

NESTLING SEX-RATIO VARIATION IN WESTERN BLUEBIRDS

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ABSTRACT.—We tested five hypotheses for facultative manipulation of sex ratios in a population of Western Bluebirds (*Sialia mexicana*) studied for 13 years in California. Based on 2,187 nestlings from 549 broods, the overall mean (\pm SE) proportion of males was $51.9 \pm 1.1\%$, not significantly different from 50%. Sex ratios of nestlings were significantly biased in only 1 of 13 years, and we failed to detect any significant bias related to brood reduction, breeder female age, presence of helper males, first-egg date, condition of the breeder female, or annual differences in environmental conditions. These results allow us to reject all five hypotheses, including: (1) nestling size dimorphism and local resource competition, both of which predict a female-biased sex ratio; (2) local resource enhancement via the “repayment model” of Emlen et al. (1986), which predicts a more male-biased sex ratio than we observed; and (3) seasonal changes in either maternal condition or nestling condition, both of which predict shifts in sex ratios not observed in our data. These results prompt us to urge caution when reporting sex-ratio biases in natural populations and when interpreting published studies, many of which suffer from small sample sizes, post hoc analyses, and insufficiently conservative statistical tests. Sex-ratio biases in birds are uncommon, and considerable data will be necessary to determine which hypotheses (if any) are sufficiently robust to regularly select for avian sex ratios that deviate significantly from 50:50. Received 22 January 1996, accepted 20 June 1996.

SEX-RATIO VARIATION in birds continues to generate considerable interest as the factors purported to cause deviations from 50:50 have grown to include life-history traits such as sexual size dimorphism, sex differences in dispersal strategies, differences in helping behavior between male and female offspring, competition between parents and offspring, seasonal changes in food availability, and differences in reproductive strategies between males and females (Trivers and Willard 1973; Clark 1978; Emlen et al. 1986; Clutton-Brock 1986; Stamps 1990; Gowaty 1991, 1993). Unfortunately, tests of these hypotheses have been slow to accumulate, if for no other reason than because nestlings of many species are sexually monochromatic and consequently the large sample sizes needed to discriminate among hypotheses are difficult to obtain.

Western Bluebirds (*Sialia mexicana*) are excellent subjects for testing sex-ratio theory. They are common in central coastal California and readily uses nest boxes. More importantly, nestlings are sexually dichromatic, males having larger and darker blue patches in the wing and tail feathers that are evident about one week

prior to fledging (Pinkowski 1974). Consequently, determining the sex of offspring is easy and unambiguous.

In our study population on and adjacent to Hastings Reservation in California, Western Bluebirds exhibit five life-history traits hypothesized to influence sex-ratio variation (Table 1). First, nestlings are sexually dimorphic in body size, with males slightly larger than females. Fisher (1958) suggested that parental investment in the sexes up through the time of independence should be equal. Thus, if one sex costs more to produce because it is larger and requires more resources, then the sex ratio should be biased toward individuals of the smaller sex.

Second, a relatively high proportion of male offspring whose parents are still alive act as helpers at their parents' nest (Dickinson et al. 1996). In a variation on Fisher's (1958) principle of equal investment, Emlen et al. (1986) proposed that the sex ratio in cooperative breeders should be biased toward the sex that helps because helpers “repay” some of the cost of their own production by helping to raise subsequent broods. This hypothesis is the converse of local resource competition, discussed below, and thus is a form of “local resource enhancement.” In Western Bluebirds at Hastings Reservation,

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TABLE 1. Theoretical reasons for a biased sex ratio and their potential applicability to Western Bluebirds in central coastal California.

Source	Expected direction of bias		Reference
	General	Western Bluebirds	
Nestling size dimorphism	The cheaper sex	Females	Fisher 1958
Helping at nest (repayment model)	The sex that helps	Males (55.2%)	Emlen et al. 1986
Differential dispersal (local resource competition)	The non-philopatric sex	Females	Clark 1978
Differential dispersal (improving seasonal conditions)	Changes seasonally	Females (increasing seasonally)	Stamps 1990 (see text)
Maternal condition	The sex benefiting from maternal investment when females are in good condition	Females in good condition produce more males	Trivers and Willard 1973

breeding males and females reduced their feeding rates when assisted by helpers, and nests with helpers fledged 12% more offspring than those without helpers due to both reduced probability of total failure and increased number of offspring fledged in successful nests (Dickinson et al. 1996). Thus, according to the repayment model, the overall nestling sex ratio should be male biased. Related to this model is the possibility that unassisted pairs and females breeding for the first time bias the sex ratio toward the sex that helps, as found in Red-cockaded Woodpeckers (*Picoides borealis*) by Gowaty and Lennartz (1985).

Third, males are significantly more philopatric than females and frequently breed near their parents. Clark (1978) proposed that if same-sex offspring compete with each other or with their parents of the same sex for food or other critical resources, then their value to the parents is reduced and the sex ratio of offspring should be biased toward the non-competing sex. Such "local resource competition," if it is important, presumably would favor overproduction of the non-philopatric sex (Gowaty 1993), which in Western Bluebirds (as in most birds) is the female. Likely candidates for such competition include food and potential nest sites.

Fourth, nestling condition increases seasonally, possibly indicating a concomitant improvement in food conditions. In species with little or no sexual dimorphism, increased provisioning late in the nestling period could increase survival of the dispersing sex (Stamps 1990). Extending this argument, it is possible that a seasonally biased sex ratio could be se-

lected for if offspring that fledge early in the season differ in condition from those that fledge late in the season, and thus are likely to be more or less successful at dispersal. Given the female-biased dispersal found in our population, we might expect that improving seasonal conditions would therefore favor the philopatric males early in the season and the non-philopatric females late in the season.

Finally, extrapair fertilizations are relatively common in our population, possibly increasing the relative variance in male reproductive success (Webster et al. 1995) and opening up the possibility that males acquiring more parental investment might yield relatively greater fitness benefits to parents than females. According to the model of Trivers and Willard (1973), this would predict a correlation between parental condition and sex ratio, with parents in better condition tending to bias the sex ratio of their offspring toward the sex with a greater rate of reproductive returns, most likely males (Frank 1990).

Here we detail the magnitude of these potential causes of sex-ratio bias and test them using 13 years of data from a population of Western Bluebirds in central coastal California. Our goal is to determine to what extent we are able to use any or all of these hypotheses to explain the observed patterns of sex-ratio variation in this population.

STUDY AREA AND METHODS

We studied Western Bluebirds that nested primarily in artificial nest boxes in the vicinity of Hastings

TABLE 2. Measurements ($\bar{x} \pm SD$, n in parentheses) of nestling Western Bluebirds 6 and 14 days after hatching.

	Mass (g)	Wing chord (mm)	Tarsus (mm)
Day 6			
Males	15.91 \pm 2.57 (753)	16.60 \pm 3.63 (639)	15.19 \pm 1.66 (562)
Females	15.90 \pm 2.67 (678)	16.39 \pm 4.11 (582)	15.14 \pm 1.63 (522)
Day 14			
Males	26.57 \pm 2.53 (796) ^a	51.04 \pm 6.17 (786)	20.84 \pm 1.07 (665)
Females	26.14 \pm 2.92 (714) ^a	50.83 \pm 6.58 (703)	20.77 \pm 1.30 (595)

^a Values significantly different ($P < 0.05$) by two-tailed Mann-Whitney U -test (with Bonferroni adjustment).

Reservation, central coastal California, approximately 40 km inland from Monterey. Plywood nest boxes were set out over a 7-km² area during a three-year period, starting with 54 boxes in 1983 and reaching 363 boxes in 1985. Since 1985, the number of boxes has been constant. Additional details of the study population are presented in Dickinson et al. (1996).

Each year, we monitored the boxes for nests, identified banded breeders, caught and banded new adults, and banded all offspring. A few pairs nested in natural cavities; such nests were opened and monitored as well. Nest occupancy was relatively low, with less than 36% of available nest boxes used by bluebirds in all years (Dickinson et al. 1996). Most nests were found at clutch initiation or shortly thereafter and followed such that the exact date of hatching was known.

Unbanded adults either were caught in the nest box or mist-netted while feeding offspring. Some unbanded adults could be aged by the color and shape of the 10th primary (Pitts 1985); when this character was ambiguous, we considered such birds to be of unknown age. Offspring were weighed (± 0.1 g) with a Pesola scale and their wing chord and tarsus measured several times during the nestling period. Starting in 1990, all nestlings were measured on days 6 and 14. Nestlings were banded when 14 days old, at which time they were sexed by the amount and hue of blue in the wing and tail (Pinkowski 1974). Fledging occurs at about day 20. During the course of the study, we determined the sex of 2,187 nestlings from 549 broods.

Statistical tests are described in the text. Significance values are two-tailed (when possible) and were corrected within tables by the sequential Bonferroni method (Rice 1989); $P < 0.05$ is considered significant. Power analyses follow the procedure detailed by Sokal and Rohlf (1981). Weather was measured at Reserve Headquarters within the study area.

HYPOTHESES AND PREDICTIONS

Nestling size dimorphism.—We tested for differences in size of nestlings in two ways. First, we restricted analyses to day 6, during the

growth phase, and day 14, by which time mass has usually reached an asymptote, and performed Mann-Whitney U -tests comparing sexed nestlings. The results indicate no sexual size dimorphism at day 6, but a significant (0.43 g, or 1.6% of female mass) male size advantage at day 14 (Table 2). The significance of this difference was confirmed by two-way ANCOVA controlling for first-egg date as a covariate and then looking at the effects of sex and year as main factors, again for days 6 and 14. In general, size measurements increased with first-egg date, and differences among years were highly significant in all cases ($P < 0.001$). After controlling for these two variables, the only significant size variable was mass at day 14 ($F = 9.2$, $df = 1$ and 1,246, $P = 0.002$). The mass difference between the sexes, adjusted for first-egg date, was 0.44 g, virtually identical to the difference based on mean values. Thus, male nestlings reach an asymptote at larger mass than do females even when controlling for first-egg date and differences among years.

If this additional mass requires that parents provide male nestlings with more food, and if parental investment does not differ between the time we sexed nestlings and the termination of parental care, then Fisherian sex-ratio theory predicts that the overall sex ratio should be biased toward females. We have no data on the second of these assumptions. Regarding the first assumption, the rate that adults fed nestling males compared with nestling females at 13 nests studied by Leonard et al. (1994) was slightly, but not significantly, greater for males ($\bar{x} = 4.74 \pm SE$ of 0.65 feedings/h for males; $\bar{x} = 4.41 \pm 0.50$ feedings/h for females). Thus, it is possible that male nestlings require more parental care than female nestlings. The extent of the sex-ratio bias expected due to this factor is difficult to determine because of our limited data on how much additional parental effort might be need-

ed to produce the larger males. Based on the feeding-rate data, male nestlings receive 7% more feeds than female nestlings, and a sex-ratio bias of 43% males might be predicted. However, given the size difference of <2% between male and female nestlings, the expected sex-ratio bias is probably less than this value.

Helping at the nest and the repayment model.—Between 1984 and 1994, the seasonal nesting attempts of 618 pairs were watched carefully enough to evaluate whether more than two adults were present and helping at the nest (Dickinson et al. 1996). Adult helpers were identified for 42 (6.8%) of these pairs. Although juvenile helpers of both sexes occur, all adult helpers thus far recorded have been males, usually offspring of the breeding pair or more rarely a brother of the breeding male (Dickinson et al. 1996).

Breeder adults of both sexes reduced their feeding rates when assisted by helpers, and nests with helpers fledged 12% more offspring than those without helpers due to both reduced probability of total failure and increased number of offspring fledged in successful nests (Dickinson et al. 1996). Thus, according to the repayment model, the overall nestling sex ratio should be male biased. The proportion of males (r^*) predicted by the repayment model, assuming offspring cost the same to produce, can be estimated to within a small error by the equation:

$$r = 0.5 + \sigma\alpha P/8, \quad (1)$$

where σ equals average brood size, α is the relative effectiveness of a helper at raising additional young compared with the average effectiveness of a parent, and P is proportion of males that act as helpers (Emlen et al. 1986). In our population (based on first nests followed between 1983 and 1994 in which both breeders were banded), $\sigma = 2.88$ ($n = 389$), $P = 0.068$, and α can be estimated (following Emlen et al. 1986) as twice the increase in number of young fledged by pairs assisted by helpers divided by the average number of helpers at assisted nests. The increase in offspring in assisted nests is 1.12, and a total of 42 adult helpers helped at 40 nests for an average of 1.05 helpers at assisted nests (Dickinson et al. 1996). These values yield $\alpha = 2.13$ and $r = 0.552$. Thus, according to the repayment model as envisioned by Emlen et al. (1986), and independent of any other potential factors, the sex ratio of our population should

be 55.2% males. This estimate is not significantly altered by the extensions of the repayment model discussed by Lessells and Avery (1987).

Differential dispersal and local resource competition.—We considered a bird as having returned if it was seen on the study area after its natal year. Of 822 male nestlings banded through 1993, 218 (26.5%) returned to the study area in a subsequent year whereas only 47 of 758 (6.2%) female nestlings did so; the difference is highly significant ($\chi^2 = 116.7$, $df = 1$, $P < 0.001$). Of the returnees, we observed 208 males (95.4%) and 46 females (97.9%) attempt to breed. Thus, the probability that returning offspring will breed did not differ between the sexes.

These data suggest that natal dispersal is female biased, with males more than four times as likely as females to return and nest in the vicinity of their parents. To the extent that parents compete for resources with nearby individuals, competition will be greater between parents and sons than between parents and daughters, and the overall nestling sex ratio should be female biased (Clark 1978, Gowaty 1993). We have not attempted to quantify the fitness effects of such competition, and thus it is not possible to derive an exact value for the expected sex ratio.

Differential dispersal and improving seasonal conditions.—In Western Bluebirds, females are the dispersing sex. Controlling for yearly differences, nestling condition (indexed by absolute body size or by the standardized residuals of either wing chord or tarsus on body mass) improves seasonally (Table 3). If we assume that nestling condition affects female fitness relatively more than male fitness because of sex-biased dispersal, then we would predict a sex ratio biased toward males early in the season and shifting gradually toward females as the season progresses and conditions presumably improve. No overall sex-ratio bias in the population is predicted.

Maternal condition.—Western Bluebirds apparently are monogamous, but approximately 16.5% of offspring are sired by extrapair males (J. L. Dickinson unpubl. data). The potential for siring extrapair offspring increases the relative variance in male reproductive success and opens up the possibility that males benefit more from increased parental investment than do females. It follows that breeder females in good condition should bias their broods in favor of males,

TABLE 3. ANCOVAs testing for seasonal effect on nestling body size and maternal condition at day 14. The main factor (year) was controlled for prior to the covariate (first-egg date). The direction of the regression of the dependent variable on first-egg date is shown in parentheses.

Variable	Sum of squares	df	F	P
Body mass				
Year	734.2	12	8.7	0.00
First-egg date (+)	3.0	1	0.4	0.52
Wing chord				
Year	4,895.6	12	11.4	0.00
First-egg date (+)	2,468.3	1	68.8	0.00
Tarsus				
Year	310.9	5	55.7	0.00
First-egg date (+)	46.5	1	41.7	0.00
Maternal condition (wing chord)*				
Year	107.9	12	10.1	0.00
First-egg date (+)	70.1	1	78.9	0.00
Maternal condition (tarsus)*				
Year	240.9	5	61.2	0.00
First-egg date (+)	31.5	1	40.0	0.00

* Maternal condition estimated from the standardized residuals of the regressions of female body mass on wing chord or female body mass on tarsus length.

whereas the reverse should hold for females in poor condition (Trivers and Willard 1973).

RESULTS

The sex ratio of offspring divided by year is presented in Table 4. The overall sex ratio was 51.9% males, not statistically different from 50% by a binomial test. The sex ratio of offspring was statistically different from 50% in only 1 of 13 years, being significantly male-biased in 1994 ($P < 0.05$ with Bonferroni correction). The overall sex ratio excluding 1994 was 50.5% males ($n = 1,743$). Considering each year as an independent sample, eight (61.5%) were male-biased and five (38.5%) female-biased, again not statistically different from 50% (binomial test, $P > 0.05$). Although the results for 1994 suggest the possibility that the sex ratio of offspring may be biased in some years, these data indicate that the sex ratio of nestlings in our population is usually even, at least by the time we are able to sex them 14 days after hatching.

In order to look for potential brood-size interactions, we also examined our data for an association between sex ratio and brood size. For broods of n nestlings (where $n = 2, 3, \dots$,

TABLE 4. Sex ratio of Western Bluebird nestlings at Hastings Reservation by year.*

Year	No. males	No. females	Total broods	No. males	% males	z
1983	13	12	25	6	52.0	0.0
1984	26	13	39	11	66.7	1.9
1985	50	49	99	25	50.5	0.0
1986	94	103	197	48	47.7	0.6
1987	59	51	110	34	53.6	0.7
1988	50	54	104	31	48.1	0.3
1989	69	80	149	43	46.3	0.8
1990	91	85	176	43	51.7	0.4
1991	46	36	82	20	56.1	1.0
1992	110	113	223	49	49.3	0.1
1993	168	41	309	70	54.4	1.5
1994	255	189	444	105	57.4	3.1*
1995	104	126	230	64	45.2	1.4
Total	1,135	1,052	2,187	549	51.9	1.8

* Values are tested against an expected 50% males by two-tailed binomial tests with Bonferroni adjustment. *, $P < 0.05$.

6), we counted the number of nests with 0, 1, ..., n males and compared those values with the number expected from a binomial expansion with a mean of 50% males. Forty-nine broods of two, 84 of three, 153 of four, and 177 of five were available for analysis (a sample of 32 broods of size six was considered too small for this analysis). None was significantly different from expected (χ^2 tests; all P s > 0.05 after sequential Bonferroni correction). Sex ratio within broods is not significantly different from random.

Although the overall sex ratio is statistically even, it is possible that the sex ratio of eggs is initially biased but that brood reduction evens out the sex ratio by the time of fledging. We tested this possibility by comparing the sex ratio among broods where brood reduction did and did not occur (Table 5). The sex ratio was not statistically different from 50% in either group, nor did the two groups differ significantly from each other. This suggests that sex-biased brood reduction does not occur. Because virtually no eggs disappear during incubation unless the nest is completely depredated, the sex ratio of eggs most likely is even as well.

If repayment by helper males influences the sex ratio, unaided pairs or young females breeding for the first time might be expected to bias the sex ratio of their offspring toward males, which might later become helpers. These possibilities are examined in Table 5. Neither the presence of helpers nor age of the breeder female was associated with a biased sex ratio. The sex ratio for pairs unassisted by helpers was

TABLE 5. Sex ratio of Western Bluebird nestlings at Hastings Reservation by presence or absence) of brood reduction, presence or absence of helpers, and age of breeder female. Numbers within categories were tested against an expected 50% males by two-tailed binomial tests (the z -value). Among categories, differences were tested by χ^2 contingency tests (all $df = 1$). All of the P -values were non-significant after Bonferroni adjustment.

	No. males	No. fe- males	No. males	% males	z
Brood reduction ($X^2 = 0.4$)					
None	867	824	393	51.3	1.0
Some brood reduction	214	190	129	53.0	1.1
Presence of helpers ($X^2 = 2.7$)					
None	1,017	919	489	52.5	2.2
Helpers present	118	133	60	47.0	0.9
Age of breeder female ($X^2 = 0.5$)					
Second year	86	75	66	53.4	0.8
≥ 3 years old	485	474	238	50.6	0.3

slightly male biased (52.5%), but the bias was not significant.

We performed several tests of whether sex ratio varied seasonally. First, the correlation between first-egg date and the sex ratio of successful broods was not significant ($r_s = 0.05$, $n = 549$, $P = 0.11$). Second, we performed an ANCOVA in which the main factor (year) was controlled for prior to consideration of the covariate (first-egg date); neither variable significantly influenced sex ratio (year: $F = 1.4$, $df = 12$ and 535 , $P = 0.17$; first-egg date: $F = 1.1$, $df = 1$ and 535 , $P = 0.30$). Finally, we performed paired comparisons using banded females that produced two successful nests within the same year. Of 45 such comparisons, both nests contained an identical proportion of males and females for five, while the remaining 40 were evenly divided between cases in which the first nest had more males than the second nest and cases in which the converse was true (Table 6).

We tested for a relationship between breeder female condition and sex ratio by correlating female body mass, wing chord, and the standardized residuals of the regression of female mass on wing chord with brood sex ratio. All females were caught during the nestling period, usually between days 6 and 14. There was no significant correlation between any of these measures and sex ratio (body mass: $r_s = 0.02$, $n = 252$, $P = 0.73$; wing chord: $r_s = -0.02$, $n = 266$, $P = 0.77$; standardized residuals: $r_s = -0.01$,

TABLE 6. Paired comparisons of Western Bluebird sex ratios within broods of females producing two successful nests within the same year. "Young" females include second-year and unknown-aged females probably breeding for the first time. "Old" females include all females known to be ≥ 3 years old.

	Proportion of males in brood		χ^2	P
	1st nest > 2nd nest	2nd nest > 1st nest		
Young females	7	9	0.25	0.80
Old females	13	11	0.20	0.84
All females	20	20	0.00	1.00

$n = 250$, $P = 0.88$). We also controlled for yearly variation in ANCOVAs in which, as before, the main factor (year) was controlled for prior to the covariate (body mass, wing chord, or standardized residuals from the female mass on wing chord regression). Significance of the covariate in all three analyses was close to 1 (body mass: $F = 0.002$, $df = 1$ and 241 , $P = 0.97$; wing chord: $F = 0.002$, $df = 1$ and 255 , $P = 0.96$; standardized residuals: $F = 0.009$, $df = 1$ and 239 , $P = 0.93$).

At the annual level, it is possible that differing conditions influence the sex ratio of offspring produced in a particular year, with more males produced in good years and more females produced in poor years. We tested for this by correlating the sex ratio of offspring fledged each year (Table 4) with five indices of environmental conditions for each year: (1) mean fledging success of all nests; (2) mean fledging success of all successful nests; (3) the earliest first-egg date; (4) mean daily air temperature between 1 April and 31 May; and (5) total rainfall between 1 April and 31 May. This period was chosen because the majority of nests (86.3% of 1,007 first-egg dates) are initiated during this period, nearly evenly divided between the two months. The results were unequivocal; none of the five correlation coefficients was significant (r_s values between -0.10 and $+0.34$, $n = 13$, all $P_s > 0.12$). Apparently, the annual variation in sex ratio documented in Table 4 is unrelated to environmental conditions that influence first-egg date or nesting success.

DISCUSSION

Few data demonstrate systematic variation in the sex ratios of nestling birds (Clutton-Brock

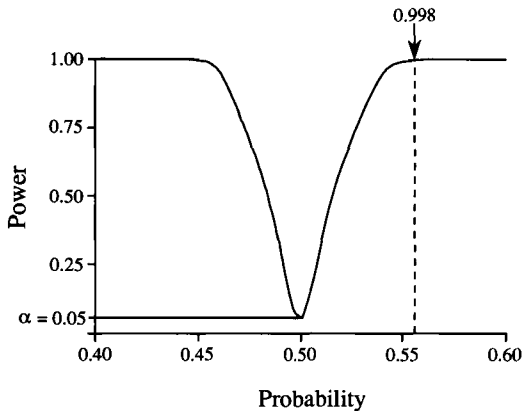


FIG. 1. Power curve for testing $H_0: \mu = 0.50$ vs. $H_1: \mu \neq 0.50$ for $n = 2,187$. Power ($1 - \beta$) is the probability of rejecting the null hypothesis when it is false and the alternative hypothesis is true. The minimum value of $1 - \beta$ is α , the critical level chosen for the test (i.e. 0.05). The dotted line is the sex ratio predicted by the repayment model, $\mu_1 = 0.552$; the power associated with this value is 0.998. Thus, given our sample size, we have a 99.8% chance of rejecting the null hypothesis of no sex-ratio bias if it is false and the true nestling sex ratio is 55.2% males, as predicted by the repayment model.

1986, 1991; Gowaty 1993). Our data offer no exception. We detected a significant sex-ratio bias in only 1 of 13 years, and overall the observed sex ratio was not significantly different from unity. Also, sex ratios within broods of particular sizes did not differ from those expected by binomial expansions. We failed to document any significant influence on sex ratio related to brood reduction, female age, presence of helpers, season, female condition, or annual environmental conditions. This failure to detect any deviation from an even sex ratio is noteworthy given the number of life-history characteristics of Western Bluebirds that predict a biased sex ratio, the relative ease with which young can be sexed compared with species in which young are not sexually dichromatic, and the large sample sizes collected over many years.

Unfortunately, only one of the hypotheses, the repayment model, predicts the magnitude of the expected sex-ratio bias (Table 1). The quantitative prediction of the repayment model allows calculation of the power with which we would be able to reject the null hypothesis of an even sex ratio ($H_0: \mu = 0.5$) if it were false and the repayment model were correct. Because of the large sample size, the power of this test

is 0.998 (Fig. 1). Using $\mu = 0.519$ (i.e. the observed value in our sample), the power of rejecting this null hypothesis if the true sex ratio is 55.2% is still high (i.e. 0.878).

How confident can we be of the conclusion that the overall sex ratio of nestlings is even? Given our sample of 2,187 nestlings, we would have detected a significant sex-ratio bias overall if 52.1% or more had been of the same sex. Based on the observed sex ratio of 51.9%, and assuming a binomial distribution, we can be 95% certain that the true sex ratio of nestlings in our population lies between 49.8 and 54.0%. Thus, we can reject the hypothesis that the sex ratio deviates by more than 4% from being exactly 50% males. We can be less certain that the true sex ratio is not slightly male biased. For example, if the true sex ratio is 51.9% males, the same as our observed value, the power of rejecting the null hypothesis is only 0.435. This problem is highlighted by the fact that the observed sex ratio was only five males short of being significantly different from 50:50. Regardless, none of the five hypotheses we considered predicts the observed sex ratio, at least when considered independently.

At least two alternative conclusions can be drawn from our results. First, it is possible that two or more of the hypotheses influence the sex ratio significantly but, because they select for biases in opposite directions, they cancel each other out. Testing this possibility would require an extensive comparative study of bluebird populations sharing some, but not all, of the life-history features that predict a biased sex ratio. For example, some Western Bluebird populations are not known to have helpers. In the absence of any potential helper "repayment," nestling sex ratios in such populations should be female biased if either nestling size dimorphism or female-biased dispersal are important determinants of sex ratio.

The second alternative is to reject all the hypotheses put forth at the start of this paper; apparently none is sufficiently strong to overcome the frequency-dependent selection tending to keep the population sex ratio at parity. Even the repayment model, which at least predicts an overall population sex ratio biased toward males, can be rejected with confidence (Fig. 1). Some corroborative evidence for a lack of gender-related behavior is the absence of sex-biased provisioning in this population documented by Leonard et al. (1994). Basically, how-

ever, we cannot discriminate between these two possibilities.

Population sex ratios of 50:50 should not be surprising given the strong frequency dependence of this character (Fisher 1958, Frank 1990). Indeed, our analyses prompt us to urge caution when analyzing or interpreting apparent sex-ratio biases in natural populations of birds. Although we do not doubt that such biases can and do occur, they appear to be rare and should be accepted with caution by workers searching for their presence. One reason for this is that there often may be multiple factors potentially influencing the sex ratio and, as in Western Bluebirds, they are likely to predict opposite patterns that may cancel each other. Consequently, observed sex ratios, both biased and unbiased, could be the result of a combination of selective agents.

A second reason for caution is statistical. Putatively biased sex ratios frequently are based on small sample sizes or only a few years of data. Biases are sometimes found only in a subset of the data, or are dependent on an arbitrary division of the data set. Analyses are frequently post hoc and fail to consider alternative hypotheses. At the very least, statistical tests should be conservative, and two-tailed tests and Bonferroni corrections should be applied when possible.

Few studies documenting nestling sex-ratio biases in birds succeed in rising above these criticisms. Unfortunately, the difficulties associated with publishing negative data tend to select against being conservative when analyzing sex-ratio data and make it unlikely that an unbiased sample of such data will be available in published form. Considerable work and reanalysis will be necessary before it will be possible to conclude that any of the hypotheses considered here are robust enough to regularly select for avian sex ratios deviating significantly from 50:50.

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