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Haematocrit correlates with tail ornament size in three populations of the Barn Swallow (*Hirundo rustica*)

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Summary

1. Handicap models of sexual selection propose that male ornaments are indicators of male quality and that honesty is enforced by the costs imposed by the exaggerated ornamental traits. In long-distance migratory birds that feed on the wing, the aerodynamic cost of exaggerated ornamental characters should be particularly high because the size of the ornaments deviates from the natural selection optimum. During migration, birds are expected to raise their oxygen consumption in relation to the energetic demands imposed by their morphology. An increase of haematocrit is an adaptive response to enhance oxygen uptake and efficiency of transfer to the muscular tissues during spells of intense muscular activity.

2. The change of haematocrit of Barn Swallows (*Hirundo rustica*) after their arrival to the breeding sites, and the relationships between haematocrit values recorded after migration and the size of ordinary and sexually selected morphological characters in three Barn Swallow populations were analysed.

3. Males had higher haematocrit values than females. Individual haematocrit values declined after arrival to the breeding sites. Haematocrit values of males were significantly and positively correlated with the size of their ornamental tail but not correlated with other characters, thus suggesting that well-ornamented males, in order to arrive early, have to raise their haematocrit above the level of short-tailed males.

4. Males and females of similar tail length did not differ in their haematocrit, thus suggesting that sexual dimorphism in haematocrit might be functionally related to dimorphism in tail length.

5. Our results are consistent with the handicap principle because long-tailed males experience lower mortality and larger seasonal reproductive success compared with short-tailed males.

Key-words: Arrival date, post-migration period, sexual dimorphism, sexually selected character

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Introduction

Advertisement models of sexual selection propose that exaggerated male secondary sexual characters could reliably signal male health and vigour by having the function of 'handicaps', i.e. characters that impose a cost to their bearer (Zahavi 1975, 1977; Heywood 1989; Grafen 1990). A commonly cited example of such characters is the ornamental tails of several bird species (Darwin 1871; Fisher 1930; Pomiankowski 1988). Extravagant tails apparently confer an advantage in the mating process because, by having a long tail, males are preferred by prospecting females. On the other hand, tail ornaments may be disadvantageous in contexts other than mate choice. It has been proposed, for example, that exaggerated tails may be costly because high androgen profiles, necessary for the development of male secondary sexual characters, have a suppressive effect on the immune system, thus reducing host immune defences against parasites, or exert a direct effect on parasites (Beckage 1983; Grossman 1985; Lawrence 1991; Folstad & Karter 1992). Large ornaments may be more conspicuous to predators than small ones, thus increasing predation risk. Moreover, aerodynamic costs may also increase with ornament size (e.g. Thomas 1993). This will be reflected in higher energy expenditure for flying or in lowered foraging efficiency determined by reduced manoeuvrability. Although the existence of aerodynamic costs of male bird ornaments has often been hypothesized, good empirical data relating ornament size with physiological measures of such costs are scarce.

A good model organism in a study of the relationship between size and costs of ornaments is the Barn Swallow (*Hirundo rustica*, Linnaeus). The Barn Swallow is a socially monogamous, migratory, aerially insectivorous passerine whose breeding range in the Western Palearctic covers a wide area from North Africa to northern Scandinavia (Cramp 1988). Wintering occurs in central and southern Africa. Barn Swallows reach their breeding ranges from February to June and leave for the winter quarters by July to October depending on latitude. The information about the reproductive biology of the Barn Swallow reported below is mainly taken from Møller (1994a). Males on average arrive some days before females and establish a small nesting territory where they try to attract prospecting females. Sexual dimorphism in morphological characters is small but it is relatively more pronounced for the outermost tail feathers. Correlational and manipulative studies have shown that females prefer to mate males with long outermost tail feathers and that fitness benefits accrue to well-ornamented males from female mate choice (see also Saino *et al.* 1997a). The outermost tail feathers of males exceed the aerodynamically optimal length (Thomas 1993). Males with comparatively long outermost tail feathers, as compared with those with short ones, capture smaller insect prey. Hence, long outermost tail feathers may impose a cost both in terms of energy expenditure for flying and in terms of foraging efficiency. However, recently it has been suggested that they might serve the function of ‘streamers’ which ultimately enables higher aerodynamic lift to be elicited from the tail with respect to a condition of shorter tail streamers (Norberg 1994).

If outermost tail feathers of males are costly to maintain, this should be reflected in a positive relationship between tail length and, for example, metabolic rate or oxygen consumption. This relationship should be particularly strong in periods of intense flying activity such as the spring migration towards the breeding grounds. Indeed, this is presumably the period of most intense flying during the annual life cycle because spring migration is faster than autumn migration. Moreover, individual time budgets during the breeding season are more skewed towards sedentary activities such as mate guarding, singing or perching in the territory. On the other hand, ordinary morphological traits, as opposed to ornamental traits, being shaped only by natural selection are presumably close to their natural selection optimum, and no correlation should be expected between their size and the energetic costs they impose during periods of intense flying activity.

The energy costs and metabolic rates associated with various activities of birds have been measured by a variety of techniques (e.g. Hails 1979; Vehrencamp, Bradbury & Gibson 1989; Andersson & Gustafsson 1995). Haematocrit is an easily measured serological variable that can be regarded both as a health status indicator and an index of metabolic activity during a period of weeks preceding the date of blood sampling (Carpenter 1975). Birds are known to raise their individual haematocrit in response to oxygen demands for thermogenesis in cold weather (Sealander 1962; Carey & Morton 1976). Intense locomotory activity has been shown to result in an increase of haematocrit (Palomeque & Planas 1978). Acclimatization to experimentally induced hypoxia and low oxygen partial pressures at high altitude involves erythropoiesis and an increase of haematocrit (Jaeger & McGrath 1974; Weathers & Snyder 1974; Clemens 1990). Mean haematocrit values in populations of migratory birds decline in the post-migration period, thus suggesting also that individual haematocrit is a negative function of time after the end of migration (Jones 1983; Morton 1994). At the interspecific level, strong flyers and migratory birds have higher haematocrit than resident ones (e.g. Carpenter 1975). Hence, birds seem to raise their haematocrit as an acclimatization to cold temperatures, low oxygen partial pressures and intense exercise, for example, during migration. From a functional point of view, raised haematocrit levels can be considered to be an adaptive physiological response that enhances efficiency of oxygen uptake and transfer by the blood stream (Gessaman, Johnson & Hoffman 1986) during spells of intense oxidative metabolic activity. The physiological mechanisms involved in the control of erythropoiesis are clearly linked to those associated with the onset of migration: migration is accompanied by an increase of thyroid activity and thyroid hormone promotes erythropoiesis. Haematocrit is sexually dimorphic in most avian species. It has been shown that administration of androgens determines an increase of haematocrit and haemoglobin while oestrogens increase blood fluids and lower red blood cell counts (Kern, DeGraw & King 1972; Nirmalan & Robinson 1972). Hence, individual differences in hormonal profile can be reflected in differences of haematocrit.

The main aim of this study was to relate post-migration haematocrit, i.e. haematocrit as measured immediately after arrival to the breeding sites, to the size of male and female ordinary and sexually selected morphological characters in Barn Swallows from three distant parts of the European breeding range. Our predictions were that: (a) haematocrit values of males and females declined after arrival to the breeding sites, (b) post-migration haematocrit of males was positively correlated with length of the outermost tail feathers (hereafter simply ‘tail length’), and (c) post-migration haematocrit of males was not correlated with the size of ordinary morphological traits. The predictions for the relationships between haematocrit of females and their morphology were weaker because no empirical data are available about the aerodynamic properties of female tails. From a theoretical standpoint, however, the optimal shape of a forked tail is triangular when the tail is fanned at 120° (Thomas 1993). To have such a shape, the outermost tail feathers have to be approximately twice as long as the innermost feathers. This ratio is actually observed, on average, in our study populations (Møller, de Lope & Saino 1995). This led to prediction (d) that no correlation should be expected between female tail length and haematocrit.

Study areas and methods

This study was carried out in three areas located in northern Jutland (Denmark, 57°12´N, 10°00´E), northern Italy (45°30´N, 9°20´E) and western Spain (38°50´N, 6°59´W) during 1992 (Denmark), 1993 (Italy), and 1994 and 1995 (Italy and Spain). The Danish study area is open farmland with scattered plantations, ponds and hedgerows. The Italian study area is intensively cultivated farmland where the prevailing crops are maize, fodder and soybean. A few poplar plantations and tree rows exist between the fields. The Spanish study area consists of open farmland with scattered groups of trees around farms and rivers.

In all the study areas Barn Swallow colonies were located in rural buildings, mainly cow stables, and just a few bred solitarily. Colonies were visited early in the morning every day (Spain) or every second day (Denmark and Italy) to record the arrival date of the first individuals. Swallows usually spend the night inside the stables where they breed, and can easily be sighted while flying between rural buildings and in open farmland, and males establish a territory and start singing immediately after their arrival to the breeding sites (Møller 1994a; N. Saino *et al.*, unpublished observations). It is therefore very unlikely that swallows escaped our prolonged (1 h or more) observation sessions during regular visits to the colonies. Individuals were captured during day time or at dawn by mist-nets starting on 10 May in Denmark, 28 March in Italy and 16 February in Spain. At the time of first capture a number of morphological characters were measured, including length of the left and right outermost tail feathers, length of the innermost tail feathers, left and right flattened wing length, and length of bill, keel and right tarsus. Tail and wing length were then expressed as the mean value of the left and right character.

At the time of first capture and, for a large proportion of individuals, at the time of subsequent recapture(s) a blood sample was taken in one to three capillary tubes after puncture of the ulnar vein. The blood samples averaged 150 μl in the three populations. Centrifugation conditions for the capillaries we used in this study were as follows: 4000 r.p.m. for 10 min in Italy, 11 500 r.p.m. for 10 min in Denmark and 11 500 r.p.m. for 7 min in Spain, always referring to a radius of the centrifuge rotor of 94 mm. In each study area, haematocrit was always measured by the same, experienced person. Haematocrit was measured in each capillary tube as the percentage proportion of the length of the part of the capillary occupied by red blood cells in respect to the total length of the part of the capillary occupied by blood components. Haematocrit in two randomly chosen capillaries from the same individual was highly and significantly repeatable in a random subsample of 500 individuals in our large set of haematocrit data collected during three years in Italy (repeatability computed according to Falconer 1989: $R^2 = 0{\cdot}91$; $F = 22{\cdot}00$, df = 498, 499, $P = 0{\cdot}0001$), and individual haematocrit was therefore expressed as the mean of haematocrit recorded for the capillaries available.

Since centrifugation conditions were different in the three study areas, geographic variation of haematocrit is not analysed here. In all the analyses in which haematocrit data from the three populations are entered simultaneously, the effect of population was controlled for by entering it as a covariate.

Correlation analyses have been run using Pearson's product moment correlation coefficient or Kendall's (when variables were not normally distributed). Haematocrit values entered in the analyses of variance and covariance (see Results) were found to be normally distributed. All statistical tests reported are two-tailed. The limit of statistical significance was set at $P < 0{\cdot}05$. For a few individuals, the value of haematocrit or some morphological variables were missing. In all analyses, however, we considered the largest sample available.

Results

HAEMATOCRIT AND CALENDAR DATE

To analyse the relationship between individual haematocrit and calendar date, two analyses were run. First, for individuals that have been sampled twice during the same breeding season, the haematocrit values recorded at first and second capture were compared by paired *t*-tests. In Italy and Spain haematocrit at second capture of both males and females was found to be significantly smaller than that at first capture (H_0: haematocrit at second capture – haematocrit at first capture = 0; males Italy, $t = -6{\cdot}87$, 369 df, $P < 0{\cdot}0001$; males Spain, $t = -7{\cdot}68$, 72 df, $P < 0{\cdot}0001$; females Italy, $t = -3{\cdot}51$, 152 df, $P < 0{\cdot}001$; females Spain, $t = -5{\cdot}64$, 73 df, $P < 0{\cdot}0001$). Danish males also had a significant decrease of haematocrit ($t = -2{\cdot}15$, 20 df, $P < 0{\cdot}05$) while no data were available for Danish female swallows. Second, the change of haematocrit of Spanish and Italian individuals were analysed by an ANCOVA in which sex and population were entered as factors and time elapsed from capture to recapture as a covariate. This analysis showed that the change of haematocrit increased with intercapture interval ($F = 24·12$, 1 df, $P < 0·0001$, $n = 670$). To check for a non-linear decrease of haematocrit the quadratic term of intercapture time was included in the ANCOVA, which, however, did not significantly covary with change of haematocrit after the linear term was included in the model. This allowed the daily decline of haematocrit to be calculated as the ratio between change of haematocrit and intercapture time (Fig. 1). Intercapture times were 25·7 days (0·95 SE) for Italian males, 24·8 days (1·17 SE) for Italian females, 105·3 days (2·12 SE) for Spanish males, 95·8 days (2·57 SE) for Spanish females, and 33·9 days (2·18 SE) for Danish males (see Fig. 1 for sample sizes).

To check if ranking of individual haematocrit was consistent, i.e. if individuals that had comparatively high haematocrit at the first capture also had relatively high haematocrit at recapture, haematocrit values at first and second capture were correlated, while controlling for the effect of both first and second capture dates in partial correlation analyses. Significant positive correlations were found both in Italy (males, $r_{\text{par}} = 0·20$, $n = 370$, $P < 0·001$; females, $r_{\text{par}} = 0·21$, $n = 153$, $P = 0·01$) and in Spain (Kendall partial correlation coefficient; males, $\tau = 0·22$, $n = 73$, $P < 0·05$; females, $\tau = 0·18$, $n = 74$, $P < 0·05$). No significant partial correlation was found in the small sample of males available from Denmark (Kendall partial correlation coefficient; $\tau = –0·01$, $n = 21$, NS).

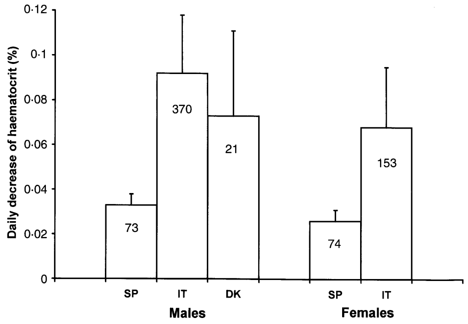

Fig. 1. Mean (SE) daily decrease of haematocrit expressed as the ratio between decrease from first capture to recapture and intercapture time (in days). Numbers are sample sizes. (SP, Spain; IT, Italy; DK, Denmark.)

HAEMATOCRIT AND MORPHOLOGY

Since it had been shown that individual haematocrit at the breeding sites is a negative function of calendar date, our analyses of haematocrit in relation to morphology had to be restricted to those individuals for which it could be assumed that the time elapsed between arrival and sampling date of haematocrit had been very short. For this purpose, for each of the study areas and years, we considered only: (1) individuals sampled for haematocrit before that 4 weeks had elapsed from the arrival of the first individual to our study colonies, and (2) individuals captured in colonies in which intense capture effort and frequent capture sessions had been made during the beginning of the breeding season. Mean capture dates of individuals are reported in Table 1, while mean post-migration haematocrit and tail length are shown in Figs 2 and 3, respectively.

The relationship between each of the morphological variables and haematocrit for the individuals chosen using the criteria described above was analysed by ANCOVAs in which haematocrit was entered as the dependent variable, population as a factor, and a morphological variable as a covariate. To have further control on the possibility that some individuals escaped our capture attempts and were captured only after several days had elapsed from their arrival, the date of first capture was also included as a covariate. This procedure allowed us partially to remove the effect of time elapsed from arrival to sampling date of haematocrit. Tail length of males significantly and positively covaried with post-migration haematocrit ($F = 12·21$, 1 df, $P < 0·001$, $n = 469$) while capture date did not ($F = 3·22$, 1 df, NS). Hence, males that had higher haematocrit also had comparatively long tails, and haematocrit of individuals that arrived early was not significantly higher when the effect of tail length was controlled statistically. The other morphological variables (bill length, tarsus length, keel length, wing length and innermost tail feathers' length) were unrelated to post-migration haematocrit (F-values from ANCOVAs always associated with P-values larger than 0·1). Analyses of covariance run for females with the same model as for males showed no significant relationship between haematocrit and length of the outermost tail feathers ($F = 0·26$, 1 df, NS, $n = 318$), or the other morphological variables (F-values from ANCOVAs always associated with P-values larger than 0·1).

Table 1. Mean (SE) haematocrit sampling dates for 'early arriving' individuals, i.e. individuals sampled for haematocrit before 4 weeks had elapsed from the arrival of the first individual to our study colonies, and were captured in colonies in which intense capture effort had been performed

	Denmark	Italy	Spain
Males	20·5 May (0·36 days) $n = 45$	14·5 April (0·44 days) $n = 243$	25·6 February (0·51 days) $n = 181$
Females	21·1 May (0·35 days) $n = 44$	16·0 April (0·59 days) $n = 133$	27·3 February (0·57 days) $n = 149$

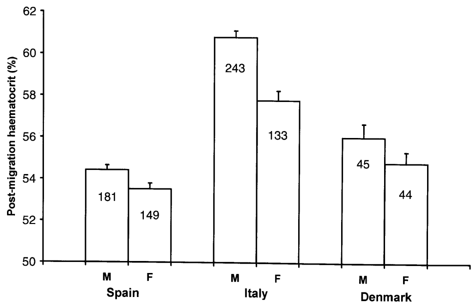

Fig. 2. Mean (SE) of haematocrit of individual Barn Swallows captured immediately after arrival and before 4 weeks had elapsed from arrival of the first individuals to our study colonies. Numbers are sample sizes.

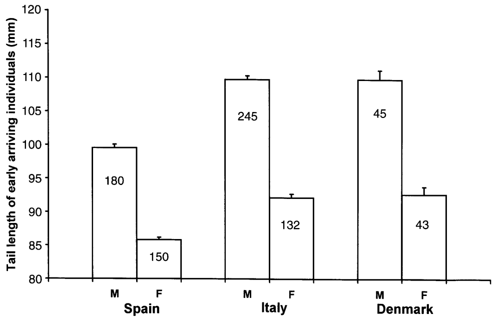

Fig. 3. Mean (SE) tail length of individual Barn Swallows captured immediately after arrival and before 4 weeks had elapsed from arrival of the first individuals to our study colonies. Figures are sample sizes.

In each of the three populations, morphological variables (see Methods) were not significantly correlated with first capture date of early arriving males (i.e. males captured less than 4 weeks after the arrival of the first male; *r*-values always statistically not significant after Bonferroni correction for multiple comparisons; sample sizes as in Fig. 2).

SEXUAL SIZE DIMORPHISM OF TAIL AND HAEMATOCRIT

A two-way analysis of variance in which sex and population were entered as factors together with their interaction term showed that sex had a significant effect on post-migration haematocrit ($F = 18{\cdot}20$, 1 df, $P < 0{\cdot}0001, n = 790$), males having larger haematocrit than females. To compare haematocrit between males and females while controlling for the effect of sexual size dimorphism in tail length, both males and females of each population were partitioned in classes of tail length and the mean haematocrit value within each class was computed. Mean haematocrits of males and females were then matched for tail length and compared by paired *t*-tests within each population. Interestingly, haematocrit of males was not larger than that of females with similar tail length (Table 2). Indeed, males tended consistently to have lower haematocrit than females in all populations.

Discussion

The results of this study can be summarized as follows: (a) individual haematocrit of males and females after arrival to the breeding sites was a decreasing function of calendar date; (b) post-migration haematocrit of males was positively correlated with a sexually selected character, tail length, whereas (c) it was uncorrelated with other morphological features; and (d) no correlation was found between haematocrit and female morphology. Hence, all of our predictions were verified. In addition, no sexual dimorphism in post-migration haematocrit existed after controlling for dimorphism in tail length.

To our knowledge, this is the first study showing that individual haematocrit declines after arrival to the breeding sites. Previous studies have shown that within-population mean haematocrit is lower as the breeding season progresses. However, this result may have been partly due to the fact that individuals that arrived late had lower haematocrit than those that arrived early. The presumed decrease of individual haematocrit after migration has been attributed to an adaptive increase of haematocrit during the prolonged migration effort and the comparatively low energy demands during breeding. Migrating birds may be better able to sustain high levels of oxidative metabolism during migration flights by increasing their haematocrit and therefore by increasing oxygen uptake and efficiency of transfer to muscular tissues involved in flight. Our results can be interpreted exactly along the same line of reasoning. Of course, Barn Swallows also experience spells of very intense flying during their breeding cycle. For example, parents have to work hard in order to provide offspring with their aerial food. However, these periods account for a relatively small proportion of the breeding season, because nestlings are fed intensively when they are 5–15-days old, and Barn Swallows rarely have more than two broods each breeding season.

A highly significant positive correlation was observed between post-migration haematocrit of males and their tail length. On the other hand, no significant correlation was observed between any of the other morphological features of males and post-migration haematocrit. Arrival date was found not to be significantly correlated with post-migration haematocrit when the effect of tail length was controlled. All these pieces of evidence when combined strongly suggest that: (1) high haematocrit is not associated with late arrival to the breeding sites, and (2) comparatively high haematocrit is associated with the condition of having a long tail and not ordinary morphological traits of any particular size. This finding is consistent with the results of an experiment in which elongation of male Barn Swallow tails determined a reduction in the natural role of decrease of haematocrit after migration (Saino *et al.* 1997b).

A fundamental assumption of honest advertisement models of sexual selection is that ornamental characters, such as tail length of male Barn Swallows, are costly either to produce or to maintain. A probable cost for a long-distance migratory bird having a tail whose length exceeds the natural selection optimum is the increased energy demands for flying. If the level of this cost is a direct function of ornament size, then well-ornamented individuals may either slow down their migration flight and arrive later or alter their physiology to meet the increased energy demands imposed by their morphology. Our results indicate that the latter is the case in the Barn Swallow. Males with long tails had higher haematocrit levels, but did not arrive later than those with short tails. Indeed, no significant correlation was observed between first capture date of early arriving males and tail length. These results do not contradict the observation consistently reported from our study areas that long-tailed males arrive significantly earlier than short-tailed males (Møller 1994a). When the analysis of arrival date in relation to tail length is extended to all males, a strongly negative correlation exists (N. Saino & A. P. Møller, unpublished observations). Haematocrit at arrival might not reflect that during migration. However, this is unlikely to be the case because (1) the ranking of individuals according to their haematocrit was consistent during the breeding season, at least in populations for which large samples were available (this suggests that relative haematocrit values are an individual’s feature which is retained during different parts of the circannual cycle) and (2) a change of haematocrit in response to experimental change in ecological conditions is known to have a latency up to several weeks and, hence, what we measured should have been representative of the haematocrit during the last part of the migration (Morton 1994).

If erythropoiesis is a costly anabolic activity, males with long tails might have to pay more for their haematocrit than those with short tails. In this respect, our results are consistent with the handicap principle because well-ornamented males could afford to have a long tail without apparently paying any additional costs (Møller 1994b). They did not delay their arrival, which might have resulted in lowered seasonal reproductive success. Moreover, long-tailed males are known to have higher survival prospects (Møller 1994a) and, thus, working harder than short-tailed males during migration does not reduce their chance to survive to the following season.

Table 2. Post-migration haematocrit (mean ± SE) of male and female Barn Swallows of similar tail length. Student’s *t*-values are derived from pairwise comparisons of mean haematocrit within classes of 0·5 mm (Italy and Spain) or 1 mm (Denmark) of tail length. The range of tail lengths considered for each population is also shown.

	Range of tail length (mm)	Males	Females	*t*	*df*	*P*
Spain	83·5–95	53·5 ± 0·75 *n* = 43	54·1 ± 0·49 *n* = 69	0·72	14	>0·4
Italy	92–99·5	58·5 ± 0·73 *n* = 31	59·0 ± 1·01 *n* = 54	0·39	11	>0·7
Denmark	94–106	54·8 ± 0·90 *n* = 10	55·7 ± 1·27 *n* = 11	0·92	6	>0·3

Post-migration haematocrit of females was not correlated with their tail length. Hence, female outermost tail feathers may actually be optimally shaped for flight as predicted from their optimal ratio between length of the outermost and innermost tail feathers (Thomas 1993).

Two of our results suggest that sexual dimorphism of post-migration haematocrit might be at least partly functionally linked to size dimorphism in tail length resulting in different flight costs. First, only tail length, which has the largest sexual size dimorphism among morphological characters, was positively correlated with haematocrit. Second, in all populations studied, no differences in haematocrit between males and females existed, for a given length of tail. Hence, sexual dimorphism in haematocrit might be partly due to flying costs imposed by tails of different size.

In conclusion, male Barn Swallows have larger haematocrit than females, and haematocrit declines after migration. Haematocrit values of males recorded immediately after arrival at the breeding sites were positively related with the size of their ornamental tails thus suggesting that well-ornamented males, in order to arrive early, have to raise their haematocrit above the level of short-tailed males. This pattern is consistent with the handicap principle because long-tailed males do not experience either increased mortality or reduced seasonal reproductive success compared with short-tailed males. Our results also suggest that sexual dimorphism of haematocrit might be functionally related to sexual size dimorphism in tail length.

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References

Andersson, M.S. & Gustafsson, L. (1995) Glycosylated haemoglobin: A new quantitative measure of condition in birds. *Proceedings of the Royal Society of London B* **260,** 299–303.

Beckage, N.E. (1983) Endocrine and neuroendocrine host–parasite relationships. *Receptor* **3,** 233–245.

Carey, C. & Morton, M.L. (1976) Aspects of circulatory physiology of montane and lowland birds. *Comparative Biochemistry and Physiology,* **54A,** 61–74.

Carpenter, F.L. (1975) Bird haematocrits: Effects of high altitude and strength of flight. *Comparative Biochemistry and Physiology*, **50A,** 415–417.

Clemens, D.T. (1990) Interspecific variation and effects of altitude on blood properties of Rosy Finches (*Leucosticte arctoa*) and House Finches (*Carpodacus mexicanus*). *Physiological Zoology* **63,** 288–307.

Cramp, S. (1988) *Birds of Europe, the Middle East and North Africa*. Oxford University Press, Oxford.

Darwin, C. (1871) *The Descent of Man, and Selection in Relation to Sex*. John Murray, London.

Falconer, D.S. (1989) *Introduction to Quantitative Genetics*. Clarendon Press, Oxford.

Fisher, R.A. (1930) *The Genetical Theory of Natural Selection*. Clarendon Press, Oxford.

Folstad, I. & Karter, A.J. (1992) Parasites, bright males and the immunocompetence handicap. *American Naturalist* **139,** 603–622.

Gessaman, J.A., Johnson, J.A. & Hoffman, S.W. (1986) Haematocrits and erythrocyte numbers for Cooper's and Sharp-shinned Hawks. *Condor* **98,** 95–96.

Grafen, A. (1990) Sexual selection unhandicapped by the Fisher process. *Journal of Theoretical Biology* **144,** 473–516.

Grossman, C.J. (1985) Interactions between the gonadal steroids and the immune system. *Science* **227,** 257–261.

Hails, C.J. (1979) A comparison of flight energetics in hirundines and other birds. *Comparative Biochemistry and Physiology*, **63A,** 581–585.

Heywood, J.S. (1989) Sexual selection by the handicap mechanism. *Evolution* **43,** 1387–1397.

Jaeger, J.J. & McGrath, J.J. (1974) Haematologic and biochemical effects of simulated high altitude on Japanese Quail. *Journal of Applied Physiology* **37,** 357–361.

Jones, P.J. (1983) Haematocrit values of breeding Red-billed Queleas (*Quelea quelea*) (Aves: Ploceidae) in relation to body condition and thymus activity. *Journal of Zoology, London* **201,** 217–222.

Kern, M.D., DeGraw, W.A. & King, J.R. (1972) Effects of gonadal hormones on the blood composition of White-crowned Sparrow. *General and Comparative Endocrinology* **18,** 43–53.

Lawrence, P.O. (1991) Hormonal effects on insects and other endoparasites *in vitro*. *In Vitro Cellular & Developmental Biology*, **27A,** 487–496.

Møller, A.P. (1994a) *Sexual Selection and the Barn Swallow*. Oxford University Press, Oxford.

Møller, A.P. (1994b) Phenotype dependent arrival time and its consequences in a migratory bird. *Behavioral Ecology and Sociobiology* **35,** 115–122.

Møller, A.P., de Lope, F. & Saino, N. (1995) Sexual selection in the barn swallow: Aerodynamic adaptations. *Journal of Evolutionary Biology* **8,** 671–688.

Morton, M.L. (1994) Haematocrits in montane sparrow in relation to reproductive schedule. *Condor* **96,** 117–126.

Nirmalan, G.P. & Robinson, G.A. (1972) Hematology of Japanese Quail treated with exogenous stilbestrol dipropionate and testosterone propionate. *Poultry Science* **51,** 920–925.

Norberg, R. (1994) Swallow tail streamer is a mechanical device for self-deflection of tail leading edge, enhancing aerodynamic efficiency and flight manoeuvrability. *Proceedings of the Royal Society of London B* **257,** 227–233.

Palomeque, J. & Planas, J. (1978) Blood volume in domestic pigeons. *Comparative Biochemistry and Physiology*, **59A,** 413–417.

Pomiankowski, A. (1988) The evolution of female preferences for male genetic quality. *Oxford Surveys in Evolutionary Biology* **5,** 136–184.

Saino, N., Primmer, C.R., Ellegren, H. & Møller, A.P. (1997a) An experimental study of paternity and tail ornamentation in the barn swallow (*Hirundo rustica*). *Evolution* **51,** 562–570.

Saino, N., Cuervo, J.J., Krivacek, M., Delope, F. & Møller, A.P. (1997b) Experimental manipulation of tail ornament size affects the haemocrit of male Barn Swallows (*Hirundo rustica*). *Oecologia* **110,** 186–190.

Sealander, J.A. (1962) Seasonal changes in blood values of deer mice and other small mammals. *Ecology* **43,** 107–119.

Thomas, A.L.R. (1993) On the aerodynamics of birds' tail. *Philosophical Transactions of the Royal Society of London B* **340,** 361–380.

Vehrencamp, S.L., Bradbury, J.W. & Gibson, R.M. (1989) The energetic cost of display in male sage grouse. *Animal Behaviour* **38,** 885–896.

Weathers, W.W. & Snyder, G.K. (1974) Functional acclimation of Japanese Quail to simulated high-altitude. *Journal of Comparative Physiology* **93,** 127–137.

Zahavi, A. (1975) Mate selection – A selection for a handicap. *Journal of Theoretical Biology* **53,** 205–214.

Zahavi, A. (1977) The cost of honesty (further remarks on the handicap principle). *Journal of Theoretical Biology* **67,** 603–605.

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