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Sexual selection in the Swallow *Hirundo rustica* – A review

Abstract: Darwinian theory of sexual selection and its development up to the present state of knowledge are sketched. The most important results of empirical studies on sexual selection in the Swallow *Hirundo rustica* are reviewed. The Swallow is a socially monogamous, slightly sexually dimorphic avian species. Long tail streamers are considered as sexual ornaments of males. Female preference for long and symmetric male tails has been inferred on both observational and experimental grounds. Experimental elongation of the tail causes short-term benefits and long-term costs in male reproductive performance. Behavioural consequences of sexual selection acting in the Swallow are discussed. An aerodynamic role of male tail streamers is also considered.

Key words: Sexual dimorphism, ornaments, sexual selection, monogamy, Swallow, birds.

1. Introduction

DARWIN (1859, 1871) put forward the theory of sexual selection to explain the evolution of a category of morphological and behavioural properties of different animal species which clearly lowered survival but enhanced mating success. These characteristics, often sexually dimorphic and exaggerated in form, should have normally been selected against by natural selection. DARWIN (1871) suggested that the exaggerated expression of such traits positively influenced fecundity by making mating easier, thus generating the sexual selection pressure able to outweigh a survival disadvantage. It is evident that sexual selection should be very intensive in polygamous animals but its pressure can also be marked in the monogamous mating system.

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Variation in mating success, in terms of both the number and quality of breeding partners, may result from two mechanisms (DARWIN 1871; ANDERSON 1994). First, a non-controversial mechanism resulting from intra-sexual competition for an access to breeding partners. Second, a partner choice mechanism resulting from choosing specific traits of partners rather than mating randomly. For DARWIN (1871) it was obvious that it was males who engaged in competition for females, and it was females who practiced choosing particular males. A general explanation of this sex role asymmetry was given by TRIVERS (1972) who proposed that the sex that makes a larger parental investment is choosy and the sex that invests less has to compete for the more investing sex. Parental investments of females are usually higher than investments of males, with some outstanding exceptions.

The intra-sexual mechanism was easily accepted even at Darwin's times. On the other hand, sexual selection by female choice was highly controversial and induced severe critique, as described by CRONIN (1991). The controversy caused stopping theoretical and empirical investigations of sexual selection for many years, with a few but most important exceptions (FISHER 1915, 1930; BATEMAN 1948; MAYNARD SMITH 1958). A new wave of sexual selection research developed in great number in the 1970s, becoming besides social behaviour studies a central topic of behavioural ecology (CRONIN 1991).

The aim of this review is to present the main results of empirical studies on sexual selection in different populations of the Swallow *Hirundo rustica* which were conducted in response to the development of theory. Since the time when it was first hypothesized that the tail of the Swallow is a sexually selected ornament (BAÑBURA 1986) the species has become a model for sexual selection studies and the tail itself has become one of the most frequently analysed secondary sexual traits in birds (MØLLER 1994a). At the same time, many studies concerning different aspects of sexual and parental behaviour of Swallows strictly linked to sexual selection started (eg. CROOK, SHIELDS 1985; MØLLER 1985, 1987).

2. An outline of sexual selection theory

The review of sexual selection theory presented here is by no means complete. It concerns only the female choice mechanism of sexual selection and its main goal is to provide an explanation of the relation between sexual dimorphism and sexual selection and some theoretical background for the results of empirical studies on Swallows. Sexual dimorphism may result from several different processes, only the last two of which can be

classified as sexual selection mechanisms (ANDERSSON 1994): (i) pleiotropy of genes; (ii) selection for occupying different ecological niches by the sexes; (iii) sex-specific signalisation of non-profitability as prey to predators; (iv) within-sex competition for mates (usually between males); and (v) preferential choice of mates.

The evolution of secondary sexual traits by means of sexual selection resulting from female choice, as hypothesized by DARWIN (1871), was initially disputed because Darwin's hypothesis seemed to assume that female preferences were based on some sort of aesthetics (CRONIN 1991). Critics would have been ready to accept the idea that female choice would generate a selective pressure but they saw no reason why females would have any preferences at all (CRONIN 1991). Consequently, an explanation of reasons for female choice is a critical point in sexual selection theory.

Two kinds of processes were proposed to explain the evolution of female preferences. The first one is represented by the runaway sexual selection process defined by FISHER (1915, 1930). When males vary, as they usually do, it is possible that a mutated allele appears which causes the females having this allele to mate with a higher probability with one male variant rather than the alternative ones. The preferred variant is assumed to be neutral or slightly advantageous with respect to survival at the beginning. The males with preferred traits have more partners, or better quality ones, and thus produce more offspring, which results in the preferred allele spreading out in the population. The preference practised by females will in addition result in developing a genetic correlation between the preference and the preferred trait because offspring produced as a result of selective mating will have both the gene of the preferred trait and the gene of preference. In this way, increasing frequency of the gene of the preferred trait will lead to an increase in frequency of preference gene as well. This is a positive feed-back process which could cause fast evolution of sexual ornaments and preferences. Once the process started working, it could result in ornaments which are disadvantageous to survival.

The second kind of process of partner choice sexual selection was most clearly presented as the handicap principle (ZAHAVI 1975, 1977). This hypothesis claims that male sexual ornaments are indicators of the genetic quality of males; similar ideas were mentioned much earlier by FISHER (1930) and WILLIAMS (1966). The handicap principle in its early version was criticised as it needs maintaining of an unrealistically high level of genetic variation in fitness (DAVIS, O'DONALD 1976; MAYNARD SMITH 1976, 1978; BELL 1978). Improved versions of the hypothesis seemed more realistic (ANDERSSON 1986, 1994; POMIANKOWSKI 1987, 1988; TOMLINSON 1988; HEYWOOD 1989; PRICE et al. 1993). HAMILTON and ZUK (1982) proposed that variation in male resistance to parasites and pathogens could

be reflected in the level of elaboration of sexual ornaments. Consequently, the ornaments would provide females with the way to discriminate between infested and non-infested males. As parasites coevolve with hosts and infest the commonest genotypes, the less frequent genotypes evolve immunity and become able to develop an ornament. Thus, the host-parasite system will tend to fluctuate, which solves the problem of genetic variation in fitness (HAMILTON, ZUK 1982; KIRKPATRICK 1986; POMIANKOWSKI 1987, 1988; TOMLINSON 1988; IWASA et al. 1991; ANDERSSON 1994). ANDERSSON (1994) suggested that it is empirical studies which should evaluate the relative importance of different mechanisms of sexual selection.

3. Sexual selection and its consequence in the Swallow

The Swallow is a small passerine bird widely distributed over the Holarctic area. In Europe it nests mostly in different buildings constructed to keep animals in farms, like cowsheds, pigsties or stables. This species has been concurring with man at least since the Pleistocene (VIETINGHOFF-RIESCH 1955). Swallows have 1–2 regular broods per year (TURNER 1994; BAÑBURA, ZIELIŃSKI 1998). Almost exclusive food of swallows are insects, mostly big flies Diptera, caught on the wings (KOŽENA 1980, 1983; TURNER 1994). A characteristic feature of the Swallow, recorded even by some older authors, is its social monogamy with high level of paternal care of nestlings (e.g. WODZICKI 1878). As a common species living in farm buildings, the Swallow has become subject to many field studies, including studies on sexual selection.

The hypothesis that the outermost feathers of the forked tail of male Swallows constitute sexual ornaments undergoing sexual selection (BAÑBURA 1986) was put forward under the direct influence of having read DARWIN (1871). DARWIN (1871) considered sexual selection as the most important mechanism of the evolution of sexual dimorphism. The outermost tail feathers are the only morphological trait of the Swallow which is clearly sexually dimorphic, with male feathers longer than female ones, and with juvenile tails still shorter and less fork-shaped (Fig. 1 and 2). As there was no ecological explanation of this dimorphism, Darwinian sexual selection was accepted as the most likely mechanism of its evolution. The process of mating in the spring turned out to be complicated but its evident component is the demonstration of male tail to females both on the wing and on perch, this sexual display having place after getting a territory by the male (own observations). MØLLER (1988a) found that breeding pairs become established only after a particular male have been visited by several females.

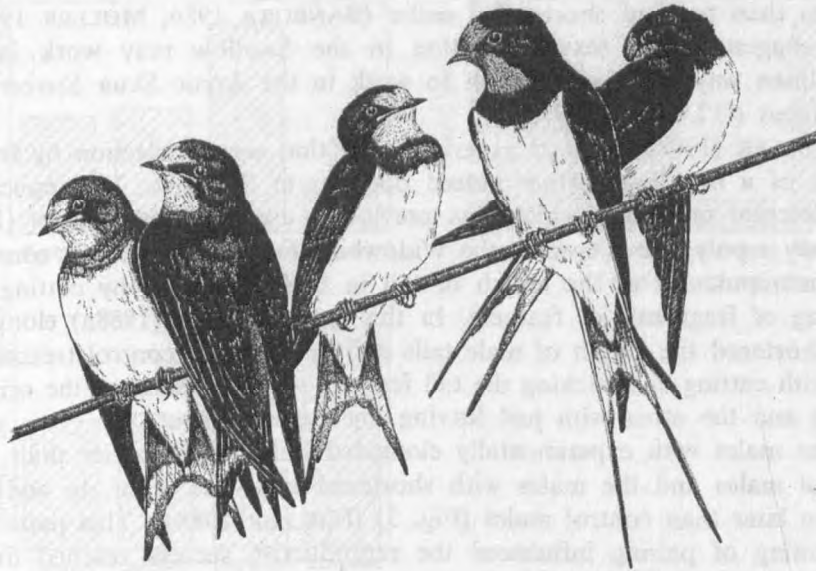


Fig. 1. Swallows – adult male (in front, right hand side), adult female (at background, right hand side) and three juvenile individuals (drawing by J. Dymitrowicz)

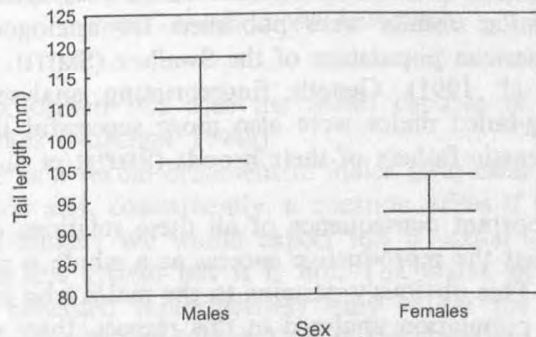


Fig. 2. Sexual dimorphism in the length of tail of Swallows in a central Poland population. Mean tail lengths \pm standard deviation are shown ($n = 302$), based on the data from BAÑBURA (1986)

The length of tail showed a slight positive correlation between male and female partners, suggesting a non-random mating, although this may or may not be a result of sexual selection (BAÑBURA 1986). DARWIN (1871) and FISHER (1930) suggested that in monogamous birds sexual selection can operate through the differentiation of fitness during the course of the breeding season. Accordingly, in the Swallow, breeding pairs which included

males with longer tails started breeding earlier and had a higher breeding success than pairs of short-tailed males (BAÑBURA 1986; MØLLER 1990a). This suggested that sexual selection in the Swallow may work in the Darwinian way, as it was shown to work in the Arctic Skua *Stercorarius parasiticus* (O'DONALD 1972).

MØLLER (1988a) showed experimentally that sexual selection by female choice of a breeding partner indeed operates in Swallows. He applied an experimental procedure which was previously used by ANDERSSON (1982) to study a polygynous species, the Widowbird *Euplectes progne*. It consisted of a manipulation of the length of tail in both directions by cutting and sticking of fragments of feathers. In this way MØLLER (1988a) elongated and shortened the length of male tails and applied two control treatments, one with cutting and sticking the tail feathers without changing the original length and the other with just leaving the feathers uncut.

The males with experimentally elongated tails paired earlier than both control males and the males with shortened tails, the latter, in addition, pairing later than control males (Fig. 3) (MØLLER 1988a). This pattern of the timing of pairing influenced the reproductive success reached during the breeding season. The breeding pairs of males with elongated tails had second broods more frequently and produced more fledglings than pairs of short-tailed and control males (Fig. 3). Moreover, the long-tailed males had also more extra pair copulations than short-tailed ones (MØLLER, TEGELSTRÖM 1997). Similar results were published for analogous experimental studies on an American population of the Swallow (SMITH, MONTGOMERIE 1991; SMITH et al. 1991). Genetic fingerprinting analyses of parentage showed that long-tailed males were also more successful than short-tailed males in being genetic fathers of their broods (SMITH et al. 1991; MØLLER 1994a).

The most important consequence of all these relations of the length of the male tail is that the reproductive success as a whole is positively related with tail lengths. This obviously pertains to the males who have been paired – in all Swallow population analysed in this respect, there exist males who have not found a breeding partner (MØLLER 1994a). Such single males have on the average shorter tails than paired males. A conceivable alternative reproductive strategy of males would be not to establish a breeding pair but to remain single and to engage in copulations with paired females. This type of behaviour proved to be rather unsuccessful (MØLLER 1994a). More successful but relatively infrequent strategy was based on attempts to pair a female by killing her nestlings and, in this way, destructing her existing pair bond (MØLLER 1994a). Infanticide resulting from attacks of foreign males was reported from both American and European Swallow populations (CROOK, SHIELDS 1985; MØLLER 1988b, 1994a; BAÑBURA, ZIELIŃSKI

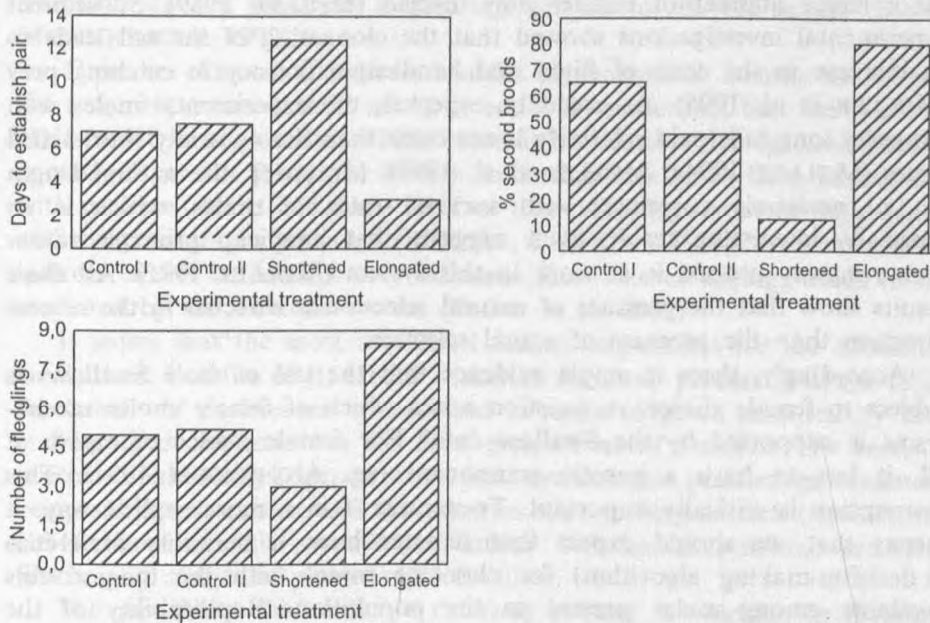


Fig. 3. Results of Møller's experiment with four treatments: elongated tails, shortened tails, control I (without manipulation) and control II (manipulation without change in length) (based on data of MØLLER (1988))

1995). Again, it turned out that the males capable of infanticide have relatively long tails (MØLLER 1994a).

The long tail as a sexual ornament of males gives clear benefits in terms of sexual selection and, consequently, a question arises if it is still evolving to become even longer? We would expect this if sexual selection were the only pressure in this system but it is not. The males with experimentally elongated tails benefited reproductively only within the breeding season when the experiment was conducted. During the moulting taking place after this breeding season, the long-tailed experimental males develop the outermost tail feathers shorter than the original feathers prior to the experiment, which puts them in a worse position in the following season (MØLLER 1989). Essentially, the costs of experimental manipulation of tail are mediated through the immune system, as shown in studies of MØLLER and co-workers (MØLLER, ERRITZOE 1996, 1998).

First costs of the experimental elongation of tails, connected with the efficiency of foraging, appeared even during the season when experiments were carried out, as the experimental males lost their ability to catch large, preferred flies (MØLLER 1994a; TURNER 1994). Hence those males had to

get a larger number of smaller prey instead (MØLLER 1989). Subsequent experimental investigations showed that the elongating of the tail leads to an increase in the costs of flight and handicap efficiency in catching prey (MØLLER et al. 1995). As could be expected, the experimental males with naturally long tails paid relatively lower costs than the naturally short-tailed males (MØLLER 1994a; MØLLER et al. 1995). Moreover, the natural length of tail positively correlates with survival rates of males, which is an especially interesting result, as it suggests that handicap principle rather than runaway process is at work in this system (MØLLER 1991). All these results show that the pressure of natural selection is directed in the reverse direction than the pressure of sexual selection.

Accordingly, there is ample evidence that the tail of male Swallows is subject to female choice. A question arises which of female choice mechanisms is supported by the Swallow data? For female choice to evolve at all, it has to have a genetic component (eg. ANDERSSOM 1994). This assumption is critically important. To express it in a more explicit way, it means that we should expect that females have a heritable preference (a decision-making algorithm) for choosing mates with the longest tails available among males present in the population. Repeatability of the choice may provide a rough estimate of the genetic component (FALCONER 1989). The first published analysis of repeatability of tail lengths of males paired to a particular females during subsequent reproductive episodes showed a low, statistically non-significant value of repeatability, 0.15 (BAÑBURA 1992). However, in this analysis only direct field measurements of mated males were taken into account, as if females trying to find a suitable mate always had males characterized by the same range of variation in the ornament to choose. MØLLER (1993a) repeated this kind of analysis using relative tail lengths with respect to the range of tail lengths available to females at the moment of mating, which showed that female Swallows are indeed consistent in their subsequent choices, as shown by significant repeatability of 0.57.

The next step in the analysis of the evolution of female choice in the Swallow would be assessing of costs and benefits resulting from practising the choice of mates. The direct costs connected with the effort put into searching for a suitable male is usually clear but not very high because single males, who come to the breeding grounds earlier than females, are very numerous at that time (BAÑBURA 1986; MØLLER 1994a). Preferring long tails of males makes females pay costs of the increased parental effort, as the male share in feeding nestlings is inversely related with their ornament size (MØLLER 1994a). This is probably the highest of the costs females pay for their preferences, which found support in Canadian populations where the male share in incubation and brooding (European male

Swallows do not incubate) is inversely related to the tail length (SMITH, MONTGOMERIE 1992).

There are direct and indirect benefits of choosiness. Among the former, the most important benefit seems to result from the fact that the preferred males are free of parasites which could infest females during close physical contact, if present (MØLLER 1994a). Indirect effects result from having sons with preferred traits and from the fact that offspring represent high quality and are resistant to parasites (MØLLER, ERRITZOE 1996). Another kind of indirect effects on females may influence their rate of ageing, which is also mediated by the immune system (SAINO et al. 2002).

It seems that the most important factors responsible for the choosiness are indirect benefits of it. Under Fisherian runaway process (FISHER 1930), the benefit of preferences is expressed in terms of genes inherited by sons, making them attractive to the next generations of females. The runaway process should always operate when there are heritable preferences, ornaments being subject to choice, and variation in male mating success (ANDERSSON 1994). However, this process can concur with handicap-related processes, which may also take place in the Swallow.

The possibility that Fisher's runaway process is working in Swallows can not be excluded. On the other hand, it is easy to find facts corroborating handicap principle at work in this species. In addition to preferring long-tailed males, female Swallows evidently choose mates characterized by bilaterally symmetric ornaments, which was shown by both observational and experimental studies (MØLLER 1992, 1994a). Randomly asymmetric development of traits, called fluctuating asymmetry, is typical of low quality individuals who are sensitive to stress (PARSONS 1993). According to MØLLER (1992, 1994a), the level of fluctuating asymmetry in the Swallow is inversely correlated with tail length. This result would support the importance of the outermost tail feathers as indicators of individual quality.

Long-tailed male Swallows are resistant to parasitic infestations, including infestations by hematophagous mite *Ornithonyssus bursa* studied by MØLLER (1990, 1994a). An adequate experimental procedure, including transferring nestlings between nests, enabled MØLLER to discover new facts of great importance. As expected, the infestation with this parasite negatively influences the host. Sensitivity of nestlings to the parasites is inherited from parents, with no influence of the nest and properties of stepparents. The long-tailed males produce offspring with low parasite load. Both genetic and early maternal effects influence the development of offspring immune systems (MØLLER 1994a; SAINO et al. 2001, 2002b). The expression of the sexual ornament in experimentally infested male Swallows was retarded. Moreover, parasite load of breeding partners tends to be positively related. All these results support the handicap hypothesis, which is also supported

by the correlation between viability of fathers and their offspring. This makes possible a reliable prediction of the chance of offspring survival on the basis of the length of paternal tail (MØLLER 1994b).

The results reviewed in this paper suggest that sexual selection plays a dominating role in the evolution of the tail length in the Swallow, which caused the species to have become a model example of sexual selection in action. In this situation a paper by NORBERG (1994) initiated much discussion. NORBERG (1994) claimed that the forked tail of the Swallow is an aerodynamic adaptation rather than a sexual ornament. The long tail streamers would enhance flight capacity and manoeuvrability and may be treated as a precise aerodynamic instrument, sensitive both to shortening and elongation (BALMFORD et al. 1993; NORBERG 1994; EVANS 1998).

It seems reasonable to take into account the strictly aerodynamic function of the tail as one of the forces involved in the evolution of its size and shape. However, a question arises what length is aerodynamically optimal, that of male tail, female tail or rather juvenile tail? Aerodynamic hypotheses do not explain sexual dimorphism of the tail nor the difference between the adult and juvenile Swallows. In central Poland, the tail of juveniles is on the average 70 mm long, i.e. much shorter than that of either females or males (Fig. 2) (WOJCIECHOWSKI 1992). This means that the mature form of the tail appears with sexual maturity, as is often the case with sexually selected traits (DARWIN 1871). Consequently, it seems that it is the length of juvenile tail which is shaped by natural selection as aerodynamic adaptation (CUERVO et al. 1996; EVANS 1998). Moreover, MØLLER and co-workers (1995) showed that the experimental elongation of the tail indeed limits capability to catch large flies but birds with the shortened tail benefit in terms of their ability to catch optimal prey. Finally, very strong support to the hypothesis that the length of streamers plays the role of a quality indicator is provided by experiments on asymmetry (MØLLER 1993b, 1994a). These studies showed that females choose males with visually symmetric tails even when symmetry or asymmetry are obtained by covering feathers with paints, not cutting. Painting, obviously, has no aerodynamic effects on birds. The last argument against the extreme variant of aerodynamic hypothesis results from the observation that long streamers often become broken during the breeding season, probably as a result of damaging contact with walls while feeding nestlings or perching (own unpublished observation). Such damage happens usually after the time of mating. Thus, it seems that the tail streamers of the Swallow are much too delicate as for structures whose length is to be maintained at optimum by natural selection.

To sum up, I presented arguments for the hypothesis that sexual dimorphism in tail length of the Swallow evolved in response to sexual

selection rather than natural selection. Sexual selection has far-reaching effects on the entire life history of this species, including its behavioural, physiological and morphological aspects. A lot is already known about mechanisms of this process, with the female choice based on the male tail length as a signal of his genetic quality being a clear one. Still it is possible that the Fisherian runaway process is also involved.

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