & Réale, 2005; Penke *et al.*, 2007a) and human studies investigating the interaction between both parents' personalities on fitness seem absent altogether.

(d) *Assortative versus disassortative mating—role of environmental conditions?*

Although we have considered assortative and disassortative mating and their fitness consequences separately, these mating strategies need not be mutually exclusive in the long term but could both be advantageous under different environmental conditions and result in a stable mix of individuals showing different levels of behavioural expressions in a population. In a three-year study, Dingemanse *et al.* (2004) found that in one year, assortatively paired individuals at the extremes of the explorative spectrum had the highest reproductive success (number of recruits). Although there were not enough data to test for an interaction between parental personalities on reproductive success in the remaining years, selection pressures on individuals of different sexes varied over the three years (see above). These changes in selection pressures coincided with fluctuating environmental conditions (food availability).

III. SELECTION FOR BEHAVIOURAL CONSISTENCY: ADVANTAGES OF BEING PREDICTABLE OR A QUALITY INDICATOR?

(1) Sex differences in consistency

We have shown that different levels of behavioural expression exist and presented explanations as to why this could be the case from a sexual selection perspective, but we still need to focus more on why individuals are consistently different from one another. We could argue that if an individual's quality is genetically determined and controls whether an individual expresses costly behavioural traits, this behavioural restriction (for low-quality individuals) is not likely to change over its life and should therefore result in behavioural consistency. However, there is some evidence that behavioural traits tend to have relatively low heritability (van Oers *et al.*, 2005). Secondly, there may be direct selection on consistency.

Dall *et al.* (2004) proposed that individuals that are consistent in their behaviour over time could acquire advantages from being predictable in competition over resources (if there is an audience). This could be the case if behaving predictably influences competitors' future responses in a way that improves the focal individual's payoffs. This idea can be applied in a sexual selection context: males, who compete aggressively over the resource females, i.e. access to mates, could have an advantage in being predictable in their aggression if some individuals are "eavesdroppers" (*sensu* McGregor, 2001; Bonnie & Earley, 2007). These eavesdroppers observe the outcome of fights between the contestants and adjust their behaviour depending on their opponents' previous behaviour (i.e. only escalate against previous losers). Consequently, individuals that are consistent in their level of aggression (low *versus* high) are favoured by selection, as their behaviour is predictable, and eavesdroppers can therefore avoid costly fights with low prospect of winning. In this way intra-sexual selection could generate consistency in male aggression. Similarly, consistency in males' behaviour could be selected for *via* female mate choice if females obtain benefits from choosing a partner whose behaviour is predictable. We propose this is most likely to occur in species that form long-term pair bonds and/or in species in which both males and females engage in parental care. In these species, mate choice has long-term consequences and males and females are required to coordinate efficiently in order to maximise the number and condition of offspring raised. A female could gain benefits not just from choosing a male who shows a high level of paternal care or territorial defence (see above) but also from a male who cares in a predictable fashion. Females can compensate and adjust their parental effort according to a male's parental care level (Sanz, Kranenbarg & Tinbergen, 2000). Johnstone & Hinde (2006) predict this is the case if there is an "informational asymmetry" between the sexes. Consequently, an estimate of male investment along with an estimate of the amount of parental effort needed to adapt to this male investment is likely to be more accurate and

less costly if the male's parental effort is stable. If the level of caring is unstable, the female might either need to assess the male's effort repeatedly - which could be costly in itself or the constant required adjustment could be costly - or she might accept an inaccurate initial estimate, resulting in over- or under-care by herself (depending on the initial estimate). The latter should lead to reduced efficiency in raising young as the female is unlikely to complement the male's parental care in the most effective way.

Other behaviours like preening/grooming of the partner might be more beneficial if expressed at a constant rate (but this should be equally true for both sexes, leading to no sex differences in consistency). Furthermore, taking the biology of the species of interest into account could help identify which behaviours are likely to be sexually selected for consistency. For instance, we found in one captive zebra finch population that male zebra finches are significantly more consistent in their exploration (but do not show a higher mean level of exploration) than females and that only males are consistent in their leading behaviour (Schuett & Dall, 2009). This makes sense given that male zebra finches lead their females around the colony and through feeding sites (Zann, 1996). A female should choose a male who explores the environment (while leading her around) in a predictable manner, as this is likely to result in a relatively predictable rate of finding feeding sites or high-quality patches within a feeding site. Generally, food is the limiting resource for females (Andersson, 1994) and a predictable access rate to food should be in the interest of the female.

In sum, from this "predictability" perspective, we would expect males to be selected for consistency in their aggressive behaviour (intrasexual competition) and parental care (female choice). Both sexes should benefit from having a partner who is consistent in his allo-preening/grooming behaviour (no difference in consistency between sexes expected). Also at a species level, we expect further sex differences in the consistency of other behaviours, depending on the biology of the species.

Unfortunately, hardly any studies have looked at sex differences in consistency (see Table 1) but rather assess repeatability of behaviours pooled for the sexes. To our knowledge, only one more study investigated sex differences in repeatability of exploratory behaviour (Dingemanse *et al.*, 2002) and two investigated aggression (Bakker, 1986; Holder *et al.*, 1991). There are also a few studies estimating repeatability of parental care for the sexes separately (Budaev *et al.*, 1999; Freeman-Gallant & Rothstein, 1999; MacColl & Hatchwell, 2003; Schwagmeyer & Mock, 2003; Nakagawa *et al.*, 2007a). However, of the latter, only Nakagawa *et al.* (2007a) tested for differences between the repeatabilities statistically, finding that male house sparrows, *Passer domesticus*, are highly consistent in their feeding rates of offspring, both within and between years, whereas females are significantly less consistent in their parental care. This fits with predictions. The same effect is apparent in a long-tailed tit, *Aegithalos caudatus*, study (MacColl & Hatchwell, 2003), in a savannah sparrow, *Passerculus sandwichensis*, study

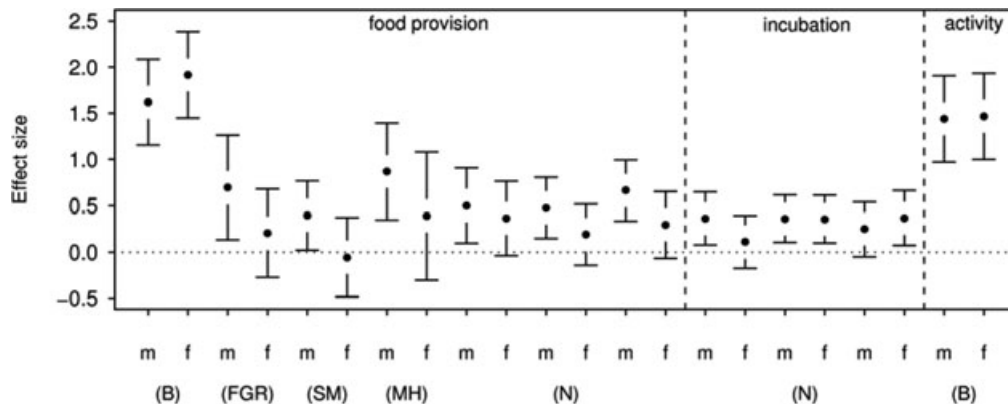


Fig. 3. Standardised repeatabilities ($z_R \pm 95\%$ confidence intervals) of parental care in males and females of different species (see Table 1). Data from: B, Budaev *et al.* (1999); FGR, Freeman-Gallant & Rothstein (1999); SM, Schwagmeyer & Mock (2003), MH: MacColl & Hatchwell (2003); N, Nakagawa *et al.* (2007a).

(Freeman-Gallant & Rothstein, 1999) and another house sparrow study (Schwagmeyer & Mock, 2003). However, in convict cichlids, *Cichlasoma (Archocentrus) nigrofasciatum*, males appear to be slightly (but probably not statistically) more unstable in terms of time spent with the brood than females (Budaev *et al.*, 1999). Finally, Dingemanse *et al.* (2002) did not detect any sex differences in consistency for exploration in great tits, whereas Holder *et al.* (1991) found that only male Midas cichlids but not females are consistent in their tendency to behave aggressively over time. On the other hand, male and female sticklebacks, *Gasterosteus aculeatus*, are similarly repeatable in their aggression, with the female even exhibiting somewhat higher absolute values (Bakker, 1986). However, in the latter study, aggression of males and females was tested in different contexts, making a direct comparison between the sexes difficult.

To assess the patterns found in more detail and in a rigorous statistical manner, we conducted a meta-analysis of studies on repeatabilities in parental care of males and females outlined above (see also Table 1). Recently, Bell, Hankison & Laskowski (2009) also conducted a meta-analysis on repeatabilities to assess sex differences in behavioural consistencies. They found that adult males were more repeatable in their behaviour than adult females, whereas no such difference was present at juvenile stages. Nevertheless, after removing some influential studies, males were not more repeatable in their behaviour than females and the pattern was even reversed. Despite being an important and comprehensive study, this meta-analysis cannot be used conclusively to assess our specific questions and predictions as a variety of behaviours and taxa were analysed collectively, therefore not considering different breeding systems, including differing patterns of parental care. Finally, in the Bell *et al.* (2009) meta-analysis, studies were included where male and female behaviours were pooled and where repeatability was just measured for one sex.

There is only a sufficient number of studies available on one behaviour, parental care, to conduct a meta-analysis on sex differences in consistency (see Table 1). To allow

us to compare the repeatabilities (and Cronbach alphas, respectively; R) of the different studies, we converted them into dimensionless, standardised effect sizes (for detailed discussion see e.g. Nakagawa & Cuthill, 2007) using Fisher z -transformations for repeatabilities, and calculated 95% confidence intervals and their variances as outlined by Stratford (2004), Bonett (2002) and Donner (1985). The obtained z -transformed repeatabilities (z_R , effect size values) were entered as the response into a weighted linear mixed-effects model (Pinheiro & Bates, 2000; REML, nlme package, in R 2.8.1; R Development Core Team, 2008), with sex as a fixed effect and study as the random term (see Nakagawa *et al.*, 2007a). The mean effect sizes for the two sexes were estimated as a weighted mean in the linear mixed-effects model following Nakagawa *et al.* (2007b). To test whether the effect sizes from the different studies were homogenous, we computed the total heterogeneity of our sample studies, Q_{REML} (for details see Nakagawa *et al.*, 2007b).

As suggested in the discussion of individual studies, the meta-analysis confirmed that males were significantly more consistent than females in their parental behaviour (Fig. 3; $F_{1,16} = 4.83, P = 0.043$; effect sizes and 95% CI: males: $R = 0.562, CI_{lower} = 0.172, CI_{upper} = 0.855, ZR = 0.725, CI_{lower} = 0.174, CI_{upper} = 1.276$; females: $R = 0.456, CI_{lower} = 0.019, CI_{upper} = 0.809, ZR = 0.571, CI_{lower} = 0.019, CI_{upper} = 1.123$). The samples were homogenous ($Q_{REML} = 0.029, d.f. = 21, P = 1$).

(2) Mate choice, male-male competition and behavioural consistency

Consistency could be sexually selected for if the expression of behaviour in a consistent manner is costly and therefore an indicator of quality that could be used (a) in mate choice by the choosy sex or (b) in male-male competition over access to females. Exhibiting consistency in behavioural expression could be particularly costly when environmental conditions change. For instance, imagine a male who shows a consistently high level of parental care. Parental care is costly from

an energetic point of view (e.g. Trivers, 1972). As long as food is abundant, we expect that a number of males can afford to show high levels of parental care (if we assume for illustrative purposes that there are no costs other than energetic ones associated with parental care). However, the less food is available, the harder it is for an individual to find enough food for its (and its offsprings) energy demands. Therefore, we assume that only very high quality individuals can maintain their high level of parental care consistently. Similar patterns may be evident during male-male competition. The expression of aggression or song in a consistent manner could be costly. For instance, consistency in certain song features may entail energetic costs or developmental constraints (for a detailed discussion on constraints and honesty of song as a signal see Gil & Gahr, 2002).

We are only aware of two published studies that tested for relationships between behavioural consistency and mate choice and/or reproductive success: Byers (2007) assessed links between male extra-pair reproductive success and consistency in song in wild chestnut-sided warblers, *Dendroica pensylvanica*. The degree of consistency in singing was positively correlated to a male's number of extra-pair offspring. Similarly, male tropical mockingbirds, *Mimus gilvus*, that are consistent within each syllable type, have higher dominance status and increased reproductive success relative to males showing low within-type consistency (Botero *et al.*, 2009). Furthermore, support for the hypothesis that male behavioural consistency is beneficial for females comes from an unpublished study on wild lance-tailed manakins, *Chiroxiphia lanceolata*. In this lekking species, females that had male partners consistent in their display behaviour (among years) were more faithful than females that were paired to behaviourally inconsistent males (E.H. DuVal, personal communication).

One recent study (de Kort *et al.*, 2009) investigated the link between male-male competition and consistency in song in the territorial banded wren, *Thryothorus pleurostictus*. In this species the number of song types expressed during a territorial encounter decreases and the same song type is often repeated a number of times (Vehrencamp *et al.*, 2007). Consistent with existing literature, in which older males often have greater success in gaining access to females than younger males (Andersson, 1994), de Kort *et al.* (2009) show first that consistency in trill notes (i.e. a series of repeated notes) increases with age within an individual (see Botero *et al.*, 2009, for similar results). Despite this increase in consistency with age, different individuals vary in their consistency. Furthermore, males presented with male song playbacks within their territories distinguish between song recorded from the same male at one or three years old. Territorial males sing significantly more when approaching the song playbacks of first-year males than those of third-year males. Finally, males sing significantly less when exposed to an inconsistent first-year song than when encountering the song of the same first-year male, manipulated to appear consistent. Although there is a debate over whether strong or weak competitors should trigger an intense song response, most studies assume that the intensity of response should increase

with decreasing competitiveness of the opponent, which also corroborates predictions from theoretical models (see de Kort *et al.*, 2009 and literature therein). Either way, what we can conclude from the study by de Kort *et al.* (2009) and to some degree also from the studies by Byers (2007) and Botero *et al.* (2009) is that consistency in at least some song traits is used as a source of information in sexual selection contexts.

We provided two possible explanations as to why behavioural consistency could be sexually selected for: as a signal of quality and/or association with advantages of being predictable. These ideas are not mutually exclusive: it could be that being consistent is in general costly, and therefore can only be displayed by high-quality individuals, but it could also be beneficial in itself. These two explanations for the existence of behavioural consistency suggest it can be selected for directly and contrast with the widespread view that behavioural consistency, or more generally limited phenotypic plasticity, results from constraints (i.e. costs and limits) to plasticity (e.g. DeWitt, Sih & Wilson, 1998; Sih *et al.*, 2004b; McElreath & Strimling, 2006; but see Dall *et al.*, 2004; Wolf *et al.*, 2008).

Finally, we want to point out two possibilities which may not favour maximum levels of consistency in a sexual selection context but which remain to be tested in future studies. First, the existence of predictability may offer incentives to deceive or to manipulate (for a general discussion about information on a partner's behaviour and credible threats, see McNamara & Houston, 2002). For instance, if females choose males whose parental care is predictable, in being predictable, males could leave it to the females to react to any environmental changes and consequent changes in the needs of the offspring, such as to increase provisioning. This could be the case if male consistency evolves to exploit existing female biases for consistency (sensory bias, see e.g. Ryan & Keddy-Hector, 1992). Alternatively, there may be cases in which females or competing males may exploit a male's behavioural predictability. Second, Sih & Bell (2008) mention a possible role of what they refer to as "social sensitivity" or "social skill" which can be applied to a sexual selection context. After an individual has chosen a time and location for mate choice, has assessed prospective partners' quality and chosen a partner, it will respond to this partner, e.g. by adjusting its display behaviour. Sih & Bell (2008) further discuss the likelihood that individuals will differ in this ability to adjust their behaviour, i.e. show different levels of "social skill", and that the choosy sex may express a preference for high levels of this skill. In support of this, male satin bowerbirds, *Ptilonorhynchus violaceus*, have increasing courtship success both with increasing displaying rates but also with decreasing startle rates of the females, which is negatively correlated to male adjustment of courtship intensity in response to female behaviour (Patricelli *et al.*, 2002; Patricelli, Coleman & Borgia, 2006).

(3) Combination of behavioural consistencies in a pair

In the same way that assortative/disassortative mate choice for behavioural levels may be important for genetic

and/or behavioural compatibility between partners and consequently their successful reproduction, combination of the level of both partners' behavioural consistency (slopes) may be crucial during mate choice. If this was the case, we would expect (a) mate choice based on consistency, with the direction depending on an individual's own level of consistency, (b) reproductive benefits of certain combinations of consistencies; (c) if (dis-)assortative mate choice by consistency plays a role, we would also expect variation in the level of consistency between individuals of the same sex.

Unfortunately, we are not aware of any studies investigating the influence of behavioural consistency of both the chosen and choosing sex on mate choice. However, there is some support for reproductive advantages for some combinations of behavioural consistencies over others (Schuett, 2008; W. Schuett, S.R.X. Dall & N.J. Royle, in preparation). Zebra finches have been shown to produce foster offspring of better condition if pairs consist of two highly consistent explorers (Schuett, 2008; W. Schuett, S.R.X. Dall & N.J. Royle, in preparation). Assortative pairs, in which both partners are behaviourally inconsistent in their exploration, raise foster offspring with reduced condition in comparison to the consistent-consistent pairing, but still show higher reproductive success than any other remaining pair combination (Schuett, 2008; W. Schuett, S.R.X. Dall & N.J. Royle, in preparation). This suggests that positive assortment in terms of behavioural consistency is important for the behavioural coordination of parental care in zebra finches (Fig. 1). However, more studies are needed to confirm these results and to shed further light into how parental care, cooperation/coordination between partners and personality interrelate. Preferably, future studies should disentangle both aspects of personality (behavioural level and consistency) experimentally as these measures are not independent of one another (Schuett, 2008; W. Schuett, S.R.X. Dall & N.J. Royle, in preparation). Therefore, only separating behavioural consistency from behavioural levels will allow us to assess the importance of behavioural consistency *per se* on reproductive performance. Finally, there is evidence for inter-individual variation in the degree of consistency (e.g. Koolhaas *et al.*, 1999; Benus, 2001; Briffa *et al.*, 2008; Schuett, 2008; Dingemanse *et al.*, 2009; W. Schuett, S.R.X. Dall & N.J. Royle, in preparation; but see: Martin & Réale, 2008), which has been anticipated theoretically (Dall *et al.*, 2004; Plaistow *et al.*, 2004; Wolf *et al.*, 2008; McNamara *et al.*, 2009), providing the scope for sexual selection to act on variation in behavioural consistency.

IV. FRAMEWORK FOR UNDERSTANDING SEXUAL SELECTION ON PERSONALITY DIFFERENCES

In general, for personality differences to be subject to sexual selection, we expect both selection on the variation in the level of behaviour expressed and on the consistency of behaviour expressed. Whereas the variation in the level of

behaviour can only be eroded or maintained, consistency could also be generated by sexual selection, if females prefer consistent males or males do better in male-male competition when they are consistent (as discussed above). Incorporating findings from the studies we have reviewed, we can construct the following predictions for a personality-based framework (see also Miller, 2007, for some overlapping predictions) (Fig. 1): firstly, sexual selection could act *via* female mate choice or *via* intrasexual competition for access to females. Both consistency and the level of behavioural expression could be an indicator of quality (indirect or direct), information that can be used during mate choice and male-male competition. Also, the behavioural expression and possibly the behavioural consistency can alternatively signal compatibility (in a mate-choice context), whereas consistency can alternatively indicate predictability (both in mate-choice and male-male competition contexts, see below).

If the personality trait (consistency or level) is an indicator of genetic quality, then this trait should exhibit some genetic variation and a positive genetic correlation with other fitness-related traits. However, if a personality trait predicts an individual's partner or parenting quality (in case of mate choice) or competitive ability (in case of male-male competition), this trait need not show genetic variation, heritability, or a positive genetic correlation to other fitness-related traits but should be correlated to parenting, partner or competitive abilities. In both cases, the quality-indicating personality traits should be expressed more often or more consistently by individuals in better phenotypic condition or quality, even under varying environmental conditions. Also, these traits should show a higher among-individual variance in the less investing sex, and should be preferred by all individuals of the choosy sex in a mate choice context (under the assumption that all individuals can assess the quality indicator in the same way). This should lead to positive assortative mating, if the same personality trait is a quality indicator in both sexes, with high-quality individuals pairing up with one another, leaving the individuals with the low-quality trait to mate with each other (McNamara & Collins, 1990; Johnstone, 1997). Reproductive success is then expected to be increased for pairs of individuals bearing high-quality personality traits, resulting in an erosion of behavioural variation over time (Fig. 1). An erosion of variation is also expected if the trait is only a quality signal in one sex.

If genetic or behavioural compatibility is important for mate choice, individuals of the choosy sex should vary in their preference for a personality trait and consider their own personality trait in their choice. This can also result in assortative or disassortative mating and increased reproductive success with increased compatibility (Fig. 1). However, the preference pattern in a population will be different to the one based on overall quality indicating personality traits, because different individuals display different preferences depending on their own personality. In the case of high behavioural compatibility, partners should display a high degree of coordination and cooperation, resulting in an increased reproductive success.

Consistency can signal predictability and predictability should be selected for *via* female mate choice as well as *via* male-male competition (Fig. 1). Females that choose a behaviourally consistent male should gain advantages from their mates' predictability in many aspects of their social life (e.g. easier coordination of parental care, general synchronisation of behaviours in a pair). Behaviourally consistent males can also experience fitness payoffs from being predictable in competitive male-male interaction resulting in increased access to females.

V. FUTURE DIRECTIONS

For future work it would be desirable to apply more holistic approaches, looking at more than one aspect of sexual selection and personality differences in one species for more detailed understanding as well as accumulating studies across species. Investigation of sex differences in both the variation in the level and consistency of behaviour (the latter is neglected completely in most studies) would be useful. A good place to start is likely to be behaviours that are generally expected to be subject to sexual selection like parental care or aggression, or behaviours that seem likely to be sexually selected given the biology of the species. We can then ask what the different selective pressures are likely to be and can test them, for instance with mate-choice trials. Do females use male behavioural context consistency in their mate choice? Do females prefer a male which is more consistent in behaviour x? Or where there is no sex difference: is assortative mating favoured?

When conducting mate-choice trials it will be important to consider the personality of both the choosing as well as the chosen sex. This will help to distinguish which behavioural traits (both in terms of consistency and level) are generally preferred (likely quality indicators) and which are preferred by some individuals but not by others. Also, it allows us to test why different individuals differ in their choice (e.g. due to disassortative or assortative choice). For mate-choice tests it would also be favourable to allow the choosing sex first to actually observe the chosen sex displaying the behaviour of interest (e.g. approaching a predator) before conducting the mate-choice trial. In combination with a manipulation of behaviour of the chosen sex, this would allow us to disentangle appearance effects from behavioural effects in mate choice and to identify direct correlations between preference and personality traits. Unfortunately, the studies of Godin & Dugatkin (1996), and Schuett (2008; W. Schuett, J.-G.J. Godin & S.R.X. Dall, in preparation) seem to be the only ones which have done so thus far. With respect to breeding experiments for investigating the combined effect of paternal and maternal personality on reproductive success, we suggest testing the personality of the parents before and after pairing. This allows investigating whether assortative/disassortative mating in itself is favoured by sexual selection, i.e. results in increased reproductive success or if partners become more similar/dissimilar after pairing

due to shared experience (behaviour contagion, convergence, or socialization, Rhule-Louie & McMahon, 2007) which could then lead to increased reproductive success. Also, observations of interactions within pairs during breeding should give information about how the interaction between male and female personality is manifest in cooperation, behavioural synchronisation *etc.*

VI. CONCLUSIONS

- (1) Whereas human studies have a long history of explaining (mainly sex) differences in behaviour from a sexual selection perspective (but mainly based on *post-hoc* interpretations), hardly any animal studies have considered a possible role for sexual selection in the evolution and maintenance of personality differences.
- (2) From the available studies, a link between personality and sexual selection is already quite convincing. Links between aspects of sexual selection, mate choice and intrasexual selection, and aspects of personality differences, variation in the level of behavioural expression and consistency in behavioural expression, have been highlighted and an outline of how these findings might be explained is proposed.
- (3) Many more studies are necessary to shed further light on the role of sexual selection acting on personality differences and to understand and test proposed underlying mechanisms in detail. We look forward to seeing more exciting results from this perspective.

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VIII. REFERENCES

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