Journal of Animal Ecology 1998,
67, 845–852

Fitness correlates of spur length and spur asymmetry in male wild turkeys

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Summary

1. Tarsal spurs play an important role in intrasexual competition for females among male wild turkeys (*Meleagris gallopavo*). Thus variation in spur development may have important fitness consequences.

2. Fitness correlates of spur development were studied in a free-living population of wild turkeys and it was found that heavier males and males with longer beards had longer spurs. Males that had longer spurs spent more time on display areas during the breeding season and less time moving among these areas compared to males with shorter spurs, independently of their body mass.

3. Otherwise ideally symmetrical spurs showed fluctuating asymmetry between left and right tarsi, the degree of absolute asymmetry decreased with spur length in adults, but not in subadults, and males that survived at least one winter had more symmetrical spurs compared to males that did not.

4. We conclude that if the ability to produce symmetrical spurs has a genetic basis, then spur length and spur asymmetry could reliably indicate individual quality and that these traits are under directional selection for increased size and symmetry in wild turkeys.

Key-words: fluctuating asymmetry, *Meleagris gallopavo*, sexual selection, tarsal spurs.

Journal of Animal Ecology (1998) **67**, 845–852

Introduction

Evolution of sexually dimorphic weapons in animals is largely favoured by intrasexual competition and by female choice of well-ornamented males (reviewed in Andersson 1994). Both processes assume directional selection for weapons of larger size because individuals with larger weapons are more successful in intrasexual competition for mates and thus have higher mating success (Brown & Bartalon 1986; Zeh 1987; Conner 1988).

Tarsal spurs are an example of sexually dimorphic weapons in many bird species (Davison 1985; Møller 1992; Sullivan & Hillgarth 1993). While variation in spur length and growth have received considerable attention in studies of sexual selection (Schantz *et al.* 1989; Hillgarth 1990; Wittzell 1991; Grahn, Göransson & Schantz 1993a, 1993b; Sullivan & Hillgarth 1993; Grahn & Schantz 1994; Buchholz 1995), the mechanism of mate choice based on spur characteristics remains poorly understood (Göransson *et al.* 1990; Hillgarth 1990; Zuk *et al.* 1990; Zuk, Ligon & Thornhill 1992; Mateos & Carranza 1996). Studies of several galliform bird species have shown that spur length is correlated with viability and reproductive success more than other sexually dimorphic morphological traits (Kelly 1975; Schantz *et al.* 1989; Steffen, Couvillion & Hurst 1990; Wittzell 1991; Mateos & Carranza 1996). Such close association of spurs with fitness is consistent with their prominence in displays and use as either weapons or ritualized ornaments during male–male competitive interactions (Hewitt 1967; Davison 1985; Zuk *et al.* 1990; Grahn *et al.* 1993a; Sullivan & Hillgarth 1993).

Female preference for males with the longest spurs could be based on female assessment of the male's fighting ability, phenotypic quality, or interaction of these factors (Zuk *et al.* 1990, 1992; Grahn *et al.* 1993a,b; Mateos & Carranza 1996). One way to infer whether longer spurs are reliable indicators of male

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quality that may have a genetic basis or whether they are just indicators of the male's fighting ability is to examine patterns of spur asymmetry (Møller 1992, 1993; Sullivan, Robertson & Aebisher 1993; Grahn & Schantz 1994; Mateos & Carranza 1996). Random deviations from ideal symmetry in bilaterally symmetrical traits [fluctuating asymmetry (FA)] may arise from individual differences in the ability to resist environmental, genetic and developmental stress (Mather 1953; Reeve 1960; Van Valen 1962; Palmer & Strobeck 1986; Zakhatov 1987; Parson 1990; Møller & Pomiankowski 1993a; Swaddle & Witter 1994). Consequently, FA is closely associated with various fitness measures (e.g. Mitton & Grant 1984; McKenzie & Clarke 1988; Thornhill 1992a,b; Thornhill & Sauer 1992; reviewed in Møller 1997) and the levels of FA could be used as an indicator of individual quality (Møller & Höglund 1991; Møller & Pomiankowski 1993a; Watson & Thornhill 1994; Møller 1997; Badyaev 1998). Specifically, if FA of a secondary sexual character is selected as an indicator of individual quality, a negative correlation would be expected between absolute asymmetry in a trait and trait size, because better quality individuals should be able not only to develop the largest weapons but also be better able to endure environmental and developmental stress (Møller & Höglund 1991; Møller 1992). If FA of a trait is not used in mate choice or intrasexual competition for mates, one can expect a flat, or positive relationship between FA and trait size, if larger traits are more expensive to produce (see discussion in Møller 1992; Evans 1993; Evans & Hatchwell 1993; Evans, Martins & Haley 1995).

The study reported here examined variation in length, mode of selection, and fitness correlates of developmental stability in tarsal spurs of eastern wild turkeys (*Meleagris gallopavo silvestris* L.) from a single population in the Arkansas Ozarks, U.S.A. In wild turkeys, only males have fully developed spurs. Indirect evidence suggests that in wild turkeys, a male's ability to grow large spurs may increase his mating success. Males compete for display areas with good acoustic characteristics and close proximity to nesting grounds, because such locations maximize encounters with females (Healy 1992; Badyaev, Etges & Martin 1996a). Because suitable nesting areas for females are limited in the study area (Badyaev 1995; Badyaev, Martin & Etges 1996c) and frequently change among years (Badyaev & Faust 1996), a male's ability to produce and maintain large spurs may directly influence his ability to fight with or to display to other males in competition for more suitable display grounds and, ultimately, lead to an increase in his mating success. In addition to tarsal spurs, male wild turkeys exhibit an array of sexually dimorphic ornamental traits, such as a long hair-like beard projecting from their chest. The function of multiple ornaments in mate choice of wild turkeys is not well known (Buchholz 1995). Thus, interactions were also examined between two ornamental traits—tarsal spur size and beard length.

Age-related variation in spur length and the relationship between spur length and body mass and beard length were first examined. The second investigation concerned whether spurs show antisymmetry, fluctuating or directional asymmetry. The predictions that spur length would be linearly negatively related to the absolute value of spur asymmetry were then examined, assuming that: (i) spur is under directional selection for increase in length; and (ii) spur size indicates male phenotypic quality (Møller & Pomiankowski 1993a). Previous investigations of the study population suggested that intrasexual competition for access to females is weaker in second-year (SY) males than in after-second-year-old (ASY) males (Badyaev, Etges & Martin 1996a,b). Thus, a stronger relationship was expected between absolute asymmetry and spur size in ASY males. Finally, spur length and spur asymmetry were examined for variation in display-range movements and overwinter survival of males.

Methods

FIELD COLLECTIONS

This study was conducted in the Ozark National Forest in northern Arkansas, U.S.A. Male wild turkeys were captured using cannon nets on prebaited sites during 30 days in February and March. Spur lengths were measured from the base to the tip (to the nearest 0·5 mm). These measurements were obtained for 209 males during 1992–95. Forty-one males had one or both spurs that were visibly damaged, recently broken, or heavily worn. These birds were excluded from these analyses. Each bird was radio-marked with motion-sensitive, radio-transmitters upon first capture and data for all recaptures were excluded from these analyses. See Badyaev (1995) and Badyaev *et al.* (1996b) for a description of the study site and details of telemetry protocols.

ANALYSIS OF SPUR ASYMMETRY

To ensure that measurements were sufficiently precise to detect the asymmetry between spurs, measurement errors associated with both spur length and asymmetry in spurs were examined (Swaddle, Witter & Cuthill 1994). During the first year of study (1992), the repeatability (R) and measurement error were determined by remeasuring spurs in every captured individual. Repeatability was then calculated following the method of Becker (1984). In addition, the variance in asymmetry of the within-individual sample ($N = 6$) was compared to the variance of the sample for all birds in the same age groups captured in 1992. The variance of within-spur measurements was significantly smaller than the variance of between-spur measurements for both age classes: SY males: 0·24 vs. 1·87, $F_{18} = 56{\cdot}45$, $N_1 = 6$, $N_2 = 14$, $P < 0{\cdot}001$, $R = 0{\cdot}88$; ASY males: 0·44 vs. 10·28, $F_{12} = 325{\cdot}92$,

$N_1 = 6$, $N_2 = 8$, $P < 0{\cdot}001$, $R = 0{\cdot}96$. The variance of asymmetry expected from measurement error was significantly smaller than the variance of observed spur asymmetry (both $F_{14,84}$ and $F_{8,48} > 6{\cdot}00$, $P < 0{\cdot}001$).

For comparison, several measures of spur length and spur asymmetry were used. Mean spur length of an individual was the mean of left and right spurs [0·5 × (L + R)]. Absolute asymmetry was calculated as the unsigned difference in length between left and right spurs (|L − R|). Relative asymmetry was (|L − R|)/0·5 × (L + R)). Asymmetry was also calculated separately for SY and ASY males as |individual absolute asymmetry − mean absolute asymmetry of age group| (Dufour & Weatherhead 1996; Whitlock 1996). Variation in the last measure, and its relation with trait size did not differ from that of absolute asymmetry, thus only the results of the two first measures are reported. According to Sullivan *et al.* (1993), regression of relative FA on mean trait size is inherently biased, while regression of absolute FA on mean trait size may produce biased slope estimates when FA is large. They recommended using the largest of the paired characters in regressions of FA on trait size (Sullivan *et al.* 1993; see also Evans & Hatchwell 1993). Neither spur length nor spur asymmetry measures differed among 3 years (ANCOVA, $F = 0{\cdot}07$, $P > 0{\cdot}3$). Therefore data were pooled among study years.

For the present study the Shapiro and Wilk test (Zar 1984) was used to determine whether the asymmetry in spurs was normally distributed and a *t*-test to test whether the mean asymmetry was zero in the population. Plots were evaluated on untransformed data and results of linear and second-order polynomial regressions to examine whether the relationship between asymmetry and spur length was linear or U-shaped. Residual plots and residual statistics were examined to ensure validity of normality and variance homogeneity assumptions in regression analyses (SAS Institute 1989; Montgomery & Peck 1992). To avoid pseudoreplications, only males that survived their first winter after capture were used in survival analyses. The mean date between the last ‘alive’ and the first ‘mortality’ mode of radio-signal was used as a reference for mortality date. Only data for males that died of natural causes, such as predation and disease, were included in the survival analyses.

Results

In both age classes males with longer spurs were heavier and had longer beards compared to males with shorter spurs (Table 1; Figs 1 and 2). When body mass was controlled, spur length increased with beard length in ASY but not in SY males (Fig. 2). Spur and beard length were smaller in SY birds than in subsequent years of life (Table 2). Absolute, but not relative asymmetry in spurs was greater in ASY than in SY males (Table 2).

Spurs of wild turkeys showed fluctuating asymmetry (FA), because the population mean of left minus right spur length did not differ from zero in either age class (Table 2) and asymmetry was normally distributed ($W = 0{\cdot}75$, $P < 0{\cdot}001$). In addition, examination of plots of |L − R| spur vs. spur length (Fig. 3) confirmed that spurs show fluctuating asymmetry rather than antisymmetry because symmetrical, or nearly symmetrical, individuals were most common in all spur size classes, but were proportionally less common among males with shorter spurs (Fig. 3). Regression analyses and examination of residual plots revealed that FA was linearly related to spur length (e.g. absolute FA on longest spur, linear regression—SY males: $F = 8{\cdot}547$, $P = 0{\cdot}004$; ASY males: $F = 4{\cdot}08$, $P = 0{\cdot}04$;—second-order polynomial regression—SY males: $F = 0{\cdot}034$, $P = 0{\cdot}85$; ASY males: $F = 0{\cdot}13$, $P = 0{\cdot}72$).

In ASY males, FA in spurs (relative and absolute) significantly decreased with spur length (Table 2). Similarly, in SY males, the relationships were mostly negative (with the exception of absolute FA vs. mean spur length), but did not reach significance (Table 2). The present study concluded that FA in spurs did not vary with spur length in SY males, but decreased with spur size in ASY males (Table 2, Fig. 3).

Spur length predicted display-related movements during breeding seasons better than did beard length (Table 1). In ASY males, longer-spurred birds spent more time within display areas and less time travelling between these areas compared to shorter-spurred males. In both age classes, males that survived a full year following capture had more symmetrical spurs compared to males that died (Table 3). Other measured traits did not differ significantly between males that survived compared to those that died (Table 3).

Discussion

The present study found that spur length appears to be a reliable indicator of viability in wild turkeys. Within each age class, spurs were longer in heavier males and in males with longer beards (Table 1, Figs 1 and 2). Males that survived to older ages had longer spurs (Table 1). These findings are concordant with the widespread use of spur length for age classification in wild turkeys (e.g. Kelly 1975; Steffen *et al.* 1990). Localized movements around female nesting areas may indicate more encounters with females and thus higher mating success (Badyaev *et al.* 1996a,b). Spur development may be associated with mating success because it closely covaried with movement pattern during the breeding season; males with longer spurs spent more time in display areas and shorter time moving among these areas (Table 1).

Several studies of galliform birds have provided evidence for strong directional selection on spur

Table 1. Pearson correlation coefficients (and sample sizes) of mean spur length and body mass, beard length, and spring display range sizes for second-year (SY) and after-second-year-old (ASY) male wild turkeys

	Spur length		Beard length	
Variable	SY (*n*)	ASY (*n*)	SY (*n*)	ASY (*n*)
Body mass	0·604* (27)	0·433* (37)	0·185 (27)	0·503* (37)
Beard length	0·577* (27)	0·293* (37)		
Display range (Hc)†	−0·162 (16)	−0·469* (17)	−0·312 (16)	−0·753 (17)
Display range (Conv)‡	0·693* (18)	−0·675* (27)	0·153 (18)	−0·198 (27)
Display range (Clust)§	0·874* (18)	−0·493* (18)	0·487 (18)	−0·223 (18)

*Significant at $\alpha = 0{\cdot}05$ after a 'trait-wide' within-age ($n = 5$) Bonferroni adjustment for multiple comparisons.

†Harmonic mean calculates area that is used must actively (Dixon & Chapman 1980).

‡90% convex polygen was calculated by correcting outer locations with 10% of the outermost locations excluded (Mohr 1947).

§Cluster estimate (Kenward 1998) was calculated by connecting actively used areas and excluding travel routes among them (see Badyaev *et al.* 1996b for further details).

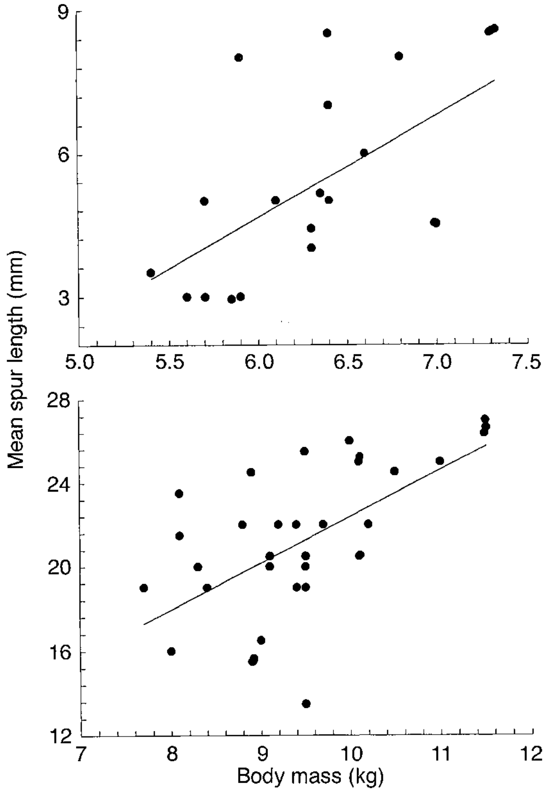

Fig. 1. Regression plots illustrating the relationship between spur length and body mass in second-year (SY) (above;. $b_{\rm ST} = 0{\cdot}62$, $t = 2{\cdot}93$, $n = 27$, $P = 0{\cdot}01$) and in after-second-year-old (ASY) (below; $b_{\rm ST} = 0{\cdot}41$, $t = 2{\cdot}14$, $n = 37$, $P = 0{\cdot}04$) male wild turkeys. b_{ST} is a standardized regression coefficient.

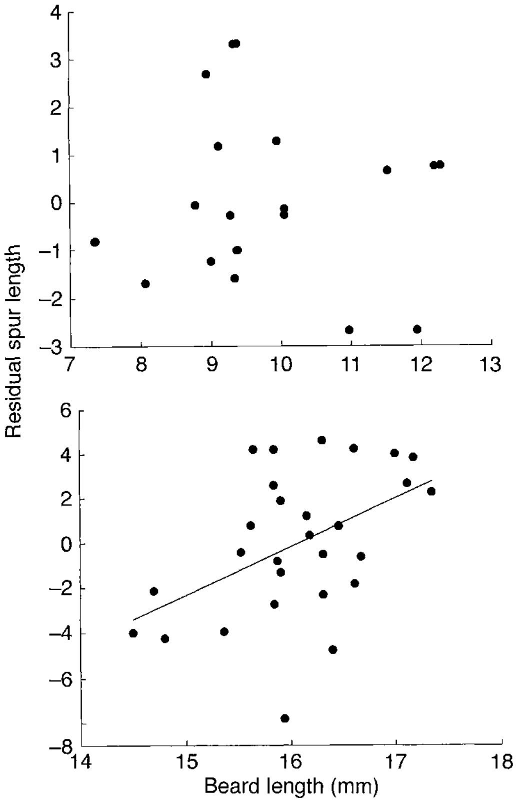

Fig. 2. Regression plots illustrating the relationship between spur length corrected for body mass, and beard length in second-year (SY) (above; $b_{\rm ST} = 0{\cdot}22$, $t = 1{\cdot}03$, $P = 0{\cdot}32$) and in after-second-year-old (ASY) (below; $b_{\rm ST} = 0{\cdot}44$, $t = 2{\cdot}10$, $P = 0{\cdot}04$) male wild turkeys. $b_{\rm ST}$ is a standardized regression coefficient.

length (Schantz *et al.* 1989; Wittzell 1991; Møller 1992; Grahn *et al.* 1993a, b; Grahn & Schantz 1994). Such directional selection for greater length may arise because individuals with larger weapons are more successful in intrasexual competition for mates and thus have higher mating success (Brown & Bartalon 1986; Zeh 1987; Conner 1988; Møller *et al.* 1996). Morphological traits under stabilizing selection typically show U-shaped distributions of asymmetry because individuals with extreme development of traits are expected to have lower ability to withstand developmental stress (SoulJ & Cuzin-Roudy 1982; Palmer

Table 2. Spur length, spur asymmetry and beard length [in mm; mean ± SD (CV)] in second-year (SY) and after-second-year-old (ASY) male wild turkeys

	SY (n = 71)	ASY (n = 97)	P†
Mean spur	5·54 ± 2·65 (47·79)	20·91 ± 3·68 (17·61)	0·000*
Difference (Left–Right)	−0·06 ± 1·02 (1816 ± 04)	0·44 ± 4·24 (971·24)	0·339
Absolute FA	0·62 ± 0·81 (131·14)	2·49 ± 3·45 (138·75)	0·001*
Relative FA	0·12 ± 0·16 (133·81)	0·13 ± 0·24 (181·36)	0·679
Beard length	89·09 ± 33·69 (37·82)	250·40 ± 23·95 (9·57)	0·000*
b_{ST} Absolute FA vs. mean spur	0·23	−0·02	0·016
b_{ST} Absolute FA vs. longest spur	−0·02	−0·22*	0·0001*
b_{ST} Relative FA vs. longest spur	−0·33	−0·39*	0·0001*

*Significant at α = 0·05 after within-table (n = 6) or within-egression (n = 2) Bonferroni adjustments for multiple comparisons.

†P value for ANCOVA of differences between age classes.

FA, fluctuating asymmetry.

b_{ST} is a standardized regression coefficient.

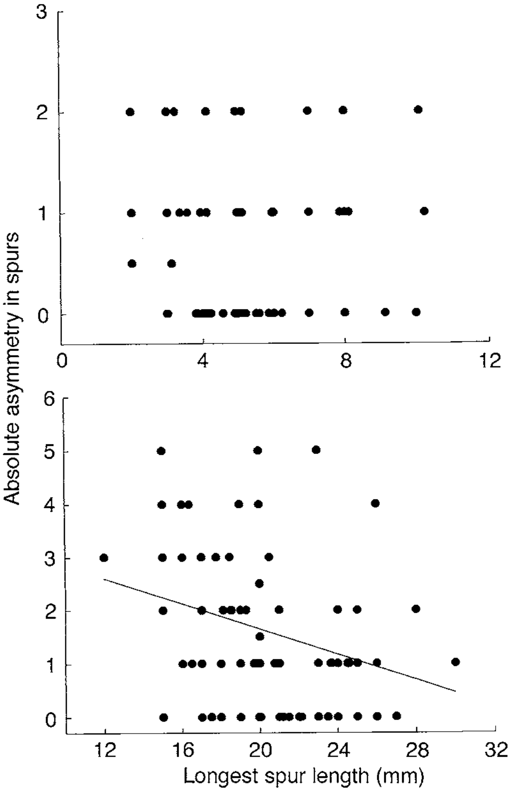

Fig. 3. Regression plots illustrating the relationship between absolute asymmetry in spurs and longest spur length in second-year (SY) (above; b_{ST} = −0·02, t = −0·19, n = 71, P = 0·85) and in after-second-year-old (ASY) (below; b_{ST} = −0·22, t = −3·25, n = 97, P = 0·01) male wild turkeys. b_{ST} is a standardized regression coefficient.

& Strobeck 1986). However, results of the present study suggest that spur length in wild turkeys is under directional selection given the linear relationship between absolute asymmetry in spurs and spur size (Møller & Höglund 1991; Møller & Pomiankowski 1993a).

In species with multiple sexual ornaments, such as in wild turkeys, only sexual traits under strong current sexual selection are expected to show high condition-dependence (Møller & Pomiankowski 1993b). Different sexual ornaments within a species could reflect several specific individual conditions (e.g. resistance to certain pathogens; Zuk *et al.* 1990, 1992), or individual conditions during various stages (e.g. during moult or growth, Bailit *et al.* 1970; Ligon *et al.* 1990; Zuk *et al.* 1990; Badyaev 1998). In wild turkeys, spurs grow continuously throughout life (Hewitt 1967). In contrast, beard growth appears to be faster in ASY males (Hewitt 1967; see also Fig. 2). Thus, spur development is likely to reflect individual condition over a long period of growth (Wittzell 1991; Grahn & Schantz 1994). Strong negative relationship between spur asymmetry and spur size (Table 2; Fig. 3) suggests that spurs are reliable indicators of individual condition in wild turkeys (Zahavi 1975; Grafen 1990; Møller & Höglund 1991; Møller & Pomiankowski 1993a and references therein). Males with longer spurs must have been in better condition over a longer period of time given the highly symmetrical development of their spurs. Indeed, the present study found that the surviving males had more symmetrical spurs compared to males that died from disease, starvation or by predation (Table 3).

Female preference for longer-spurred males in the Phasanidae (Schantz *et al.* 1989; Wittzell 1991; Møller 1992; Grahn *et al.* 1993a,b; Grahn & Schantz 1994) could be confounded by female preference for older males (Hillgarth 1990; Zuk *et al.* 1990; Grahn *et al.* 1993b; Buchholz 1995; Mateos & Carranza 1996). For example, observed associations between territory quality and spur size in ring-necked pheasant (*Phasianus colchicus* L.) was due mostly to a close association of spur size with age and several other morphological measurements (Göransson *et al.* 1990; Grahn *et al.* 1993a,b; Mateos & Carranza 1995, 1996; but see Schantz *et al.* 1989). Buchholz (1995) did not find female preference of spur size when he controlled

Table 3. Spur length, spur asymmetry, beard length (mm), and body mass (kg) (least-squared mean ±SD) of male wild turkeys that survived compared to those that died during the 3 years of study

	SY			ASY		
	Survived $n = 15$	Died $n = 18$	*P*†	Survived $n = 22$	Died $n = 14$	*P*†
Mean spur	9·61 ± 2·28	5·77 ± 1·98	0·22	18·50 ± 1·43	21·36 ± 2·16	0·28
Longest spur	9·55 ± 2·23	5·00 ± 1·95	0·14	17·75 ± 1·36	19·29 ± 2·06	0·54
Absolute FA	0·07 ± 0·16	0·78 ± 0·13	0·002*	0·68 ± 0·15	1·50 ± 0·24	0·009*
Relative FA	0·03 ± 0·06	0·26 ± 0·05	0·006*	0·07 ± 0·02	0·17 ± 0·03	0·02
Beard length	11·20 ± 0·92	9·00 ± 0·80	0·09	14·9 ± 0·58	15·9 ± 0·87	0·34
Body mass	6·34 ± 0·32	6·84 ± 0·27	0·25	8·78 ± 0·32	8·89 ± 0·49	0·85

*Significant at $\alpha = 0{\cdot}05$ after within-age class 'table-wide' ($n = 6$) Bonferroni adjustments for multiple comparisons.
†*P* value for ANCOVA of differences between survival classes.
FA, fluctuating asymmetry.

for age class in wild turkeys. Similarly, in the present study no difference in survival was observed among males with spurs of different length (Table 3), but spur asymmetry was a reliable indicator of male quality (see above; Table 3). These results suggest that spur asymmetry (or perhaps traits that are closely associated with spur asymmetry) may be used by females or by rival males to distinguish between high and low quality males.

In wild turkeys, SY males usually do not participate in breeding, because dominant older males prevent SY males from displaying (Healy 1992). Males typically establish their spring display areas at 3 years of age, but the age of participation in breeding can vary with population density and with the proportion of older males in a population (Healy 1992). The spurs of SY males in the present study population, were not a reliable indicator of individual condition because spur asymmetry did not vary with spur length (Table 2; Fig. 3). It is possible that still-growing SY males invest proportionally less to spur development than fully grown older males (Hillgarth 1990; Wittzell 1991; Grahn & Schantz 1994). The most likely explanation for the apparent lack of condition-dependence in spurs of SY males, as indicated by Fig. 3, was the absence of sexual selection on spur developmental stability and size in this age class (see also Hillgarth 1990; Grahn & Schantz 1994). Consequently, if the regression of spur length on spur asymmetry is an indicator of sexual selection intensity (Grahn & Schantz 1994; Badyaev 1998), geographical variation in the relationship may be predicted, because wild turkey populations vary strongly in age and sex ratios. In particular, a significant negative relationship would be expected between spur length and spur asymmetry for SY males in populations where SY males have higher breeding opportunities compared to this study.

Acknowledgements

We thank R. Bullington, C. Cirriano, D. Frick, K. Gardner, D. Hasenbeck, A. Hodgson, B. Infield, T. Lane, K. Lynch, A. Mouhalis, K. Teter, and M. Widner for assistance with various aspects of the field work. This article was considerably improved by comments from Steve Albon, Alison Banks, Shannon Garner, Cameron Ghalambor, Geoff Hill, Paul Martin, Toni Rapone, Richard Repasky, Wendy Parson, Marlene Zuk, and two anonymous reviewers. The support of the Arkansas Game and Fish Commission and the Arkansas Cooperative Fish and Wildlife Research Unit is gratefully acknowledged.

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Received 18 September 1997; revision received 2 February 1998