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REPRODUCTIVE CONSEQUENCES OF AUTUMNAL SINGING IN BLACK REDSTARTS (*PHOENICURUS OCHRUROS*)

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ABSTRACT.—In a migratory population of Black Redstarts (*Phoenicurus ochruros*) in central Europe, males were territorial and sang in autumn between the end of molt in early September and the abandonment of territories in October. Participants in autumn singing were adult males past their first potential breeding season; subadults rarely defended territories in autumn. Prior to the autumn singing period, unmated males and males after their first breeding season often dispersed to new locations within the study site. Pair associations with experienced female breeders still present on the breeding ground were preformed. Low winter mortality, site dominance, and fidelity to autumn territories allowed the reformation of 59% of autumnal pair bonds in the following spring. The mating pattern was assortative by age because the initiation of territory acquisition and pair formation was temporally segregated by more than six months between subadult and adult breeders. Males benefitted from mating with experienced females because they started breeding earlier and initiated more breeding attempts per season. Autumnal singing and territoriality, a phenomenon that has not attracted much attention, may play a key role in the understanding of age-related reproductive asymmetries in Black Redstarts. Age-related reproductive performance may be the underlying cause for the evolution of delayed plumage maturation in this species. *Received 16 November 1998, accepted 5 May 1999.*

THE REPRODUCTIVE CYCLE of most north-temperate bird species starts in spring and ends in late summer (Murton and Westwood 1977). Preparation for nesting is thought to be displayed only a few weeks or months before nest building actually starts. Among the few exceptions to this rule are cavity-nesting ducks that prospect for breeding opportunities for the next year during the present breeding season (Patterson and Makepeace 1979, Eadie and Gauthier 1985, Zicus and Hennes 1989), and Spotted Sandpipers (*Actitis macularia*) that inspect potential breeding territories for next year during late-summer movements (Reed and Oring 1992).

The autumnal song of several passerines also may yield benefits for breeding in the subsequent year. For example, Hegner and Wingfield (1986) showed that territorial activities of resident House Sparrows (*Passer domesticus*) in autumn may enhance next year's breeding success. Autumnal song of nonmigratory Northern Mockingbirds (*Mimus polyglottos*) serves to attract mates, and birds that are paired in autumn may benefit from a longer breeding season the next year (Logan and Hyatt 1991). Lawn (1994) suggested that nonbreeding Willow Warblers (*Phylloscopus trochilus*) that settle late in the breeding season intend to stake out next year's breeding territories rather than breed in the current year, and Yamagishi (1991) revealed that resident male Meadow Buntings (*Emberiza cioides*) advertise their settlement or site tenacity by singing in autumn.

Male Black Redstarts (*Phoenicurus ochruros*) breeding in central Europe sing intensively during two phases: (1) from late March immediately after their arrival on the breeding territory until the onset of molt in July, and (2) from mid-September until mid-October before the birds leave their breeding grounds to migrate to their winter quarters (Glutz and Bauer 1988, Schmidt 1992). It is not known whether males that sing in autumn are mainly transient birds or males on their breeding territories, and possible reproductive consequences of autumnal singing heretofore have not been investigated.

Here, I present evidence that autumnal singing in a migratory population of Black Redstarts helps male breeders to secure access to territories and high-quality females for the following breeding season. Because subadult males (i.e. hatched in the current calendar year)

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TABLE 1. Population size and seasonal timing of mortality of banded Black Redstarts. The breeding season lasted from the day of arrival until 31 July (ca. 4 months), and the nonbreeding season lasted from 1 August until late March/early April. "Winter" mortality tended to be lower than summer mortality in males ($\chi^2 = 3.52$, df = 1, $P = 0.061$) and females ($\chi^2 = 2.62$, df = 1, $P = 0.105$).

Variable	Year			
	1994	1995	1996	1994 to 1996
Males				
Breeding population in April	25	28	25	—
No. of deaths April to July	10	12	14	36
No. of deaths August to March	5	5	2	12
Total no. of deaths	15	17	16	48
No. surviving to next year	10	11	9	30
Females				
Breeding population in April	24	29	20	—
No. of deaths April to July	12	15	7	34
No. of deaths August to March	1	6	5	12
Total no. of deaths	13	21	12	46
No. surviving to next year	11	8	8	27

rarely sing in autumn, autumnal singing by older males may help to explain age-specific reproductive performance and the evolution of delayed plumage maturation in this species. My aim was to (1) identify the origin and age of autumnal singers and (2) explore relationships between autumnal singing and behaviors related to subsequent breeding attempts and reproductive performance.

METHODS

Study species and population.—In central Europe, the breeding habitat of Black Redstarts consists of alpine cliffs and rocky slopes (primary habitat), as well as human settlements (secondarily). Within human settlements, nests are located in walls or roofs of dwellings and huts. The species is multibrooded and regularly produces two (rarely up to three) broods per season.

Between 1994 and 1996, I studied a breeding population of Black Redstarts in two villages (167 dwellings and huts in total) in the Swiss Alps. The annual number of birds fluctuated between 25 and 28 males and 20 and 29 females (Table 1). Males were strictly territorial, and territorial arrangement varied only little between years. Mean territory size was 0.48 ha (range 0.12 to 1.32 ha, $n = 28$). Most (77%) of the 78 males that were recorded as breeders at least once were mated monogamously, 10% were bigamous, and 13% were unmated. These numbers refer to the situation on 10 May of each season. However, because summer mortality of females and males was high (Table 1), and the breeding season was long, pair bonds and mating systems changed frequently in the course of the breeding season.

Breeding birds in both villages were marked with unique combinations of three colored plastic bands, and the age of all birds could be determined as subadult (younger than 1.5 years) or adult (older than 1.5 years) based on plumage characters (Glutz and Bauer 1988, Andersson 1991). Breeding males consisted of two differently colored age classes: (1) first-time breeders (i.e. subadults) with dull plumage, and (2) adults with conspicuous black plumage and a white patch on each wing. The age class of females could be determined only with birds in the hand. The presence or absence of breeding birds was determined by daily censuses conducted from 1 March to 15 August of each season.

Monitoring identity and age of autumnal singers.—To identify the origin and age of autumnal singers, I tallied all males that displayed full song after 15 September based on four census periods (three days each) between 15 September and 10 October in 1994 and two census periods during this same range of dates in 1995 and 1996. For all singing males, I recorded the identity (banded or unbanded) and age class according to plumage characters. The exact number of males that did not sing could be determined only for banded individuals.

To quantify song output of males, I performed 10-min focal watches of all singing males during the first two daylight hours on three days in autumn 1994. During these focal watches, I counted the number of 30-s intervals during which a male was continuously singing and then calculated the mean number of intervals for all males recorded on that day. To compare song output between fall and spring, the same focal watches were performed on all breeding males at regular intervals from March to August 1994.

Spatial position, territorial behavior, and pair associations.—To address whether autumnal singing is accompanied by behaviors that are related to breeding, I mapped the spatial positions of all singing males in the autumns of 1994 to 1996 and compared them with positions at the start of the subsequent breeding seasons of 1995 to 1997. Territory-related behaviors other than singing were noted continuously. To explore possible triggers for observed movements between summer and subsequent autumn positions, I related the occurrence of such late-summer shifts to the age of the male and his mating status on 1 August. I checked for the presence of females by searching all summer territories for at least 30 min on three different days after 15 September. The identity of males that followed females or chased them around was noted.

Autumnal singing and breeding performance the fol-

TABLE 2. Number of Black Redstarts seen by the end of the breeding season (1 August), number seen in autumn of the same year (after 15 September), and number seen in the subsequent spring. Autumn birds are classified as to whether they were singing when observed. Data are combined for 1994 to 1996 for breeding season and autumn and 1995 to 1997 for subsequent spring.

	1 August	15 September		Subsequent spring	
Age class	Seen	Singers	Non-singers	Total	Seen previous autumn
		Males			
Adult	42	40	2	30	30
Subadult	?	5	?	44	?
		Females			
Adult	39	0	22	27	18
Subadult	?	0	?	44	0
		Sex unknown			
Subadult[a]	71	0	9	0	0
Unknown[a]	1 to 5	0	5 to 25	—	—

[a] "Subadults" were born on study area; "unknowns" were born outside of study area and observed on daily censuses.

lowing spring.—To relate autumnal singing to breeding performance in the following year, I first explored how frequently autumnal singers reclaimed their autumn "possessions" (i.e. territory and/or female) in the following spring. I further evaluated which of the following three factors possibly contributed to the persistence of autumnal possessions: (1) site fidelity, (2) winter mortality, and (3) site dominance. Mortality rate of birds was derived from censuses carried out between March 1994 and May 1997. Vanished birds were considered to have died. I discounted the possibility that birds recorded as residents in autumn dispersed out of the study area because (1) birds seen repeatedly at a site in autumn almost exclusively were adults, (2) only 2 of 73 breeders that entered the population between 1995 and 1997 presumably had been immigrating adults, and (3) none of the adult breeding males from 1995 to 1997 was missing in the fall of the previous year.

Second, I explored whether territory and/or mate possessions gained by autumnal singers were relevant to reproductive success. I measured seasonal reproductive performance by recording all nesting attempts and fledgling success from mid-April until August of 1994 through 1996 and compared these data among males based on the consequences of autumnal singing. I eliminated possible effects of polygyny by selecting a subsample of pairs that was mated monogamously throughout the season. To find a possible explanation for differential reproductive success depending on achievements gained in autumn, I analyzed timing of arrival and the onset of breeding for the two different age classes of females.

RESULTS

Identity of autumnal singers.—Fall singers were almost exclusively adult males, although most of the males were subadults at that time. The total number of adult versus subadult males singing in the autumns of 1994 to 1996 (40:5; Table 2) was significantly different from the ratio of adults to subadults in the breeding population of the subsequent springs of 1995 to 1997 (30:44; Fisher's exact test, $P < 0.0001$; Table 2). The vast majority of breeding males from the preceding nesting season sang in fall: 40 of 42 (95%) breeding males present by the end of the nesting season on 1 August were recorded singing persistently after 15 September (Table 2).

Subadult males, as well as females, were mostly silent but not absent from the study site during autumn (Table 2). Non-singing Black Redstarts in fall could be assigned to four different groups: banded adult males ($n = 2$), banded adult females ($n = 22$), banded subadults of unknown sex born on the study site ($n = 9$), and unbanded dull-colored birds of unknown sex and age ($n = 5$ to 25 in each census). Most birds in the last group presumably were on migration and were roosting and foraging during daytime within the study site. Their numbers increased from mid-September until early October and declined thereafter.

The pronounced difference in the age composition of singing males between autumn and spring revealed that most subadult males did not sing in autumn. However, because the five subadult males that sang in autumn were not marked, it is possible that subadults occasionally settle as yearlings on sites at which they

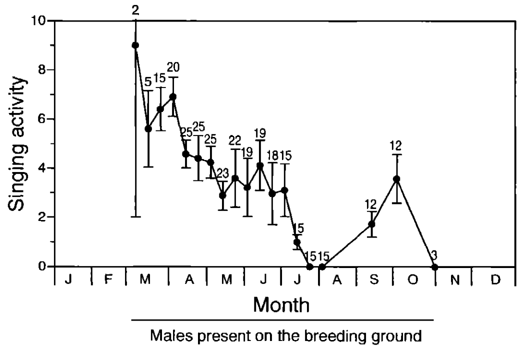

Fig. 1. Singing activity of male Black Redstarts between March and October expressed by the mean number of 30-s intervals (±SE) a male was singing during 10-min focal watches. Sample sizes are above error lines.

sang the previous autumn. Four subadult breeders that were marked as nestlings but not recorded as singers in their first autumn provided further evidence that subadult males rarely sing in autumn at the territory they occupy in their first breeding season.

Territorial and intrasexual activities in autumn.—The territorial behavior of males in autumn resembled the situation in the second half of the breeding season, when territories were firmly established and most males were already mated. The amount of song output of autumnal singers was considerably lower than in early spring but comparable to that in May and June (Fig. 1). The singing activity of males in autumn accompanied activities typical for territorial birds; i.e. singing males chased neighboring males out of their territories, fought vigorously with transient birds, and perched on sentinel positions within their territories.

All 22 females seen in fall lived within a territory of an adult male, and all of them were involved in pair chases with the male territory holder. Twenty of the 22 females were guarded by the adult territory holder in a manner similar to that I observed in spring. While females moved around the territory foraging, males followed them at a distance of less than about 10 m and sometimes drove off rival males that approached the female. Although pair interactions were not studied in detail, the 22 pairs of adults that I observed maintained close spatial proximity for up to two months between the end of the nesting season and early October.

Spatial position of birds in autumn and timing of breeding dispersal.—Breeding dispersal by males occurred mostly between the end of the breeding season and the autumn territoriality period rather than between autumn and the next spring; 29% of adult males present in autumn ($n = 42$) dispersed to a new autumn territory between 1 August and 15 September (Fig. 2), whereas autumn territories were reoccupied by returning males in the next spring in 93% of cases (28 of 30 returning males). Consequently, the territorial position of adult males in autumn matched the situation in the following spring more closely than that in the preceding breeding season.

Dispersal movements at the end of the breeding season toward a new autumn territory were triggered by the absence of a female within the breeding territory and were carried out more often by males that selected their breeding territories while young and inexperienced rather than when they were adults. A logistic regression relating the occurrence of late-summer dispersal to mating status on 1 August showed that males that were unmated by the end of the breeding season were significantly more likely to disperse to a new location than were mated males, and that first-year breeders dispersed significantly more often than adults ($\chi^2 = 23.8$, df = 2, $P < 0.0001$, $r^2 = 0.47$). In total, 11 of 20 (55%) unmated males dispersed, versus only 1 of 22 (5%) mated males, and 11 of 23 (48%) adults breeding for the first time dispersed versus only 1 of 19 (5%) males with more breeding experience.

Dispersing males in late summer probably sought access to females. After their spatial shift, males tended to be associated with a female more frequently in autumn (5 of 12) then before they dispersed (1 of 12; Fisher's exact test, $P = 0.069$), and males that dispersed were mated as frequently (5 of 12) as males that did not disperse (17 of 30; $\chi^2 = 0.29$, df = 1, $P = 0.592$).

Breeding females showed strict site fidelity from spring to autumn and also into the next spring. All 22 female breeders were seen in autumn exclusively within the range they lived in by the end of the breeding season, and all of them returned the next spring to the same sites.

Frequency of female presence in autumn.—Only 56% of the breeder females from the preceding nesting season were seen during autumn. On

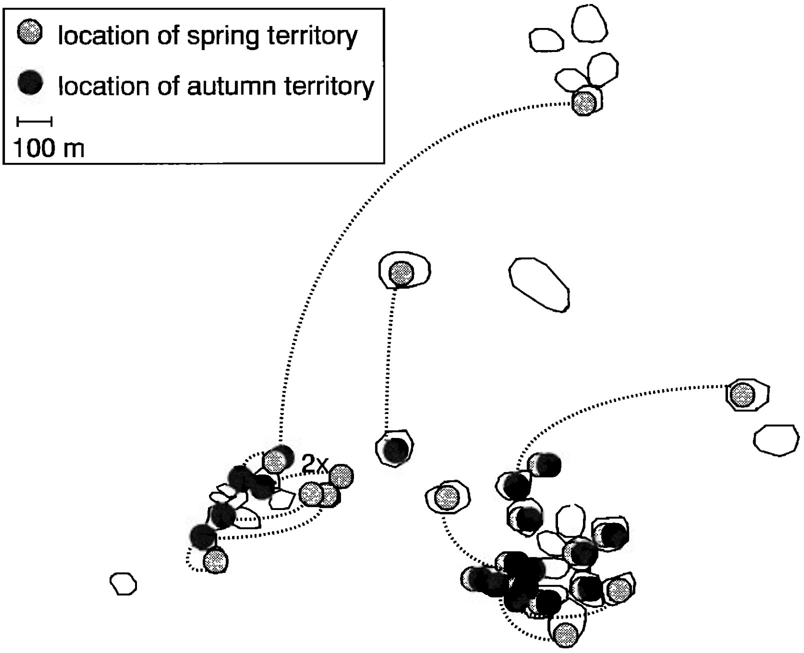

FIG. 2. Territory map with dispersal movements between breeding and late-summer territories of 12 breeding male Black Redstarts. Data are combined for 1994 to 1996.

1 August, 39 breeding females were present, and 22 of them were seen until after 15 September (Table 2). However, the number of female breeders in autumn may have been as high as 34 (87%) given a female detection rate of 67% in autumn (only 18 of 27 spring-to-spring survivors were seen in autumn). It is unknown whether the difference between the real and estimated number of females in autumn arose because some females had already left the breeding ground by 15 September, or because they were present but undetected during fall censuses.

Autumnal pair associations and reformation frequency in spring.—Thirteen of the 22 observed autumn pair associations (59%) were reestablished the next spring. Three pair bonds dissolved because both partners died, one because the female died, three because the male died, and two pairs split although both partners survived and returned. The frequent reformation of previously formed pairs resulted in adults being mated with adults more often than would be expected by chance ($\chi^2 = 9.39$, df = 1, $P < 0.01$).

Newly formed pairs of adults were established in the previous autumn in six cases and in the spring in four cases. In 11 cases, adult-adult pairs persisted from one spring to the next. However, the significance of the autumn period for males to acquire an adult female may be even greater than these figures suggest, because the detection of adult females in autumn was incomplete.

High site fidelity, low winter mortality, and successful defense of former territory sites all may have favored the frequent reclamation of autumn possessions. Adult males and adult females almost invariably returned to the site they had occupied in the previous autumn (28 of the 30 returning males obtained a territory that broadly overlapped the one they had during the previous autumn). Two males shifted one territory away from their previous territory without apparent pressure from rival males. These two males did not disperse to a new late autumn territory in the previous autumn.

All 27 returning females settled within the territory they occupied on 1 August of the previous year. The mean distance of a female's nest between years was significantly shorter than the mean nearest-neighbor distance in the population (Mann-Whitney *U*-test, $z = -4.63$, $n_1 = 27$, $n_2 = 117$, $P < 0.0001$). Adult females fre-

TABLE 3. Arrival dates and laying dates of the first egg per season for subadult and adult female Black Redstarts. For comparison, arrival dates of males are also indicated. Arrival dates of age/sex classes carrying the same superscript are equivalent ($P > 0.05$). Sample sizes for laying dates differ from arrival dates because six nests were impossible to inspect.

Age class	Median arrival date	n	Median laying date	n
		Females		
Subadult	16 April	49	8 May	44
Adult	3 April^{A,B}	24	29 April	23
		Males		
Subadult	1 April^{B,C}	44	—	—
Adult	27 March^{A,C}	34	—	—
		Overall		
	7 April	73	4 May	67
	29 March	78	—	—

quently constructed a nest in the same dwelling in subsequent years (19/27), and most females (15/27) occupied the nest they had used in the previous year.

The probability that pair bonds dissolved owing to mortality was smaller in winter than during the breeding season. In males and females, mortality between August and March tended to be lower than in the four months of the breeding season (Table 1). Pooled for both sexes, the difference was significant ($\chi^2 = 7.45$, df = 1, $P = 0.006$).

Once in possession of their former territory, resident males and females never lost their position to incoming rivals. However, in defense of their former territories, adult males had to drive off subadults that were already present in 4 of 30 cases and also had to chase off later-arriving subadult challengers. Competition for former breeding sites probably was less severe for adult females, because they settled on their breeding sites about two weeks before subadult females arrived (Table 3).

Reproductive consequences.—Being mated to an adult female yielded reproductive benefits for males. Within monogamously mated pairs, female age contributed significantly to seasonal reproductive success, whereas male age did not ($F = 4.4$, df = 2, $r^2 = 0.21$; age of male, $P = 0.861$, age of female, $P < 0.02$). Pairs with an adult female raised 7.8 ± SD of 4.1 offspring per year, whereas pairs with a subadult female raised only 3.4 ± 3.7 offspring per year. Lower reproductive success of subadult females presumably arose because these females were temporally delayed in breeding and therefore initiated significantly fewer breeding attempts (Mann-Whitney U-test, $z = 3.74$, $n = 23$ adults and 44 subadults, $P = 0.0002$). Compared with adult females, subadult females occupied their breeding territories 13 days later and began egg laying about 10 days later ($z = -3.80$, $P = 0.0001$; Table 3).

DISCUSSION

Male Black Redstarts sang and exhibited other territorial behaviors during autumn after the breeding season had ended. Young males and unmated male breeders dispersed in late summer toward new territory positions. Experienced male and female breeders associated together in these autumnal territories. The territory and pair setting in autumn frequently was reestablished in spring because of high site fidelity, low winter mortality, and site dominance of experienced breeders. Subadult males (which would be first-time breeders the next spring) rarely participated in territorial activities in late summer. Temporal segregation of age classes during territory establishment and pair formation promoted assortative mating by age, which in turn impaired reproductive success of subadult males because subadult females are inferior breeders.

A period of singing and/or pair formation in autumn has been reported in several passerines (Alexander 1935, Snow 1958, Homann and Gwinner 1963, Matthijsen and Dhondt 1983, Rost 1990, Logan and Hyatt 1991). Because late-summer territoriality can be very "cryptic" (Lawn 1994), it is not clear how widespread this behavior is among passerines. Hegner and Wingfield (1986) proposed that in the temperate zone of the Northern Hemisphere, the annual cycle of reproductive activities generally begins in autumn. However, only a few studies of passerines were able to relate autumn territorial activities to breeding performance in the following breeding season (Lawn 1982, 1994; Hegner and Wingfield 1986; Logan and Hyatt 1991).

Territoriality and mate searching during autumn are likely to yield two benefits for male Black Redstarts. First, because prior ownership of territories is known to increase reproductive performance (Krebs 1982, Jacobsson 1988), autumn territoriality may yield special benefits for males that try to disperse to a new territory with better breeding prospects. By dispersing in late summer immediately after breeding, males can begin to acquire new breeding territories in the absence of first-time competitors and can firmly take possession of their new territories for almost two months. The decision to disperse after breeding seems to follow the "win-stay/lose-disperse" rule. Young males and unmated male breeders were the most likely individuals to disperse. Beletsky and Orians (1987) observed a similar pattern of dispersal in Red-winged Blackbirds (*Agelaius phoeniceus*) between late summer and spring rather than between late summer and autumn. Male blackbirds that moved had below-average reproductive success in the preceding breeding season and predominantly were young males that had established their subsequently abandoned territories when they were unfamiliar with the sites.

The second advantage of territoriality in autumn lies in monopolizing matings with experienced females. Experienced females return to their breeding sites earlier, lay their first eggs on average 10 days earlier than novice females, and have higher seasonal reproductive success. Earlier spring nesting, mate evaluation, and enhanced nutrition of females have been proposed as benefits of autumn or winter pairing (Hegner and Wingfield 1986, Rohwer and Anderson 1988). Black Redstarts abandon their autumn territories by October, and according to observations on the wintering grounds, pair bonds are not maintained over the winter (Cuadrado 1995). However, high site fidelity and low winter mortality of both sexes result in a high rate of autumn pairs (59%) being reformed the next spring. This suggests that territoriality and pairing activity in autumn are important for understanding variation in breeding performance of some migratory species in which territories and pair bonds are reestablished each spring.

I can only speculate as to why subadult males do not participate in contests for territories and adult females in autumn. Subadult males may not be sufficiently mature at the age of one to four months to display full song or aggression, two behaviors necessary to successfully participate in territorial disputes. Ultimately, selection to participate in autumn territoriality as a subadult simply may not be feasible because subadults miss necessary information that is only available during the breeding season. Breeding male Black Redstarts assess the distribution of successfully breeding females throughout the breeding season, e.g. by inspecting nests in adjacent territories (Weggler 1997). This information may be crucial for knowing the location of successfully breeding adult females and of vacant territories. Therefore, conditions and uncertainties for subadults are the same in autumn as in spring. Under these circumstances, autumn territoriality may not be favorable for subadults because it yields costs but no benefits.

The temporal segregation of age classes during the process of pair formation passively promotes assortative mating by age in Black Redstarts. A significant age correlation without a preference for mating with experienced birds has also been described for Great Tits (*Parus major*; Perrins and McCleery 1985). Reid (1988) modeled correlation between age and mating under different degrees of pair stability and mate preference and showed that high correlations with age are possible even when mate preference is weak and annual survivorship is low, because low survivorship reduces potential variation in ages of mates. A spatial or temporal segregation of the few main age classes during pair formation can then easily lead to a strong age correlation. All of these factors (low mate preference, low annual survival, and temporal segregation of age classes during pair formation) seem to prevail in Black Redstarts.

My results suggest that temporal segregation of male age classes during pair formation is the cause of a reproductive handicap for subadult male Black Redstarts (Weggler 1997). This, in turn, may set the stage for the evolution of delayed plumage maturation, i.e. a nondefinitive plumage in subadult males during their first breeding season (Studd and Robertson 1985). Several ecological and life-history factors may favor age-related asymmetries in Black Redstarts. The temporal pattern of mortality risk may be an important trait because high summer mortality relative to winter mortality means that early acquisition of breeding resources is not heavily disrupted by mortality (Reid 1988). Therefore, the time window for a temporal segregation of age classes for competition over breeding resources is wide. Second, high summer mortality of males may favor age-specific asymmetries. High summer mortality of males selects for females that are independent from males for brood care because the risk of losing the mate during brood rearing is high. When settling, female Black Redstarts may use a reliable resource-based cue (e.g. territory characteristics) rather than a potentially unreliable one (e.g. male characteristics). These conditions may explain why experienced females are highly faithful to a proven site and suggest that subadult females should choose territories carefully. Careful site selection is time consuming (Dale et al. 1990, 1992; Choudhury and Black 1993; Badyaev et al. 1996), which may explain why subadult female Black Redstarts delay the start of breeding and why they experience relatively low reproductive success in their first year. The age-related asymmetry in female reproductive performance promotes selection on males to secure access to adult females. Experienced males cope much better than subadults with this task because they can use their current knowledge about the presence and spatial position of adult females and occupy these sites in autumn in preparation for the next breeding season.

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