# Demographic consequences of sexual selection in the long-tailed manakin

Demographic divergence between the sexes is a major consequence of sexual selection. Matrix-based demographic measures, including the sensitivity and elasticity of  $\lambda$  (population growth rate, fitness) to survival and fertility rates are powerful indexes of intersexual divergence. Many morphological, behavioral, and ecological differences distinguish males and females in lekking long-tailed manakins (Chiroxiphia linearis), and none is more dramatic than the demographic divergence. Only 16 of 142 (8%) banded males copulated during an 8-year period. The mean estimated age of male copulators was 10.1 years (SD = 2.2), and only 5 of 166 copulations were by males  $\leq 8$  years old. Females probably begin reproduction at age 1 or 2. The reproductive value curve reached a peak of 15.0 for 12th-year males, versus 2.7 for sixthyear females. The matrix-based elasticity of  $\lambda$  to survival rates was greater in males (91% of total elasticity) than in females (80% of total). In a literature-based, interspecific comparison, the difference in elasticity to survival between the male and female manakins (91-80=11); ranks 2 and 9 of 16 species/sex combinations) was greater than that between the sexes in northern elephant seals (90-84=6); ranks 3 and 8), which have the highest variance of male mating success documented for mammals; red deer (88-87=1); ranks 4 and 5); Galapagos cactus finches (79-74=5; ranks 10 and 12); and acorn woodpeckers (76-74=2; ranks 11 and 13). In the face of continuing debate over appropriate measures of sexual selection, matrixbased demographic techniques facilitate quantitative, comparative analyses of the life-history consequences of sexual selection. Measures of intersexual demographic divergence may provide insights into heretofore puzzling instances of sexual selection in species with little dimorphism in size or ornament. Key words: age structure, comparative demography, delayed reproduction, elasticity, life history, manakin, Pipridae, reproductive value, sensitivity analysis, sexual selection. [Behav Ecol 4:297-309 (1993)]

 $\mathbf{S}$  exual selection has important consequences both inter- and intraspecifically. Interspecifically it may play a role in speciation (Lande, 1981), a topic I will not address in this paper. Intraspecifically, sexual selection is of interest because of its role in creating dramatic differences between the sexes. Such differences may include not only morphological traits but also divergence in demographic traits, such as age at first reproduction or age-specific fertility or survival. Changes in age-specific survival or fertility may have many important evolutionary consequences (Caswell, 1989; Charlesworth, 1980). For example, increasing the disparity in reproductive success among age classes will decrease effective population size, increasing the force of genetic drift (Emigh and Pollak, 1979; Felsenstein, 1971). If mating success is restricted to older individuals in one sex but not the other, the result may be ageand sex-specific selection pressures that could have important evolutionary consequences, including delayed maturation, effects on age-specific survival rates, and increased genetic drift.

Intersexual differences in age structure, therefore, should be of central concern to students of sexual selection. Age has long been considered an important factor in the reproductive success of individuals under sexual selection (e.g., Apollonio et al., 1990; Clutton-Brock et al., 1988; Kruijt and de Vos, 1988; Snow, 1962; Wiley, 1991). Nevertheless, few demographic analyses of both sexes are available for species under intense sexual selection, especially tropical species with lek mating systems. Lek mating systems provide a useful opportunity for studying the consequences of intersexual selection (female choice) without confounding influences of male control of resources valuable to breeding females (Bradbury, 1981). The lack of sexual size dimorphism in many species of lekking birds, accompanied by lack of plumage dimorphism in a few species, has been noted (Payne, 1984; Trail, 1990), but little attention has been devoted to examining demographic differences between the sexes. Further, few data exist with which to assess the relative roles of inter- and intrasexual selection in producing demographic divergence between the sexes (Clutton-Brock et al., 1988).

Demographic analyses can complement analyses of the variation in lifetime reproductive success among individuals (Clutton-Brock, 1988; Newton, 1989) by assessing the consequences of sexual selection on age structure and population dynamics. Studies of lifetime reproductive success have been useful in examining life-history components that contribute to differential success among individuals within populations. Such studies have combined life-history components to measure the opportunity for sexual selection (Wade and Arnold, 1980) that results from variance of mating success among individuals. Nevertheless, it is also of interest to assess the consequence of those differences for the David B. McDonald Archbold Biological Station, PO Box 2057, Lake Placid, FL 33852, USA

Received 20 September 1990 First revision 1 August 1991 Second revision 13 January 1992 Third revision 15 September 1992 Accepted 28 September 1992 1045-2249/93/\$5.00 © 1993 International Society for Behavioral Ecology age structure and population dynamics of the species or sex in which they occur.

Recent developments in stage-classified matrix and life-cycle graph models (Caswell, 1989; Cochran and Ellner, 1992; McDonald and Caswell, 1993) allow one to search quantitatively for demographic divergence driven by sexual selection. Matrix-based measures include (1) population growth rate,  $\lambda$ , which can be used as a measure of fitness, (2) eigenvalue sensitivities of  $\lambda$  (fitness) to changes in life-history traits such as fertility or survival rates, (3) elasticities, which measure the sensitivity of  $\lambda$ to proportional changes in life-history traits, (4) reproductive value, defined as the importance of individuals of a given age class or stage to population growth (see Caswell, 1989: 67, 108, 136), and (5) age-based statistics from stage-classified models (Cochran and Ellner, 1992). Because they are directly equivalent to selection gradients in quantitative genetics (Caswell, 1984), the sensitivities also provide an important life-cycle-level parallel to measures such as  $I_s$ , the selection gradient assessed from the variance of mating success among individuals (Wade and Arnold, 1980). All the matrix-based measures are inherently focused on age structure.

The purpose of this paper is to compare male and female life histories in a long-lived, lek-breeding neotropical bird, the long-tailed manakin (Chiroxiphia linearis, Pipridae). In previous papers (McDonald, 1989a,b), I discussed the behavioral correlates of male mating success and male-male cooperation in a color-banded population of manakins in Costa Rica. I use matrix-based techniques to develop summary elasticity and sensitivity measures, and demonstrate their use in comparing the life cycles of males and females. I then analyze published data for two species of mammals where strong sexual selection has been demonstrated and for eight other avian species with a variety of mating systems and life histories. I show that matrix-based demographic analyses, in general, and the elasticity measure, in particular, provide a useful way of assessing the consequences of sexual selection. I suggest tentatively that intersexual demographic divergence may be greatest in mating systems where female choice predominates, and should be looked for in species where sexual selection has not resulted in morphological divergence.

#### **METHODS**

The study area is 80 ha of premontane, moist forest in Monteverde, Costa Rica (10°18' N, 84°48' W, described in McDonald, 1989a,b). Courtship displays begin as early as February and last until August, but the bulk of mating activity occurs from March to June, with a peak in April and May.

For courtship display, males form teams at scattered lek arenas or perch zones, each of which may contain several perches traditionally used for dance displays (McDonald, 1989a). I use the term "lek" to refer to the group of males. Each lek consists of an alpha and beta male, with 2–12 associated males (McDonald, 1989a), arranged in a dominance hierarchy that is linear, at least for the top few males. Subordinate males, sometimes including the beta male, may associate with more than one lek simultaneously, leading to a complex network of malemale alliances that spans many years. The courtship displays are cooperative. Two males, usually the alpha and beta, perform the unison "toledo" calls, coordinated, backwards leapfrog dances, and "butterfly" flight that are correlates of male mating success (McDonald, 1989b). With rare exceptions (4 of 166 in this study), all copulations are by alpha males. Females are heavier than males during the breeding season, and female choice among leks appears to be unrestricted by the multiyear period of intrasexual selection that determines male status within leks (McDonald, 1989a,b).

Male long-tailed manakins undergo numerous morphological and behavioral changes with age (McDonald, 1989a). A 3-year sequence of distinct, age-specific predefinitive plumages precedes the acquisition of definitive male plumage in the 4th year. I use the term "predefinitive" (Foster, 1987) rather than "subadult" to avoid implying anything about reproductive state. Males with predefinitive plumage rarely displayed for females and were never seen to copulate (McDonald, 1989a). Females could not be aged by plumage. As with all lek mating systems, all parental care is by the female. For other species of manakins, Snow and Lill (1974) indicated that females begin breeding at age 1, as did Foster (1976) for long-tailed manakins.

The study period included behavioral observations from the 1984 through 1991 breeding seasons and netting data from 1981 to 1990. Netting effort varied within and between seasons. Typical effort was semiweekly deployment of 14-18 nets, 12 m in length, for 4–6 h. The great majority of sightings occurred during 5816 h of scheduled 2-h observation periods in blinds 8-12 m from dance perches (Table 1; see McDonald, 1989b), but also included ad libitum sightings. Daily effort per lek arena was approximately 2 h per day during 12-15-week field seasons. Between 1981 and 1990, I color-banded 342 long-tailed manakins, of which 142 were males, 108 females, 32 "probable females," and 60 of undetermined sex. I identified females by vascularized brood patches (N = 27), retention of green plumage for >1 year (N = 5), nest or dance perch attendance with female behavior (N = 10), or two or more of the previous criteria (N = 66). Assignment as a "probable fe-male" was based on higher weights (>20 g) characteristic of females (McDonald, 1989a) as well as on bill and tarsus measurements (McDonald DB, unpublished data).

For survival analysis, I constructed a matrix in which columns were years and rows were individuals. "Detection" meant either a resighting or a renetting. Each cell had three possible values: 0, no detection; 1, detection; 2, died in the net as a result of handling or predation (N = 2). Using the data matrix, Jolly-Seber and related models provided the estimates of survival rates and detection probabilities (Jolly, 1965; Seber, 1965). Detection probability is an estimate of the probability of a resighting or recapture and is not necessarily directly correlated with the survival rate. If they survived, for example, males were usually resignted each year (high detection probability), whereas this was not so for females, despite rather similar survival rates. I used Program JOLLY (Brownie et al., 1986; Pollock et al., 1990) to estimate survival and detection rates for females and for the entire set

of males and females taken together ("all individuals"). To analyze differences in detection probabilities between males and females, I used a test for differences in means with unequal variances (Sokal and Rohlf, 1981: 411).

I used Program JOLLYAGE (Pollock et al., 1990) to estimate survival rates of younger males versus those of older males. JOLLYAGE was designed to distinguish only between younger (first-year) and older (adult) categories typical of temperate species. Because of the more extended maturation of the manakins, and because sample sizes of firstyear males were small, I categorized males as follows: at first capture, males with any of the predefinitive plumages (age 1-3) were categorized as "younger"; at any capture in a subsequent year, they were classified as "older" (even if they still had predefinitive plumage), as were all birds with definitive plumage. The analysis therefore compared survival from first predefinitive capture with that for a somewhat heterogeneous category of older birds. The estimated survival rates then served as parameters in matrix-based demographic models.

I used the matrix-based, stage-classified models of Caswell (1989) to calculate the growth rate,  $\lambda$ , stable-stage distribution, reproductive value vector, sensitivities, elasticities, and other demographic measures. The sensitivity of  $\lambda$  to changes in lifehistory traits is defined as

$$s_{ij} = \frac{\partial \lambda}{\partial a_{ij}} = \frac{v_i w_j}{\langle \mathbf{w}, \mathbf{v} \rangle},$$
 (1)

where  $a_{ij}$  is the life-history trait found in row *i* column j of the projection matrix (e.g.,  $a_{13}$  is the fertility of individuals in stage or age class 3, and  $a_{32}$  is the survival of individuals from stage or age class 2 to stage or age class 3),  $v_i$  is the *i*th element of the reproductive value vector,  $w_i$  is the *j*th element of the stable-stage distribution, and  $\langle w, v \rangle$ is the scalar product of the reproductive value vector, v, and the stable-stage distribution, w. In summarizing sensitivities, I used only possible transitions; that is, I used only sensitivities for transitions with non-zero arcs in the life-cycle graph (one can, for example, calculate the sensitivity of  $\lambda$  to the probability of surviving from age 2 backwards to age 1, but this has little biological relevance). The elasticities,  $e_{ij}$ , are derived from the sensitivities and are defined by

$$e_{ij} = \frac{a_{ij}}{\lambda} \times s_{ij}.$$
 (2)

The elasticities help circumvent the problem that fertility and survival are measured on different scales. They assess, instead, the effect a proportional change in a given life-history trait will have on  $\lambda$ . They also have the advantage of summing to unity, and of being non-zero only for possible transitions. I present the elasticities on a scale of 0–100 (%) rather than 0–1.0.

Because of their intuitive appeal, and to facilitate construction of the demographic projection matrices, I used life-cycle graphs (Caswell, 1989; McDonald and Caswell, 1993). A life-cycle graph comprises numbered nodes that represent the age classes or stages in the life cycle and arcs that represent transitions between stages (e.g., survival rates, fertility rates, changes in size or social status). Caswell (1989: Figure 2.1) discussed the relationship between the continuous variable, x, for age and the discrete variable, *i*, for age class when formulating matrix models. Further, all the analyses in this paper use birth-pulse (as opposed to birth-flow) formulations, which better characterize most birds and many mammals. The life-cycle graph is mathematically equivalent to the projection matrix. Thus, the projection matrix coefficient,  $a_{ij}$ , equals the coefficient on the arc from node j to node i in the lifecycle graph. For convenience, the arc coefficients of the life-cycle graph are labeled  $F_i$  for the  $a_{1i}$  that represent fertility rates and  $P_i$  for the  $a_{ii}$  that represent survival rates. As noted by Caswell (1989: 13), the fertility coefficients,  $F_{j}(a_{1j})$ , contain a survival term,  $P_j$ , as well as a maternity or paternity function term,  $m_i$ .

I used the following parameters or assumptions in formulating the survival elements of the matrices for long-tailed manakins: (1) an estimate of 0.50 for the unmeasured fledgling-to-yearling survival, from reports in the literature (e.g., Koenig and Mumme, 1987, for the acorn woodpecker, Melanerpes formicivorus), and (2) survival estimates for younger individuals of both sexes based on the younger male survival estimate. For both sexes, I used the younger survival rate through the age class of plumage maturation in males (year 4). For mathematical convenience, or when lacking life-long agespecific data, one can condense age classes during which survival and fertility are known or assumed to be essentially age-independent into a single stage in the life-cycle graph (Caswell, 1989; McDonald and Caswell, 1993). I refer to individuals at this age-independent stage as being in their prime. Coefficients associated with the prime stage have the subscript p. The age-independent survival rates for males and females were based on the estimates from the Jolly-Seber models.

To generate the paternity function,  $m_i$ , for males, I first calculated an age-specific copulatory schedule for 70 color-banded males that met two criteria: (1) they were active at a dance perch at least once after banding, and (2) they were  $\geq 5$  years old, the youngest age at which a male copulated. The males meeting those criteria were categorized as known age (N = 35), if first captured and banded in one of the three age-specific, predefinitive plumages or minimum-age (N = 35) if captured when already in definitive plumage ( $\geq$  fourth year). The sampling effort per male was equal to the number of hours of scheduled 2-h observations at the lek arena that he attended most frequently at each age. The definition of a copulation included the following restrictions: (1) it occurred during a scheduled 2-h observation period, (2) multiple mountings constituted a single copulation, (3) if females could not be distinguished by bands or plumage from other females that copulated the same day, with the same male, I recorded only a single copulation for that day.

I used two different methods for calculating an age distribution of male copulations. For the basic analysis, I used estimated ages for the minimumage males using criteria described in the results. As a variant, I used the strict minimum possible age for all minimum-age males, except for two alpha males who were highly successful in the year they were banded. Because no known-age male copu-

# Table 1 Observer effort and copulatory success for 35 known-age and 35 minimum-age males, 1984–1991

Age class or stage Cumula-Male category 5 6 7 8 9 10 11 12 13 14 Prime<sup>a</sup> tive Known age Observations (h) 1974 1262 804 502 258 746 1506 5816 No. of males 22 20 12 7 6 2 35 No. of copulations 2 2 0 2 0 4 10 2 3 No. of copulators 1 0 1 0 6 Estimated aged Observations (h) 736 856 2114 1974 1098 530 516 398 516 314 5346 5816° No. of males 7 7 26 18 12 9 8 5 3 2 9 35 0 0 7 No. of copulations 1 37 50 4 18 33 6 155 156 No. of copulators 0 0 1 7 2 5 4 2 1 1 10 4 Minimum age<sup>e</sup> Observations (h) >2296 2454 2980 1264 362 646 444 456 388 5816<sup>c</sup> No. of males 22 28 18 10 6 5 4 3 18 35 No. of copulations 49 31 10 8 17 35 0 6 66 156 No. of copulators 4 6 2 2 4 4 0 6 10 Copulations/h × 100<sup>f</sup> Estimated + known 0.074 0.094 0.034 1.434 3.375 0.888 0.7754.523 6.395 1.911 2.350ª Minimum + known 0.7451.202 0.484 0.718 2.431 4.986 0 1.546 1.894\*

<sup>a</sup> Prime was  $\geq 10$  years old for the estimated age distribution, and  $\geq 7$  for the minimum distribution.

<sup>b</sup> Maximum age attained by known-age males by end of study period was 10.

<sup>c</sup> Cumulative sampling effort represents total number of hours in scheduled 2-h observations.

<sup>d</sup> Minimum-age males that were assigned their estimated age, as described in the text.

<sup>e</sup> Minimum-age males that were assigned their minimum age, with two exceptions, as described in text

<sup>f</sup> Copulatory rate includes the sampling effort and copulation data from known-age males.

lated at less than 5 years old, I assumed that these two minimum-age copulators were 5 years old, a highly conservative assignment given the social status and copulatory success of known-age males at that age. From either the estimated or strict distribution, I calculated a stage-specific copulatory rate (Table 1) and then assumed that it was directly proportional to the stage-specific fertility function,  $m_j$ . For females, I assumed linearly increasing success with a slope equaling that of sparrowhawks (Accipiter nisus; Newton, 1988), which had the steepest increase among recent analyses of lifetime reproductive success in birds (Clutton-Brock, 1988). I assumed that fertility reached an age-independent rate,  $m_p$ , in year 7.

Although I knew or could estimate the relative fertilities of age classes or stages for males and females, the absolute values were unknown. I therefore calculated the fertility coefficients by using a stationarity assumption (McDonald and Caswell, 1993). By assuming that population growth is stationary ( $\lambda = 1.0$ ), one can solve for an unknown parameter in the characteristic equation. In this study, that unknown was the absolute value of the maternity (paternity) function,  $m_j$ . The  $m_j$  are one component of the fertility coefficients,  $F_i$ . The methods described above provided basal distributions of the stage-specific  $m_i$ . I then multiplied the set of  $m_i$  by constants, using trial-and-error adjustment, until the matrices yielded  $\lambda = 1.0$ . Thus, the absolute values for the stage-specific maternity or paternity functions were adjusted, but not their values relative to other stages.

I used separate projection matrices derived from

life-cycle graphs for each sex. Many demographic analyses use a females-only approach, assuming female demographic dominance, largely because female fertilities are fundamental and are usually easier to assess. Caswell and Weeks (1986) showed that two-sex matrix models can be nonlinear with the sort of competition between age classes found in long-tailed manakins, a complication I avoided by performing separate analyses for each sex.

Certain cautions are necessary when using the separate sex matrices and stationarity assumption. The stationarity assumption is based on the argument that populations that are neither growing nor shrinking have a mean growth rate of 1.0. Clearly, one cannot then use the resulting calculations to assess growth rates. It is also inappropriate to use the separate sex analysis to assess population growth rates for males and females. Nevertheless, the separate-sex matrices and the stationarity assumption do permit calculation of other demographic measures, such as eigenvalue sensitivities and reproductive values (McDonald and Caswell, 1993). Those measures allow comparison of stage- or age-specific selection pressures on males and females. The criteria for changing a number of the assumptions and parameters of the basic model are outlined in the results.

#### RESULTS

I begin by presenting survival estimates. Next, I address reproductive rates, and then synthetic aspects, such as reproductive values and sensitivities, that integrate features of both the survival and re-

Category the estimates	No. of returns	No. of individuals	Modela	Survival rate ( $\bar{x} \pm SD$ )		
	275	46	D2	$0.78 \pm 0.03$		
	96	96	D2	$0.68 \pm 0.06$		
	236	140 60	В	$0.75 \pm 0.04$		
	667	342	В	$0.70 \pm 0.02$		

<sup>a</sup> D2, reduced parameter model with constant survival rate per unit time, constant capture probability per unit time. B, reduced parameter model with constant survival rate per unit time, time-specific capture probabilities.

<sup>b</sup> Individuals included in analysis of survival rate of all individuals.

productive rates. I then examine the effect of changing some of the assumptions and parameters of the matrix models. Finally, I compare the manakin results to my parallel analyses of published studies that had  $l_x m_x$  life tables or equivalent data on survival and fertility.

#### Survival rates

Table 2 lists estimates of annual survival rates. The annual survival rate of older males was 0.78 and that for younger males was 0.68. The probability of detection (resighting or renetting in a subsequent year) for a marked male, after first capture, was 0.83. Of 142 males banded, only one was recaptured in a subsequent year without being resighted. The lack of recaptures without sightings suggests that few established males were unsighted within the study area. However, 52 (37%) males that were resignted were never recaptured. For 18 males that were never recaptured, the interval between banding and the most recent resighting record was at least 3 years; for an additional 5 males the interval was 7 years. Many surviving males, therefore, avoided recapture for months or years, even though they remained in the study area.

Resighting data complemented the recapture data because lek attendance changed as a function of age. Males not sighted in a particular season sometimes reappeared in later years. For example, of the 45 color-banded males resignted in 1989, 7 had a 2-year span between successive sightings, 2 had a 3-year span, and 1 had a 4-year span. Long spans between sightings were limited to lower-ranking males; no alpha or beta male was ever resighted after a gap lasting more than a few weeks within a field season. Because their attendance rates at lek arenas were much higher than those of lower-ranking males, alphas and betas were unlikely to be missed, even in years with lower sampling effort (McDonald, 1989b). Gaps in sightings, therefore, probably represented mortality for high-ranking males but might not for lower-ranking males. A few cases where banded males were discovered outside the study area suggested that mortality rates might further differ from disappearance rates among young ( $\leq 6$  years old), lower-ranking males that emigrated. The documented emigrations, however, occurred more often in early definitive stages (age classes 5–7, N = 4) than during the predefinitive stage (N = 1). True survival, therefore, may be higher than the estimated level for both categories.

Attainment of alpha status had no obvious effect on survival rate. The two males most successful in mating (60 and 63 of the 166 copulations included in Table 1) survived 5 years beyond their first observed copulations. Other copulators survived 3-6 years beyond first copulation. All had peak years toward the end of that span. Six different alpha males outlived one or more of their beta partners. As a result, eight beta males disappeared before their alpha males, whereas only four alpha males disappeared before their only recorded beta partner. Differences in weight among males, and between males and females, were clearly related to rank but not to survival rates. During the breeding season, males of high social status, especially copulators, weighed significantly less (16-18 g) than females (20-23 g) and predefinitive males (18-20 g). High-ranking males also weighed less in the breeding than in the nonbreeding season, when their weights did not differ significantly from the female weights (McDonald, 1989a).

The estimated survival rate of females was 0.76. Sightings and recaptures of the wide-ranging females were more widely dispersed in space and time than were those of males, whose activities consistently centered on the dance perches at which observations occurred. The probability of detection (resighting or renetting) for a female was 0.38 (SD = 0.11, N = 140), significantly lower than that for a male ( $\bar{x} = 0.83$ , SD = 0.03, N = 142; t' = 48.1, p < .001, two-tailed test).

#### Age, reproduction, and social status

I derived the data for age- and stage-specific copulatory success in Table 1 using two different methods. The first used estimated ages for minimumage males by inference from their social status and success relative to that of known-age males. The second assigned the strict minimum possible age. The strict method required the implausible assumption that minimum-age males developed social status and mating success in an age-specific pattern different from that established for known-age males. I therefore used the more plausible estimated age distribution for the primary demographic analyses.

Social and copulatory data for known-age males provided a basis for the estimated ages of minimum-age males. Known-age males rarely attained alpha or beta rank or danced more than once for a female before their eighth year, and by the end of the study none had the opportunity to reach an



#### Figure 1

Life-cycle graphs for longtailed manakins. (A) Males. Nodes 1-9: age classes (firstyear birds, second-year birds, etc.); node Pr-10: prime stage, comprising males  $\geq 10$  years old, assumed to have ageindependent fertility and survival. (B) Females. Nodes 1-6: age classes; node Pr-7: females in their prime.  $F_i$ , fertilities (all arcs directed to node 1, including the leftmost self-loop);  $P_i$ , annual survival probabilities (horizontal arcs and rightmost self-loops). The subscript p denotes a transition (annual survival or fertility) that is age-independent.

age class greater than 11. For many males, their first dance for a female occurred 1 to several years before they danced regularly for females or attained beta rank. The 4 copulations by known-age males in their sixth to eighth years were by a beta male (N = 1) or occurred under unusual circumstances (N = 3). The 3 established, known-age alpha males that performed the remaining 6 of the 10 known-age copulations did so in their ninth and 10th years. By the end of the study period, no known-age male had yet attained the high copulatory rates achieved by a few of the top minimumage males. Further, 3 minimum-age males first attained beta rank in at least their ninth year, and 2 minimum-age alpha males had still never copulated in at least their 11th year. Of the 54 known-age males, 4 were alpha males, and 6 were beta males. During the study period, all other alpha (N = 13)and beta (N = 16) males were minimum-age. In estimating ages, therefore, I assigned betas to age class 8 and copulators to age class 9, which is still likely to have been conservative for several of the highly successful males responsible for the majority of the copulations.

The distribution of copulations was highly skewed toward older males (Table 1), whether using estimated ages ( $\bar{x} = 10.1$ ; SD = 2.2) or strict minima ( $\bar{x} = 7.4$ ; SD = 2.1). Four males were responsible for 143 of the copulations. The 2 most successful were responsible for 123 copulations. Two males responsible for three copulations were betas of the two most successful alpha males. The only other copulation by a nonalpha was by a beta vying for a position at the most successful lek arena in 1991. The copulation occurred during a brief and unusual period of social turmoil after the rapid, sequential disappearances of the beta, the alpha, and the successor alpha, who had been beta for only 1 year.

Fewer data were available for the relationship between age and reproduction in females. Females of other species of manakins appear to begin nesting the year after hatch (Snow and Lill, 1974), and Foster (1976) suggested this was the case for longtailed manakins also. In this study, a female banded in the nest copulated 350 m from her natal site 2 years after hatch. Further, nine females had spans of 7–9 years between first and last documented reproduction, longer than any reproductive spans documented for males. Females (N = 29) attempted reproduction in successive years, as judged by vascularization, copulations, or nests. Because females do not delay plumage maturation and do not engage in long-term, complex networks of social interaction (McDonald, 1989a), and because of the data for long reproductive spans, I assumed provisionally that females begin reproduction at age 1. As a variant, I also modeled the consequences of a 1-year delay in reproduction. Nesting success was low. Two banded fledglings from different nests survived at least 1 year from 18 2-egg clutches; 6 additional nestlings had unknown fates, yielding a minimum of 6% survival from egg to fledging and a potential maximum of 22%.

#### Life-cycle graphs for males and females

I modeled the life cycle of male long-tailed manakins with the 10-node life-cycle graph shown in Figure 1A. The first nine nodes represent age classes (first-year birds, second-year birds, etc.). The final node (Pr-10) represents males in their prime, a multiyear stage during which both survival and fertility are assumed to be independent of age. The prime stage includes all males in their 10th year and older. The prime stage, therefore, begins just before the mean age of copulation (Table 1). Arcs (directed lines) describe the transitions between nodes. Self-loops are arcs that return to the same node. The arcs and self-loops have coefficients as follows:  $F_i$  for the number of first-year birds produced at time t + 1 per individual in node j at time t (i.e., the  $F_i$  are the coefficients on all the arcs or self-loops directed to node 1);  $P_j$  for annual survival rates (i.e., all the coefficients on right-pointing, horizontal arcs plus the self-loop on the final node). At the stage where either fertility or survival rates become independent of age, I used the subscript p ("prime"). Note that I assumed males to achieve age-independent survival rates,  $P_{\mu}$  (from node 5 on, after plumage maturation), 5 years before attaining an age-independent paternity rate,  $m_p$  (at node Pr-10).

The life-cycle of females can be modeled with seven nodes (Figure 1B). The first six nodes represent age classes, and the final node (*Pr-7*) again represents individuals during their prime. For survival, the female survival schedule mirrored that of males, becoming independent of age from node 5. The coefficients on the arcs of the life-cycle graphs in Figure 1 are directly equivalent to those in the demographic projection matrix used for the actual calculations (Caswell, 1989). The simplifying assumption of an age-independent prime stage means that the matrices are stage classified, as opposed to the strictly age-classified matrices developed by Leslie (1945).

#### Sensitivity and elasticity analysis of the life-cycle graph and matrix

Eigenvalue sensitivity analysis assesses the effect on population growth ( $\lambda$ ) of a change in a life-history trait, such as stage-specific survival or fertility (Caswell, 1989). Elasticity is the sensitivity of  $\lambda$  to a proportional change. The mathematical definitions are given by Equations 1 and 2 in Methods. The dominant eigenvalue of a demographic projection matrix is  $\lambda$ , the population growth rate. Assuming weak selection and no frequency dependence, one can equate  $\lambda$  with fitness (Caswell, 1989: 171; Lande, 1982a,b). The sensitivities are directly equivalent to selection gradients, which measure the direct force of selection on life-history traits (Arnold, 1983: 96–100).

I present the elasticity measures in two ways: as coefficients on life-cycle graphs and in summary, percentage-based graphs or tables. All the elasticity measures are presented as percentages rather than frequencies. Figure 2A is the life-cycle elasticity graph for males, and Figure 2B the graph for females. To facilitate comparison between the sexes, and as a prelude to interspecific comparisons, Figure 3 summarizes elasticities for the two major sorts of life-history transitions: the percentage of the total elasticity represented by the summed elasticities to fertility transitions and the percentage represented by the summed elasticities to survival rates. For brevity, I refer to the percentage of the total elasticity of  $\lambda$  attributable to changes in the survival rates as the "survival elasticity."

The survival elasticity of males was higher than that of females (Figure 3; 91.4% of total versus 79.6%). The percentage of possible survival sensitivities was even more different between males (95.4%) and females (68.7%). The simplifying assumption of a prime stage scarcely affected the result, as demonstrated by elasticity analyses of fully age-expanded, Leslie matrices with 14 age classes. The paternity function for males in the full Leslie matrix was based on the entire estimated age distribution for copulatory success in Table 1. Because survival beyond the 15th year remains undocumented, the matrix was truncated at that age class for both males and females. Using the full Leslie matrices (Table 3), the survival elasticity changed little (from 91.4% to 90.4% in males, from 79.6% to 77.8% in females).

#### **Generation times**

I used the method of Cochran and Ellner (1992) to calculate generation times and age at prime from the projection matrices. When  $\lambda = 1.0$ , the cohort generation time,  $T_c$ , equals the mean age of parents at the stable age distribution,  $\overline{A}$  (see Caswell, 1989: 109). For females,  $T_c$  was 4.9 years, for males, 11.7. The structure of the life-cycle graphs and the data for age-specific copulatory success in Table 1 reflect the demographic differences between the sexes. Females had 6 years of reproduction before prime and reached their prime in the seventh year, which was one age class earlier than male reproductive success began to rise steeply. The estimated age distribution in Table 1 shows that male copulatory success peaked in the 13th year, 3 years after the beginning of the prime stage (tenth year and older) used for analysis. Cochran and Ellner's method allowed calculation of mean age of individuals in the stable-stage distribution. At equilibrium, the 7.6% of males in their prime have a mean age of 12.6 (SD = 4.1); the 13.5% of females in their prime have a mean age of 9.1 (SD = 3.5).

Table 4 lists the stable-stage distribution and reproductive values for males and females for the stage-classified analyses represented by the life-cycle graphs of Figures 1 and 2. Note that the peak



reproductive value of males was considerably greater than the peak value of females. That is, a male manakin in his ninth year is worth 14.4 first-year males, whereas a female in her prime (seventh year or older) is worth 3.0 first-year females. This difference is due, in large part, to the fact that fewer males (12.4% surviving through the fifth year) than females (50% surviving through the first year) survived to the age of first reproduction. Using the variant model of a full Leslie matrix uses all the data on male mating success as a function of age. With the Leslie matrix analysis, the reproductive value of males peaked at 15.0 in their 12th year, followed by a rapid decline (Figure 4). The peak reproductive value of females under the Leslie matrix variant was 2.7 in their sixth year (Figure 4), followed by a gradual decline. The minor difference between peak reproductive values using the stageclassified model versus the Leslie model indicates that the simplifying assumption of a prime stage had little effect on the major results. The difference between the reproductive value curves of males and females was considerably more pronounced than the intersexual difference in elephant seals (Figure 4; data from Le Boeuf and Reiter, 1988).

## Effects of changing other assumptions, including maturation events

What effect would changing various assumptions and parameters have on the summary survival elasticity measure? Using the stationarity assumption to solve for the unknown maternity functions, fe-



#### Figure 2

Elasticity (expressed as percentage rather than frequency) graph for longtailed manakins. The nodes and arcs refer to the same stages and life-history transitions as depicted in Figure 1, but the coefficients here represent the elasticity of  $\lambda$  (fitness) to changes in stagespecific survival or fertility rates. The arcs with bold lines in each graph represent the three transitions to which  $\lambda$  is most elastic. (A) Males, (B) females.

#### Figure 3

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Summary elasticity measures for male and female longtailed manakins. The measures are the summed percentages of the elasticity of  $\lambda$  to survival rates, or to fertility rates (i.e., they can be derived from the coefficients of Figure 2 by summing across either survival or fertility arcs).

McDonald • Male--female life-history differences

#### **Figure 4**

Reproductive values of longtailed manakins, using a Leslie matrix with 14 age classes, and for male and female northern elephant seals, from data in Le Boeuf and Reiter (1988). For the femalemanakin Leslie matrix, the prime stage of Figure 1B was expanded into age classes, and the matrix was truncated at the 15th age class, as for males. (Open symbols) males, (filled symbols) females, (solid lines) manakins, (dashed lines) elephant seals.



males in their prime produced a mean of 0.96 fe-

male fledglings per year  $(m_p = F_p/P_p; 0.726/0.755)$ 

= 0.96). Of the known parameters, only first-year survival was not based on data from this study. For that reason, and because  $\lambda$  was sensitive and elastic

to its value (Figure 2;  $e_{12} = 16.8\%$  of total elasticity;

 $s_{12} = 0.34 = 19.0\%$  of total sensitivity), it is of

interest to see what changing this rate would do to

the  $m_{p}$  required to maintain stationarity ( $\lambda = 1.0$ ).

Changing first-year survival to 0.35 raised the re-

quired  $m_p$  to 1.37. Given my evidence for low nest-

ing success, it seems likely that the values used in

the primary model of Figure 1 ( $m_p = 0.96, P_1 =$ 

(0.5) may be the closest to the true values. With the

lower initial survival rates (" $P_1 = 0.35$ " variant of Table 3), the survival elasticity remained un-

changed at 79.6%. Using the less plausible assumption that females first bred at age 2 ("delay"

variant of Table 3) had the greatest effect on the

only minor changes in the survival elasticity. I mod-

eled two variants, and each was analyzed with a

Leslie as well as a prime-stage matrix (Table 3). In

the first variant, I used the strict, minimum-age

distribution of copulatory success from Table 1,

with a prime at ages  $\geq$  7, the mean age at copulation

in that formulation. With the strict minimum dis-

tribution, the total survival elasticities became

slightly less important (89.5% versus 91.4% of the

total elasticity). As noted above, using the full Leslie

Changing the distribution of male fertility caused

survival elasticity (to 83.0% from 79.6%).

#### Table 3

Survival elasticity under variants of matrix models for male and female long-tailed manakins

Model type	Male fertility distribu	, ation <sup>a</sup>	Param female			
	Esti- mated	Strict	Orig- inal	Delay	$P_1 = 0.35$	
	91.4 <sup>6</sup> 90.4	89.5 87.7	79.6⁵ 77.8	83.0 —	79.6	

Survival elasticity is the percentage of total elasticity of  $\lambda$  attributable to changes in survival rates.

Table 1 shows the estimated and strict minimum age distributions used to calculate male fertilities.

Primary models, illustrated in Figures 1 and 2. See text for parameters used for formulating variants.

matrix formulation left survival elasticities virtually unchanged (to 90.4% from 91.4% using the estimated paternity distribution; to 87.7% from 89.5% using the strict minimum distribution), again indicating that the stage-classified prime simplification did not affect the major results. Of the variants considered in Table 3, therefore, the highest elasticity to survival transitions for females (81.7%, assuming a delay in age of first reproduction) was still considerably lower than the lowest elasticity total for males (87.7% using the Leslie model with the strict paternity distribution).

### Interspecific comparisons of survival elasticity

Table 5 shows life-history traits for male and female long-tailed manakins, eight other species of birds, and two mammals, including the survival elasticity measures of Figure 3. The species in Table 5 are listed in decreasing order of survival elasticity. The selection of data was based on availability and was neither systematic nor random. The data sets used, however, represent a wide range of mating systems, taxonomy, habitat, body mass, and life histories, and may, therefore, be representative of much of the spectrum among birds. The two mammals were

#### Table 4

Demographic measures for model with prime stage for male and female long-tailed manakins

Stage	Males 54			Females				
	distribution	Reproductive value	Mean age <sup>a</sup> (±SD)	Stable stage distribution	Reproductive value	Mean age <sup>a</sup> (±SD)		
1	0.36	1.0		0.37	1.0	0		
2	0.18	2.0		0.18	1.7	1		
	0.12	2.9		0.13	2.0	2		
	0.08	4.3		0.09	2.3	3		
5 -	0.06	6.3		0.06	2.8	4		
6	0.04	8.0		0.04	2.9	5		
7	0.04	10.1			4.0	•		
8	0.03	12.8						
9	0.02	14.4						
Prime <sup>b</sup>	0.08	13.6		0.14	3.0	9.1 (±3.5)		

<sup>a</sup> Age at time of census, at beginning of stage.

<sup>b</sup> Prime stage is 10th node for males (Figure 1A) and 7th node for females (Figure 1B).

# Table 5 Comparison of demographic measures across species and sexes

Species and reference	Sex	SE	SS	Sexual difference <sup>a</sup>	λ (growth rate) <sup>b</sup>	AS	MSc	Body weight (g) <sup>d</sup>
Northern spotted owl (Strix occidentalis: Lande, 1988)	and a	98.1	93.5	-	0.96	0.94	М	610 <sup>e</sup>
Long-tailed manakin (Chiroxiphia linearis)	М	91.4	95.4	11.8	1.00	0.78	L	18
Northern elephant seal (Mirounga angustirostris: Le Boeuf and Reiter, 1988)	М	89.5	92.6	5.4	1.00	0.82	FHP	$3.7 \times 10^{6}$
Red deer (Cervus elephus: Clutton-Brock et al., 1988)	M F	87.9 87.2	61.4 49.2	0.70 0.70	1.00	0.98 <sup>t</sup>	FHP	$6.5 \times 10^{3}$ 4.5 × 10^{3}
Florida scrub jay (Aphelocoma coerulescens: Woolfenden and Fitzpatrick, 1984; McDonald and Caswell, 1993)		85.7	88.2	-	1.00	0.82	C	80*
Yellow-eyed penguin (Megadyptes antipodes: Ricklefs, 1973)		84.6	89.1	-	1.09	0.84	М	5385 <sup>s</sup>
Northern elephant seal (Mirounga angustirostris: Le Boeuf and Reiter, 1988)	F	84.1	78.0	5.4	1.00	0.80'	FHP	$9 \times 10^{5}$
Long-tailed manakin (Chiroxiphia linearis)	F	79.6	68.7	11.8	1.00	0.76	L.	21
Cactus finch (Geospiza scandens: Grant and Grant, 1992)	М	79.0	82.1	4.8	1.12	0.84'	М	21 <sup>h</sup>
Acorn woodpecker (Melanerpes formicivorus: Koenig and Mumme, 1987)	М	75.8	73.3	3.7	1.02	0.69	С	83
Cactus finch (Geospiza scandens: Grant and Grant, 1992)	F	74.2	75.6	4.8	1.32	0.80 <sup>r</sup>	М	20
Acorn woodpecker (Melanerpes formicivorus: Koenig and Mumme, 1987)	F	72.1	74.2	3.7	1.08	0.69	С	78
Screech owl (Otus asio: Ricklefs, 1983)		61.6	67.4	-	1.01	0.75	М	181
Prairie warbler (Dendroica discolor: Nolan, 1978)		52.4	81.1	-	1.27	0.65	М	8
Blue tit (Parus caeruleus: Dhondt, 1989)		25.1	58.4	_	1.15	0.28	М	11

SE, Survival elasticity; SS, survival sensitivity; AS, adult survival; MS, mating system.

<sup>a</sup> Difference between male and female survival elasticity.

<sup>b</sup> Stationarity assumption ( $\lambda = 1.0$ ) used to solve for unknown parameter.

<sup>c</sup> M, monogamous; L, lek; FHP, female herding polygyny; C, communal breeding.

<sup>d</sup> For single-sex analyses, value is mean of male and female weight.

<sup>e</sup> Body weight data from Dunning (1984).

<sup>f</sup> Mean of survival rates from age of first reproduction, excluding ages at which survival declined sharply

<sup>8</sup> Body weight data from Richdale (1973).

<sup>h</sup> Body weight data from Grant and Grant (1989).

selected as well-documented examples of intense sexual selection on males. For the species listed, spotted owls (*Strix occidentalis*) had the highest survival elasticity. The survival elasticity scores of male (91.4%) and female (79.6%) long-tailed manakins showed the greatest intersexual difference both in absolute number and ranking in Table 5 (91.4 – 79.6 = 11.8; ranks 2 and 9). Two of the published avian data sets had separate-sex analyses. For Darwin's cactus finch (*Geospiza scandens*), the male and female score and rank differentials (79.0 - 74.2 = 5.2; ranks 10 and 12) were lower than those of the manakins, as were those of male and female acorn woodpeckers (*Melanerpes formicivorus*; 75.8 - 72.1 = 3.7; ranks 11 and 13). Red deer (*Cervus elaphus*) males and females had similar survival elasticities, and the intersexual difference (87.9 - 87.2 = 0.7; ranks 4 and 5 in Table 5) was less pronounced than those of any of the birds. Male and female northern elephant seals (*Mirounga angustirostris*) had an in-

tersexual difference (89.5 - 84.1 = 5.4; ranks 3 and 8) that again was less than that of the manakins, but greater than that of the other two birds.

The difference between male and female longtailed manakins was robust to changes in the assumptions used to generate the matrices. The less plausible variant models that produced the lowest male and highest female survival elasticities (87.7 -83.0 = 4.7) were nevertheless approximately equivalent to the largest of the other intersexual contrasts. Using sensitivity to rank the species/sex combinations made the intersexual difference in the manakins even more extreme. Males (95.4%) had the highest survival sensitivity of any of the 16 species/sex combinations, while females (68.7%) ranked 12 of 16. Using survival sensitivity further widened the intersexual differential of manakins relative to that of the two mammals and the two birds, in score as well as in ranking (Table 5). Indeed, the intersexual survival sensitivity (selection gradient) difference in the manakins (95.4 - 68.7)= 26.7) was approximately equivalent to the difference (89.1 - 58.4 = 30.4) between long-lived yellow-eyed penguins (Megadyptes antipodes) and weedy blue tits (Parus caeruleus). For those species that had only a single life table, differences between the sexes are likely to be so slight as to be overshadowed by sampling error or other problems of data collection or interpretation (e.g., Woolfenden and Fitzpatrick, 1984).

No correlation was apparent between the survival elasticity and mating system or body size in Table 5. A pattern did, however, emerge regarding delayed reproduction, and, more weakly, regarding survival rate. Each of the eight species/sex combinations at the top of the table (high survival elasticity) delayed reproduction for 1 or more years, and most had high adult survival rates. In each of the seven species/sex combinations that had the lowest survival elasticities, 25% or more of the population reproduce at age 1, and most had lower adult survival rates. Female long-tailed manakins fell at the boundary of species/sex combinations that delayed and those that did not.

#### DISCUSSION

The elasticity analyses of this study provide a quantitative measure of divergence between male and female life-history traits and the selection gradients on those traits. Further, they provide a basis for comparative approaches (Ricklefs, 1983), as data become available for a wider variety of species and mating systems. Debate continues concerning which measure of selection is the most appropriate and consequential (Downhower et al., 1987; Wade and Arnold, 1980), proper null models (Sutherland, 1987), the influence of stage of enumeration (Cabana and Kramer, 1991), and the role of constraints and selection on correlated traits (Price et al., 1987). Grafen (1987) suggested that measuring the intensity of sexual selection might be of little consequence in itself. The results presented here suggest an additional and potentially powerful approach to the problem. Before setting out to measure and interpret variance of male mating success, one can work backwards, in a manner analogous to that used in dynamic programming, and let evolutionary consequences reflected by intersexual demographic divergence serve as a guide to patterns in the history of sexual selection, especially in cases where little size dimorphism occurs.

# Survival rates, plumage, and life-history patterns among manakins

Karr et al. (1990) provided annual survival rate estimates for three species of manakins: 0.51 for Pipra coronata, 0.72 for Pipra mentalis, and 0.47 for Manacus vitellinus. The estimated survival rates of male and female long-tailed manakins lie along the upper bound for all species analyzed by Karr et al., but at the lower bound of the 0.80–0.90 estimates traditionally ascribed to tropical species (Fogden, 1972; Snow and Lill, 1974). The first several years of a manakin's life may entail extensive wandering (see McDonald, 1989a, for evidence at a local level) and higher mortality (Graves et al., 1983), whereas high survival rates are characteristic of established birds. Support for the latter point comes from the studies of M. manacus by Snow (1962) and Snow and Lill (1974). This species is similar to M. vitellinus, and yet Snow's estimate of a 0.89 survival rate for established males is higher than the estimate by Karr et al. (1990) from analysis of all individuals, regardless of sex, age, or social status. Nevertheless, a difference in survival rate is only one of a suite of differences that separate manakins in the genus Chiroxiphia from other dichromatic, lekking genera in the family.

Plumage maturation in male long-tailed manakins occurs in the fourth year (Foster, 1987; McDonald, 1989a). Manakins in the important genera Pipra and Manacus achieve the definitive male plumage in the first or second year (Foster, 1987). The variance of male mating success in long-tailed manakins is apparently greater than that in Pipra and Manacus (McDonald, 1989a; Wiley, 1991). The longer delay and relatively high survival rate of male long-tailed manakins are aspects of intergeneric differences that culminate in the apparently unique phenomenon of obligate, cooperative male-male courtship display in the long-tailed manakin and its three congeners (Foster, 1987). The results of this study suggest that when comparable data are available for other manakins, the intersexual differences in survival elasticity, reproductive value curves, and other demographic measures may serve as a guide to the species in which sexual selection has been most intense.

### Life-history divergence as a major consequence of intersexual selection

The considerable demographic difference between male and female long-tailed manakins was attributable largely to the difference in the age distribution of reproduction. Male copulatory success peaked late in the life span (Table 1 and Figure 4). Males, therefore, simply had to survive to their fifth year to have any chance at copulatory success and to their ninth year before expected success rose dramatically. Reproduction in male long-tailed manakins is restricted to approximately the final third of a fairly long life span. The distribution of reproduction against age for male long-tailed manakins may, therefore, be more skewed than it is for any other long-lived bird or mammal. This skew is reflected in the shape of the reproductive value curve of Figure 4. A typical reproductive value curve peaks much earlier in the life span (cf. Roughgarden, 1979: Figure 18.8) and has a gradually decreasing tail.

The intersexual difference in the manakins was greater than that in elephant seals, which have the highest variance of male mating success reported for a mammal (Le Boeuf and Reiter, 1988). The reproductive value curves for female manakins and female elephant seals were similar to each other and far less skewed than those of the males. The reproductive value curve of male elephant seals was less sharply peaked and less skewed than that of male long-tailed manakins, especially in comparison to that of the female seals. The contrast between male and female manakins was also reflected in the interspecific comparisons of Table 5. The male survival elasticity resembled that of species with delayed reproduction, while the female survival elasticity resembled that of species with no delay. It seems unlikely that the actual pattern of female age-specific success is any more skewed than the strong linear increase assumed for this analysis. Data for age-specific reproductive success of females in this and other tropical lek-mating species will be difficult to obtain but would be especially valuable for comparative analyses, especially as data accumulate for the roles of intra- and intersexual selection in lek-mating species (Borgia, 1985; Gibson and Bradbury, 1987; Hill, 1991; Höglund and Robertson, 1990; Trail, 1985).

Intense sexual selection on male long-tailed manakins was due largely to females' being nearly unanimous in choosing a few of the oldest males (123 of 166 copulations by two males  $\geq 8$  years old in Table 1; McDonald, 1989a,b). An intriguingly similar case of major sexual differences in age of first reproduction occurs in the nonlek mating system of spotted hyenas (Crocuta crocuta; East and Hofer, 1991; Hofer H, East ML, personal communication). Whereas orderly male queues are enforced by female choice among leks in long-tailed manakins (McDonald, 1993), female dominance over males enforces orderliness in the hyenas, such that males maintain rank beyond their peak of physical vigor. In mating systems where intersexual selection is of primary importance, success might continue beyond the age of peak physical vigor because of female copying of mate choice or female preference for familiar mates. In contrast, male-male combat is likely to produce peak success at intermediate ages, followed by a decline. Such a pattern occurs in black grouse (Tetrao tetrix), where both size dimorphism and the importance of male combat for territories point to the predominance of intrasexual selection (Kruijt and de Vos, 1988). Declining success with advanced age may make the demographic divergence caused by intrasexual selection relatively less pronounced than the divergence driven by female choice. Accepting such a hypothesis, however, will require more demographic data, on a wider array of species, than are now available.

The sensitivities of  $\lambda$  to life-history transitions are equivalent to selection gradients, and the results presented here show very different selection pressures on survival rates for males and females. Intense sexual selection has led to demographic divergence that now produces very different natural selection on survival for males and females. In many cases, demographic traits may be more useful in examining sexual selection than the morphological traits more commonly assessed in studies and models of sexual selection.

Many traits often used to characterize sexual selection, such as ornaments or size dimorphism, may point only weakly to intensity of sexual selection, especially intersexual selection. For example, despite the monochromatism and lack of size dimorphism in lekking hermit hummingbirds, tentative evidence suggests intense sexual selection that could be reflected in major life-history differences between the sexes (Stiles and Wolf, 1979). Long-tailed manakins are not size dimorphic (McDonald, 1989a), and whether their plumage is more extravagant than that of other species of manakins is debatable. Indeed, quantifying the brightness of ornaments poses difficult challenges (Kiltie and Laine, 1992; Read and Harvey, 1989). Conversely, despite the huge size dimorphism between male and female elephant seals, and the less dramatic size dimorphism of red deer, the intersexual difference in survival elasticity in seals (5.4) and deer (0.7) was less than that in the long-tailed manakin (11.8; Table 5). The lesser demographic difference between the sexes in the two mammals, where malemale combat plays the predominant role in male reproductive success, again hints at the possibility that demographic differences may be greatest in those species where female choice predominates.

A number of questions arise as a result of the demographic approach taken in this paper. Other lekking species are likely to exhibit the large skew in the age distribution of reproduction that I argue should be associated with intense sexual selection through female choice. Male birds of paradise (Paradisaeidae) and bowerbirds (Ptilonorhynchidae), for example, have long delays in plumage maturation (Lawton and Lawton, 1986). Will intersexual demographic differences be greater in avian species where female choice is important than in those species with a high degree of size dimorphism, such as various members of the Icterinae (Payne, 1984). where male-male interactions appear to be the primary determinant of male success? Can female choice operate to produce extravagant ornaments without also producing intersexual demographic divergence, and vice versa?

Attention to patterns of demographic divergence between the sexes may provide the elements necessary for answering such questions and then assessing patterns of inter- and intrasexual selection that can be applied to the behavioral, demographic, and genetic data collected by field workers. Moreover, the demographic measures and techniques (Caswell, 1989; Cochran and Ellner, 1992) used here should be widely applicable to problems in behavioral ecology that concern the life-history consequences of variation within and among populations, even when age is not the primary determinant of reproductive success. One example is the use of stage-classified models to describe behavioral transitions (e.g., satellite to resident, searcher to guarder; see McDonald and Caswell, 1993, for an application to the demography of cooperativebreeding Florida scrub jays, Aphelocoma coerulescens). Sensitivity analysis of age-structured or behavior-based matrix models allows quantitative comparisons that can focus precisely on the key transitions measured by behavioral ecologists.

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