Brothers and sisters are stabbing each other in the back: long-term effects of sex of siblings on barn swallow offspring

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Prenatal and early postnatal conditions can prime developmental trajectories, with short- as well as major long-term effects on phenotype. Variance in perinatal conditions may be caused by many factors, including number of siblings of either sex, which is expected to influence individual phenotype for two complementary reasons. First, male and female offspring can differ in susceptibility to extrinsic conditions. Second, the effect that an individual has on its siblings can differ according to their sex. Yet, few studies of vertebrates and only one of birds have addressed the long-term consequences of family sex composition on offspring of either sex. We analysed the effect of brood sex composition on adult phenotype and breeding performance in the barn swallow, *Hirundo rustica*. Male offspring growing with more sisters had shorter wing length, an aerodynamically important trait, and tail length, a condition-dependent, sexually selected trait. In addition, tail length of females decreased with increasing brood size but more steeply so when they grew with more female siblings. Body size of females also declined with increasing brood size. Notably, breeding output of females declined with an increasing proportion of male siblings and also with increasing brood size. This study thus suggests that social environment has major consequences for phenotype and breeding performance in adulthood and that variation in brood sex composition has long-term effects which depend on the sex of the individual as well as on the specific trait considered. Hence, optimal parental sex allocation decisions depend not simply on additive fitness costs and benefits of producing males or females, but also on the long-term effects that sons and daughters exert on each other.

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Phenotypic variation in populations of organisms arises partly as the expression of norms of reaction to the extrinsic factors to which individuals are exposed early in life (Schlichting & Pigliucci, 1998). The flow of causation between the conditions that individuals experience during the pre- or early postnatal stages and performance later in life has been dissected in a number of animal and plant models (Lindström, 1999; Metcalfe & Monaghan, 2001 Mousseau & Fox, 1998). The studies of such carryover effects have hinted at long-term effects that are eventually expressed after sexual maturation, potentially being as important in determining individual fitness as are short-term effects (Cam, Monnat, & Hines, 2003; van de Pol, Bruinzeel, Heg, van der Jeugd, & Verhulst, 2006).

In essence, so called 'silver spoon' (Grafen, 1988) effects of early life conditions, whereby maternal effects or rearing environment

may have life-long consequences on performance, depend on three, tightly linked processes. First, variation in parental quality contributes to setting the environmental scene for the growing offspring. High-quality parents can secure favourable conditions with 'developmentally entrenched' effects, possibly mediated by egg quality or by pre- or postnatal care (Badyaev, 2008; Cam & Aubry, 2011; Carere & Balthazart, 2007; Groothuis & Schwabl, 2008; Mousseau & Fox, 1998; Ruuskanen, Doligez, Pitala, Gustafsson, & Laaksonen, 2012). Second, habitat quality can add to variation in the extrinsic conditions experienced by the offspring via, for example, effects of nutritional conditions (Metcalfe & Monaghan, 2001; van de Pol et al., 2006; Sergio et al., 2009). Parental and environmental quality are likely to covary positively and, by acting independently or in concert, can have long-term consequences for fitness traits of mature offspring as diverse as development of 'ordinary' and secondary sexual characters (Gustafsson, Qvarnström, & Sheldon, 1995; de Kogel, 1997; de Kogel & Prijs, 1996; Nowicki, Peters, & Podos, 1998), dispersal (Nicolaus

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et al., 2012), viability or recruitment (Cam et al., 2003; Potti, 1999a, 1999b), offspring number and quality (Cam et al., 2003; van de Pol et al., 2006; Potti, 1999b) or breeding habitat quality (Verhulst, Perrins, & Riddington, 1997; see also Cam & Aubry, 2011; Tilgar, Mänd, Kilgas, & Mägi, 2010). The intimate connection between parental and environmental effects (see Sergio et al., 2009) is exemplified by seasonal effects. In spatially heterogeneous, seasonally varying temperate habitats, low-quality individuals may settle in poor-quality habitats (Rodenhouse, Sherry, & Holmes, 1997) and fail to achieve reproductive state at the time when conditions for breeding are optimal. Under such circumstances, the frequently observed negative covariation between offspring quality/viability and birth date (e.g. Naef-Daenzer, Widmer, & Nuber, 2001; Saino et al., 2012; Verboven & Visser, 1998) may be ultimately caused by the concomitant effects of habitat and parental quality on breeding date.

Third, social environment, and interactions with competing kin in particular, can produce huge variation in offspring growth trajectories and general physiological state at the within-family level (Mock & Parker, 1997; Wright & Leonard, 2002), with immediate but also persistent consequences for morphological and physiological traits, and thus for survival and/or reproductive success (Lindström, 1999). A potentially major determinant of the long-term outcome of interactions between siblings that has remained neglected is sex, despite straightforward molecular sexing techniques having been devised many years ago. Yet, there are two compelling, complementary reasons to expect that the number of male or female siblings sharing a rearing environment can influence the long-term fitness consequences of sibling competitive interactions. First, asymmetries often occur between male and female siblings in competitive interactions over limiting resources (see Uller, 2006). These can result from a variety of proximate causes including intersexual variation in social behaviour which is established early in life, differences in resource demands or size-related dominance in species with early established sexual dimorphism, or parental favouritism for either sex (e.g. Badyaev, 2002; Bonisoli-Alquati, Boncoraglio, Caprioli, & Saino, 2011; Lessells, 2002; Saino et al., 2010; Uller, 2006). Second, young of either sex may differ in their susceptibility to the same features of their rearing habitat, whereby competition over limiting parental resources with any given offspring can have different effects on male or female siblings (Bonisoli-Alquati et al., 2011; Gustafsson, 1989; Lindström, 1999; Oddie, 2000; Uller, 2006).

Short-term sex-dependent competitive behaviour and its consequences for growth and survival before independence have been investigated in some studies of altricial birds (Boncoraglio, Martinelli, & Saino, 2008; Saino, de Ayala, Martinelli, & Boncoraglio, 2008; Uller 2006). However, few studies exist on the consequences of family sex composition for phenotype and performance in adulthood in vertebrates in general (Uller, 2006) and, to our knowledge, only one of them has concerned birds (Radersma, 2011). Yet, such studies are expected to shed more light on, and potentially also add a further level of complexity to, the analysis of the evolution of reproductive strategies and of sex allocation decisions in particular.

In the present study we thus used a small passerine bird, the barn swallow, *Hirundo rustica*, as a model to investigate the effects that brood sex composition and brood size have on morphology and seasonal breeding success of the offspring that were eventually recruited into the study population as breeding adults.

In the barn swallow, male offspring are penalized more than females by adverse rearing conditions and when they compete with female compared to male siblings (Bonisoli-Alquati et al., 2011; Saino, de Ayala, et al., 2008; see also Boncoraglio et al., 2008). Average nestling phenotypic quality declines with brood size

(Saino, Calza, & Møller, 1997; Saino et al., 2000). In addition, hatching date negatively predicts life expectancy after sexual maturation and lifetime reproductive output, implying that early maternal effects and postnatal conditions and/or parental quality have major consequences for viability and fecundity (Saino et al., 2012). While the studies of barn swallows to date have focused on the effects of brood sex composition on growth and general state during the nestling period, no study has been carried out on the consequences of brood sex composition in adulthood. We predicted that phenotypic values of traits that reflect growth (keel length), body condition (adult body mass, plumage growth and ornamental tail length; Møller, 1994) and breeding performance would decrease, and particularly so among males, with an increasing proportion of female siblings. Generally negative associations between phenotypic values or breeding performance and brood size were also expected irrespective of fledgling sex. Because hatching date may affect adult performance (Saino et al., 2012), in the analyses we controlled for the effect of hatching date. In addition, because the effect of hatching date on performance may be partly mediated by the order (first or later) of the clutch of origin, in the analyses we also controlled for this potentially confounding effect.

METHODS

Study Organism

The barn swallow is a small (ca. 20 g), insectivorous, long-distance migratory passerine (Møller, 1994; Turner, 2006). Breeding typically occurs in colonies of two to tens of pairs, inside rural buildings such as cowsheds (Møller, 1994; Turner, 2006). Socially monogamous pairs have one to three clutches of two to seven eggs per breeding season. Hatching asynchrony is small (hatching spread: 24–36 h), with first-laid eggs hatching first (Saino, Incagli, Martinelli, Ambrosini, & Møller, 2001). Altricial nestlings fledge when ca. 18–20 days old. The single annual moult of rectrix (tail) and remex (wing) feathers occurs during wintering in Africa (Ginn & Melville, 1983). Sexual dimorphism in size is small, but males have longer wing and tail feathers (Møller, de Lope, & Saino, 1995).

Field Methods

In spring–summer 2010–2012 we studied 38 barn swallow colonies (=farms) in the Magadino Plain (southern Switzerland, barycentre of the study farms: 46°9′54″N, 8°55′47″E). The study area (10 × 4 km) mainly consists of farmland and is dominated by maize and hay fields. In 2010 and 2011 we visited the nests every 10–12 days to record breeding events, ring the nestlings ($N = 1248$ in 2010 and 1353 in 2011), and collect a small blood sample by puncturing the ulnar vein for molecular sexing (Saino, Martinelli, & Romano, 2008). Hatching date could be either directly identified upon nest inspection or estimated according to several cues (e.g. chick feathering; see Ambrosini & Saino, 2010).

We intensively captured the adults at the colonies in 2011 and 2012 by placing mist nests before dawn at the exits of the rural buildings in which breeding individuals usually spend the night. Upon capture we identified the recruits and measured body mass, keel length (a proxy for body size), the length of the longest (ninth) primary wing feather (a proxy for wing length) and the length of the left outermost tail feather (a sexually selected trait in males; Møller, 1994). Recruits were colour-ringed to assign them to breeding pairs and to identify their nests, which were regularly inspected to record the size of the clutches and breeding output (number of nestlings at last visit). Total numbers of eggs and fledglings were used as indicators of seasonal fecundity and