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PEREGRINE FALCON EGGS: EGG SIZE, HATCHLING SEX, AND CLUTCH SEX RATIOS

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Abstract. Eggs ($n = 367$) collected from wild Peregrine Falcon (*Falco peregrinus anatum*) nests between 1976 and 1990 in Colorado and New Mexico were artificially incubated and hatched. We retrospectively examined these data for variation in egg length, breadth, and initial mass of hatchlings to resolve questions about relationships among egg size, chick size, and sex; and egg size related to first and second clutches and years. Egg length and breadth were significantly related to chick mass at hatching. Neither egg size nor hatchling mass were related to sex. Egg breadth slightly increased and then decreased over the years eggs were collected, which possibly reflects a re-established and then aging wild falcon population or other environmental variation. We also evaluated clutch sex ratios relative to theory based on sexual size dimorphism and local resource competition. Sex ratios did not significantly differ from 1:1 within first or second clutches separately or when combined. Thus, Peregrine Falcons in this population apparently did not skew clutch sex ratios in accordance with local resource competition or Fisherian theory.

Key words: chick mass, clutch sex ratio, Colorado, egg size variation, Falco peregrinus anatum, New Mexico, Peregrine Falcon.

Huevos de Halcones Peregrinos: Tamaño, Sexo de los Pichones y Proporción de Sexos en la Nidada

Resumen. Huevos ($n = 367$) colectados de nidos silvestres de halcones peregrinos (*Falco peregrinus anatum*) entre 1976 y 1990 en Colorado y New Mexico fueron incubados artificialmente hasta eclosionar. Examinamos esos datos retrospectivamente en cuanto a la variación en la longitud y ancho del huevo y el peso inicial de los pichones para contestar preguntas sobre las relaciones entre tamaño del huevo, tamaño del pichón y sexo, y entre el tamaño del huevo con relación a primeras y segundas nidadas y años. La longitud y el ancho del huevo estuvieron significativamente relacionados con la masa del pichón al eclosionar. El tamaño del huevo y el peso del pichón no estuvieron relacionados con el sexo. El ancho de los huevos aumentó ligeramente y luego disminuyó a través de los años en que los huevos se colectaron, lo que posiblemente refleja una población silvestre de halcones re-establecida y posteriormente senescente, u otro tipo de variación ambiental. También evaluamos la proporción de sexos en las nidadas con relación a la teoría basada en el dimorfismo sexual de tamaño y la competencia local por recursos. Las proporciones de sexos no difirieron significativamente de 1:1 entre primeras o segundas nidadas separadamente o de forma combinada. Por tanto, los halcones peregrinos en esta población aparentemente no sesgaron la proporción de sexos en sus nidadas de acuerdo a la competencia local por recursos o a la teoría Fisheriana.

INTRODUCTION

In the mid-twentieth century, chlorinated-hydrocarbon-induced shell thinning resulted in high embryo mortality and low natural reproduction by wild falcons, endangering populations of some species (Peakall 1976). As part of the recovery effort for Peregrine Falcons (*Falco peregrinus anatum*), J. Craig, D. Berger, J. Enderson, W. Heinrich, and W. Burnham removed

clutches of thin-shelled Peregrine Falcon eggs from eyries and replaced them with nestling falcons to bolster "natural" reproduction in the Rocky Mountains (Burnham et al. 1978, 1988). Thin-shelled eggs from first and second (induced) clutches were hatched in artificial incubators and resulting young were released into the wild (Burnham 1983, Burnham et al. 1988). This management action not only helped stem population declines but also provided opportunity to examine a large number of wild-laid Peregrine Falcon eggs and retrospectively examine relationships among eggs, clutches, chicks, sex-

es, and years. Therefore, to help understand relationships among falcons and the chicks they produce, we asked (1) how was chick mass related to egg size, sex, and clutch number (first or second), (2) how did clutch sex ratios vary by clutch number or year, and (3) how did egg size vary by year of study?

Recent studies have illustrated the ability of female birds to adjust both the primary (at laying) and secondary (at hatching) sex ratio of their clutches (Sheldon 1998), often in agreement with theories of adaptive sex allocation. Among these theories, Fisher (1958) hypothesized that investment in the sexes should be equal at the termination of parental care, and this results in sex ratios skewed toward the less costly sex. For many raptors, where females are larger than males, this predicts male-biased sex ratios at the end of parental investment. Secondly, when the offspring of one sex differentially compete with each other or with their parents for food or other resources, local resource competition is hypothesized. Such competition decreases their value to parents and leads to a bias toward the noncompeting sex (Clark 1978). Gowaty (1993) showed that within a variety of passerines, where males tend to be more philopatric, sex ratios often are skewed toward daughters. In contrast, among waterfowl where males disperse, sex ratios tend to favor sons (Gowaty 1993). In Peregrine Falcons, female fledglings disperse farther than males (Mearns and Newton 1984, Tordoff and Redig 1997, Restani and Mattox 2000) so, if local resource competition occurs, sex ratios should be skewed toward females in Peregrine Falcons. Local resource enhancement may occur when the philopatric sex helps or otherwise benefits parents, resulting in sex ratios biased toward the helping sex (Gowaty and Lennartz 1985, Emlen et al. 1986). In Seychelles Warblers (Acrocephalus sechellensis), individual parents bias the sex ratio of their offspring toward females (the principal helping sex) when on high-quality territories with few helpers, which is when additional helpers are expected to significantly increase reproductive success (Komdeur 1996). Such helping likely does not occur in Peregrine Falcons, so the selective pressures of local resource enhancement likely are not great. Finally, parental condition (Trivers and Willard 1973) also may affect offspring sex ratios. Under this notion, females in superior condition are expected to invest in the sex with

a greater rate of reproductive returns, which in general means males; however, Olsen and Cockburn (1991) suggested that in species with reversed size dimorphism, female nestlings would benefit more from extra provisioning. Thus, their modification of Trivers and Willard's hypothesis suggests female-biased broods in Peregrine Falcons and other raptors, which indeed they found (Olsen and Cockburn 1991). Our study also allowed us to retrospectively evaluate sex-ratio variation in Peregrine Falcon clutches within the framework of these hypotheses.

METHODS

From 1973–1990, eggs laid by wild Peregrine Falcons were removed from cliff nest sites as clutches. Nest site locations varied among years. Females producing eggs were unmarked and probably differed over years when eggs were removed from the same sites. When more than one clutch was removed at the same site within a single year the laying female, because of time between clutch removal and renesting, was almost certainly the same bird. Most clutches had more than five days of incubation before removal, as determined by observation of females beginning incubation. Either artificial eggs or captive-hatched young falcons usually were substituted for removed eggs. On occasion, clutches were removed and not replaced with artificial eggs or young, causing falcons to lay a second clutch, which was again removed but then replaced with nestlings. Eggs were transported to laboratories in portable incubators by aircraft or vehicle and, upon arrival, were coded, weighed, measured (length and breadth), and artificially incubated as described by Burnham (1983). Eggs were measured to the nearest 0.01 mm with vernier calipers and to the nearest 0.01 g with a weighted balance or electronic scale. Fresh egg weight (calculated weight at laying) was calculated according to Hoyt (1979) and Burnham (1983). Upon hatching, the eggshell, chick, and residual cell contents were weighed to the nearest 0.01 g. Contents of eggs that failed to hatch were routinely analyzed for contaminant levels but are not reported here.

Young were raised as described in Cade and Weaver (1983) and released into the wild by fostering to wild nesting pairs of Peregrine Falcons (Burnham et al. 1978) or by hacking (Sherrod et al. 1981). In 1976 and 1977 young were fostered into eyries before gender could be accu-

rately determined. Post-1977, prior to transport from the propagation facility, nestlings were banded with gender-specific U.S. Fish and Wildlife Service leg bands. Peregrine Falcons exhibit reverse size dimorphism, and sex could be accurately determined by size and appearance (head and beak shape and size, tarsus breadth, and foot size) at banding. From 1978 forward, young released by fostering were placed with wild adults at about 21 days after hatching. Young released by hacking were transferred to release sites at about 35 days of age.

STATISTICAL ANALYSIS

To assess relationships among egg and chick parameters, we used generalized linear models employing the Generalized Estimating Equations (GEE; Diggle et al. 1994) within PROC GENMOD in SAS software (SAS Institute Inc. 2000). Using the repeated statement within this procedure allowed for correlation among eggs within any site × year combination; that is, eggs from a clutch were not independent so this approach allowed for their clustering in the analysis. In addition, we assumed that error structure held no specific relationship with egg number (i.e., we imposed exchangeable structure on correlation matrix among the observations within each cluster), meaning that differences between eggs 1 and 2 were the same as 2 and 3, and so forth. This latter assumption was necessary because we could not determine laying sequence based on field protocols, so assignment of eggs number 1 through the total clutch size was arbitrary. Because it was not possible to determine the identity of nesting pairs each year, the analyses assume that different sites and different years represent independent observations. Collinearity among predictor variables was assessed prior to analyses using the diagnostic statistics in PROC REG (Allison 1999). Briefly, both Pearson correlation analyses and variance inflation factors (VIF) were evaluated. High correlations ($r \sim 0.5$) and VIF values greater than 10 generally indicate strong collinearity among predictor variables (Marquardt 1980). Finally, calculated weight at laying was highly correlated with both egg length ($r = 0.61$, $n = 366$, $P < 0.001$) and egg breadth ($r = 0.91$, $n = 366$, $P < 0.001$), as calculated weight at laying is calculated directly from egg length and breadth. In all cases results of models using calculated weight at laying were qualitatively similar to models using egg length and egg breadth as predictor variables. Thus, we report results of the latter models only.

We analyzed clutch sex ratio in clutches for which we had complete data (i.e., all eggs hatched and sex was discernible for each hatchling). We considered clutches to be complete when within a clutch each of the eggs hatched and sex was discernible. To determine whether sex ratios deviated from a uniform distribution (1:1), we calculated proportion of males within the clutch and tested the null hypothesis that mean proportion of males = 0.50 using the Wilcoxon signed-ranks test.

We also examined trends in sex ratios for first and second clutches separately by regressing proportion of males against year while including clutch size as a covariate, calculating Durban-Watson statistics (Freund and Littell 1991) to rule out autocorrelation. Results are presented as means ± SE throughout, and we accepted significance at $P < 0.05$.

RESULTS

Overall, 367 eggs ($n = 306$ from first clutches and $n = 61$ from induced, second clutches) were collected between 1976 and 1990 from 28 sites located in Colorado and New Mexico. There were 24.5 ± 2.2 eggs collected per year (range 11–41), representing 3.9 ± 0.2 eggs per nest per year, including second-clutch eggs (see below). The average number of eggs in first clutches was 3.3 ± 0.1 ($n = 93$ nests). The mean number of years during which eggs were collected from each site was 3.3 ± 0.5 (range 1–10). Second clutches were induced at 12 different sites ($n = 6$ in one year; $n = 6$ in two different years).

Eggs averaged 52.2 ± 0.1 mm (range 48.2–56.5 mm) in length and 41.4 ± 0.1 mm (range 36.8–44.2 mm) in breadth ($n = 366$ for each). Calculated weight at laying was 49.1 ± 0.2 g (range 36.2–57.9 g; $n = 366$). The average mass of emerging chicks was 34.7 ± 0.2 g (range 23.7–40.7 g; $n = 154$). Sex was determined for birds from 232 eggs, of which 100 were females and 132 were males. Sex of birds from 135 eggs (116 from first clutch and 19 from second) was not identified because eggs either did not hatch or young were released before sex could be accurately determined.

INFLUENCES ON CHICK MASS

We examined relationships between chick mass at hatching and egg length, egg breadth, sex, and
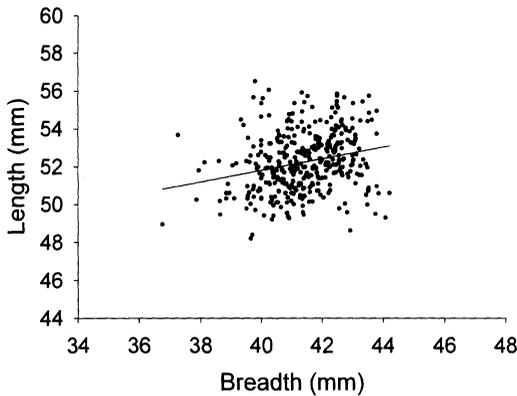
FIGURE 1.   Relationship between egg length and egg breadth for 366 Peregrine Falcon eggs collected from wild nests and incubated in captivity (1976–1990). These two variables were only weakly (although significantly) related, so both were used in subsequent multiple regression analyses as explanatory variables.

clutch number. Although the first two of these predictor variables (length and breadth) were significantly correlated, the relationship between them was quite weak ($r = 0.24$, $n = 366$, $P < 0.001$; Fig. 1), and the low P-value likely reflects the large sample of eggs. Regression diagnostics indicated little collinearity (VIF <1.3 for both) between these two variables. Therefore, regression models included both egg length and egg breadth without further concern about their collinearity.

Egg length and egg breadth both were significantly related to chick mass at hatching (Table 1), and this was especially true for the latter (Fig. 2). Larger chicks hatched from larger eggs, both in terms of length and breadth. Specifically, for each 1-mm increase in length, on average
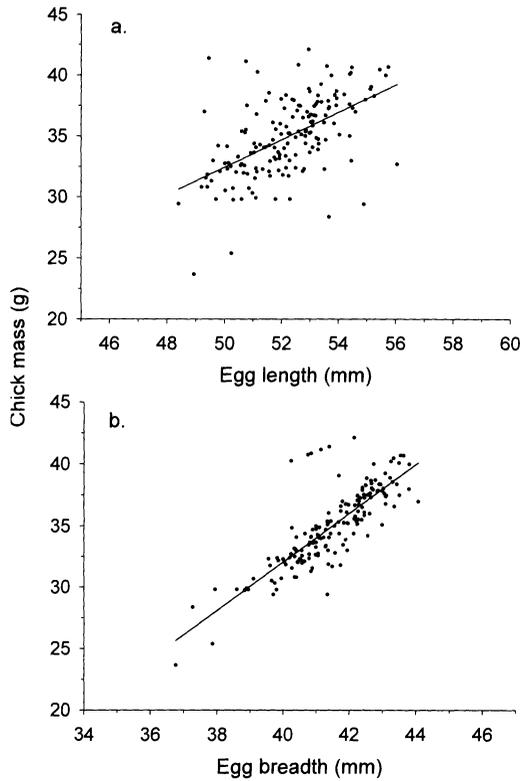

FIGURE 2.   Mass of newly hatched Peregrine Falcon chicks as a function of (a) egg length and (b) egg breadth; $n = 157$ in each case. Lines are for heuristic purposes based on simple linear regression; see Table 2 for results of multivariate analysis.

there was a corresponding 0.54-g increase in chick mass (Table 1). Similarly, for each 1-mm increase in breadth, there was a corresponding 1.70-g average increase in chick mass. Overall, males weighed 34.8 ± 0.3 g (range 28.4–40.2

TABLE 1.   Results of multiple linear regression using Generalized Estimating Equations (GEE) and the identity link function for relationship between Peregrine Falcon chick mass at hatching (g) and egg length (mm), egg breadth (mm), sex, and clutch number (first or second). The GEE accounted for individual eggs clustered within nests using exchangeable correlation structure, and the analysis was based on 156 eggs where chick mass, sex, egg length, and egg breadth were known. Zeros indicate class variables serving as reference categories. Note that chick mass increased with both egg length and egg breadth. Additionally, relative to second clutches, chick mass at hatching was greater in first clutches.

Parameter	df	Estimate	SE	z	P
Intercept	1	−64.77	4.86	−13.3	<0.001
Egg breadth	1	1.70	0.07	23.2	<0.001
Egg length	1	0.54	0.08	6.4	<0.001
Sex female	1	0.01	0.20	0.0	0.99
Sex male	0	0.00	0.00		
First clutches	1	0.80	0.25	2.2	0.02
Second clutches	0	0.00	0.00		

TABLE 2. Results of logistic regression using Generalized Estimating Equations (GEE) for relationship between chick sex and egg length (mm), egg breadth (mm), and clutch number (first or second) for Peregrine Falcon eggs collected from the wild and hatched in captivity. Odds of being male were modeled. The GEE accounted for individual eggs clustered within nests using exchangeable correlation structure, and the analysis was based on 227 eggs where chick sex, egg length and breadth, and clutch number were known. Zeros indicate class variable serving as reference category.

Parameter	df	Estimate	SE	z	P	Odds ratio
Intercept	1	1.91	5.42	0.3	0.78	
Egg breadth	1	–0.17	0.14	–1.2	0.22	0.84
Egg length	1	0.10	0.22	0.8	0.40	1.11
First clutches	1	0.27	0.34	0.8	0.43	1.31
Second clutches	0	0.00	0.00			

g; n = 84) and females weighed 34.4 ± 0.4 g (range 23.7–40.7 g; n = 73) at hatching, but mass at hatching was not significantly different by sex (Table 1). Finally, relative to eggs from second clutches (33.1 ± 0.6 g, n = 25), chick mass was greater in eggs from first clutches (35.0 ± 0.3 g, n = 133; Table 1).

SEX RATIO

We examined relationships among egg measures and sex to uncover potential predictors of chick sex. GEE modeling indicated that the odds of being male were not related to egg length, egg breadth, or clutch number (Table 2). Therefore, nothing we measured about wild-laid eggs in first or second clutches was a useful predictor of Peregrine Falcon chick sex.

For first clutches, there were 80 females and 110 males identifiable from eggs collected at 77 individual nests. There were 29 clutches for

FIGURE 3. Sex ratio (proportion of males) in first (n = 29) and second (n = 10) clutches of Peregrine Falcon eggs where sex was discernible for all eggs within a clutch. Proportion of males did not differ from 0.5 for either first or second clutches.

which sex was known for all eggs within the clutch. These clutches spanned the years 1978–1990 and contained one egg (n = 2), two eggs (n = 2), three eggs (n = 8), and four eggs (n = 17). Of these, 19 contained both males and females (Fig. 3). Of the 10 single-sex clutches, five contained all males, and five contained all females (Fig. 3). The overall proportion of males was 0.55 ± 0.06, which did not differ significantly from 0.50 (Wilcoxon signed-rank test: T = 26.5, P = 0.42).

Eggs (n = 61) from second clutches were obtained during 10 different years (1976–1989). Ultimately sex was discernible for 42 of these eggs (22 males, 20 females), and 10 second clutches (two 2-egg and eight 3-egg clutches) provided complete information about sex of chicks (these were collected in 1978–1988). The proportion of males in complete second clutches was 0.59 ± 0.10, which also did not differ significantly from that expected under a uniform distribution (Wilcoxon signed-rank test: T = 11.5, P = 0.19).

There was no relationship between first-clutch sex ratio as measured by proportion of males and year of study while accounting for clutch size ($F_{2,26}$ = 1.1, P = 0.34; Fig. 4). For second clutches, however, the proportion of males increased with time (proportion males = −4.16 + 0.06(year) − 0.05 (clutch size); $F_{2,7}$ = 6.8, P = 0.02), although this relationship was largely driven by small sample size and by two specific nests in the sample: one in 1978 with no males, and another in 1988 with only males (Fig. 4).

EGG SIZE BY YEAR AND CLUTCH

When we evaluated trends in egg length and egg breadth over the years of study, the relationship
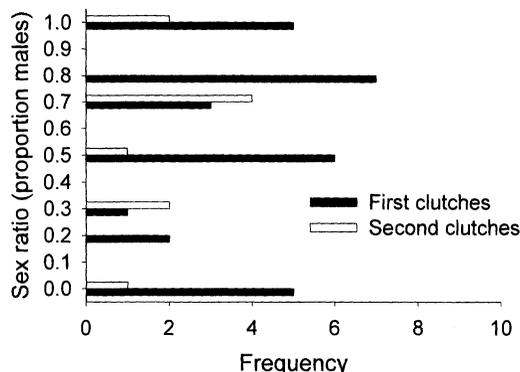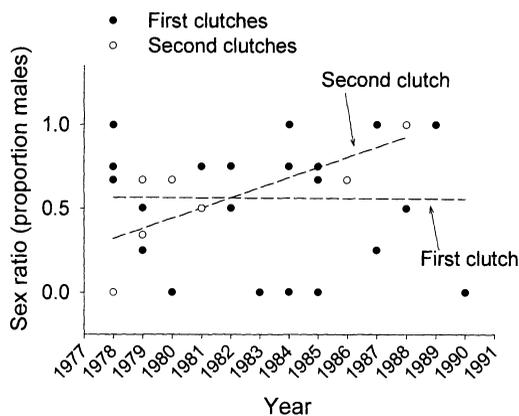
FIGURE 4. Relationship between sex ratio (proportion males) and year of study (1977–1990) for first (n = 29) and second (n = 10) clutches of Peregrine Falcons where sex was discernible for all eggs within a clutch. Regression lines are for illustration; see text for multiple regression results. There was no relationship between sex ratio and year for first clutches, but sex ratio in second clutches increased during the study period.

FIGURE 5. Relationship between (a) length and (b) breadth (mean ± SE) of Peregrine Falcon eggs and year of study (1976–1990). Egg length did not differ between first and second clutches, so overall means are presented. Because breadth differed by clutch, means for first and second clutches are denoted in (b). Number of eggs measured by year is indicated. In (b), number of first-clutch eggs measured is above the error bars, and number of second-clutch eggs measured is below error bars. See Table 3 for results of analysis of trend over the study period.

was more linear for length than for breadth (Fig. 5). Thus, we modeled the latter relationship by fitting a quadratic term, which was significant (Table 3); fitting cubic terms did not improve model fit. The relationship between egg length and year (Fig. 5) was not significant (Table 3). Similarly, eggs in first clutches (52.3 ± 0.1 mm, n = 306) were no longer than eggs in second clutches (52.1 ± 0.2 mm, n = 61, Table 3).

In contrast to egg length, egg breadth varied significantly by year and between first and second clutches (Table 3). Egg breadth tended to increase in the early years of this study but then declined in later years (Fig. 5). Moreover, eggs were significantly broader in first clutches (41.5 ± 0.1 mm, n = 305) compared with second clutches (40.9 ± 0.2 mm, n = 61; Table 3).

DISCUSSION

Larger Peregrine Falcon chicks hatched from larger eggs, but no relationship between chick mass at hatching and sex of chicks could be determined. Differences in body size related to gender must therefore arise sometime later, as average mass for fully grown *F. p. anatum* is 992 ± 12 g (n = 7) for females and 616 ± 18 g (n = 7) for males (C.S., unpubl. data). Only chick mass was assessed, and no other measurements of size were taken at hatching or during growth of chicks. Egg length and breath also
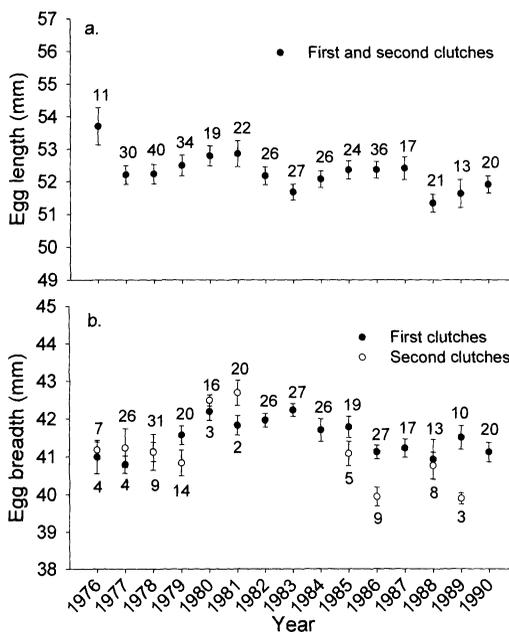
were poor predictors of chick sex. In fact, we detected nothing about eggs that was useful in determining sex of chicks.

These results differ from those reported for American Kestrels (*F. sparverius*) by Anderson et al. (1997). They found that eggs producing males were significantly larger than eggs producing females, and they speculated that laying females may thus control not only egg size but also sex of their offspring. The larger size of male eggs was interpreted as adaptive compensation in favor of the survival of nestling males in sibling competition, as males are the smaller sex (Anderson et al. 1997). Larger eggs of males also are found in White-crowned Sparrows (*Zonotrichia leucophrys oriantha*), which Mead et al. (1987) interpreted along the lines of Trivers and Willard (1973). Because reproductive success is more variable in males, female White-crowned Sparrows in good condition are expected to facultatively manipulate allocation in

TABLE 3. Results of multiple linear regression using Generalized Estimating Equations (GEE) examining relationships between (1) egg length and (2) egg breadth and year of study (1976–1990) and clutch number for Peregrine Falcon eggs collected from wild nests and hatched in captivity. Analyses were based on 366 eggs where egg length and breadth and clutch number were known. As relationship between egg breadth and year was not linear, a quadratic term also was modeled (see text).

Parameter	df	Estimate	SE	z	P
Egg Length					
Intercept	1	56.09	2.84	19.8	<0.001
Year	1	–0.05	0.03	–1.4	0.16
First clutches	1	0.16	0.28	0.6	0.56
Second clutches	0	0.00	0.00		
Egg Breadth					
Intercept	1	–93.59	48.79	–1.9	0.06
Year	1	3.26	1.18	2.8	0.005
Year^2	1	–0.02	0.01	–2.8	0.006
First clutches	1	0.54	0.13	4.2	<0.001
Second clutches	0	0.00	0.00		

favor of males, and this can be facilitated by diverting more resources into male eggs (Mead et al. 1987). Because male House Sparrows (*Passer domesticus*) in good condition may attain higher reproductive success than females, for example through polygyny and extra-pair paternity, Cordero et al. (2000) also interpreted larger male eggs in this species as adaptive extra investment by females in sons. In contrast to these studies, we found no evidence that egg size varied between males and females in Peregrine Falcons from wild-laid eggs from the southern Rocky Mountain states.

Our study determined sex for 190 chicks that hatched from eggs in first clutches, of which 80 were females and 110 were males. When these data are subjected to ordinary chi-square analysis, the null hypothesis of a uniform distribution is rejected (χ^2_1 = 4.7, P = 0.03). However, one potential limitation with this approach is the nonindependence of offspring sexes within broods. As Krackow and Tkadlec (2001) discussed, pooling broods for straightforward chi-square analysis of offspring sex ratios results in potential pseudoreplication. This is the logic that prompted us to analyze relationships among egg parameters in the current study using the GEE approach, which handled clustered observations. Thus, to avoid potential pseudoreplication in the analysis of Peregrine Falcon sex-ratio data, we calculated each clutch sex ratio as an individual datum. When doing so, we detected no deviation from a 50:50 sex ratio. These results are consistent with those of Newton and Mearns (1988)

who examined 133 Peregrine Falcon broods in south Scotland and found that among nearly fledged young, the sex ratio did not differ from unity. Similarly, during a long-term study of Peregrine Falcons in Greenland in which 1846 nestlings were banded between 1972 and 1998, W. Mattox (pers. comm.) reported 870 males, 897 females, and 79 nestlings of undetermined sex (eyries were visited when nestlings were too young to determine sex). This must be one of the largest data sets for a wild population of medium-sized falconiforms, and the results suggest the lack of a skew. These and our own results do however contrast with those of Olsen and Cockburn (1991), who reported significantly female-biased sex ratios for Australian Peregrine Falcons and other falconiforms. They suggested that such data fit a modified version of the Trivers and Willard (1973) hypothesis in that parents in good condition invested in the sex that would benefit from extra provisioning (i.e., the larger females). However, those results, as well as others cited above, are based on ordinary chi-square analysis, where any effects of nonindependence of eggs or nestlings within clutches remain unknown.

Thus, we cannot reject the null hypothesis that brood sex ratios were 1:1 in first or second clutches of Peregrine Falcons in the current study. Gowaty (1993) discussed the fact that the lack of statistically significant differences from a 50:50 sex ratio may have obscured biologically interesting phenomena associated with sex-ratio variation in birds when describing potential

effects of local resource competition on passerine and anseriform sex ratios. For example, she found that passerine sex ratios across species tended to be slightly rather than significantly female biased, whereas sex ratios among many waterfowl species were slightly biased toward males. However, even when considering mean proportion of males per brood (0.56 and 0.59 for first and second clutches, respectively) in Peregrine Falcons in the current study, our results are not consistent with the local resource competition hypothesis. This hypothesis predicts sex-ratio skews (statistically significant or otherwise) toward the dispersing sex, which in Peregrine Falcons is young females. However, because of reverse size dimorphism, a skew toward males may be expected under Fisherian theory (Fisher 1958). Because adult females never were captured during this study, we cannot evaluate effects of female body condition on offspring sex ratios as predicted by Trivers and Willard (1973).

Mass at hatching was significantly greater for chicks from first clutches. Moreover, egg breadth and mass also were significantly larger for first-clutch eggs than second. As egg size reflected chick mass, this result is predictable. In addition, eggs in third clutches laid by captive Peregrine Falcons are smaller still (Burnham et al. 1984) despite having access to a consistent level of food throughout reproduction. Thus, size differences in both eggs and hatchlings between clutches likely result from clutch sequence rather than seasonality or food availability.

Egg breadth varied by year, increasing in early years, and then decreasing in later years. There was also a gradual, but not significant, decrease in egg length over the period of egg collection. Burnham et al. (1984) reported egg size decreased over the years captive Peregrine Falcons laid. One possibility is that the initial size increase followed by gradual decline in egg size in the wild Peregrine Falcons that we report here reflects a population of young females newly established by restoration efforts. As this population aged during the period eggs were collected, females eventually laid smaller eggs. Alternatively, annual environmental influences could have affected mean egg size across the study period.

The information we report is unique for wild raptors because we know which egg a particular

young came from and that young's sex. We conclude that larger chicks hatch from larger eggs, but egg size is unrelated to hatchling sex. Finally, because clutch sex ratios did not differ significantly from 1:1, Peregrine Falcons in this population apparently did not skew clutch sex ratios in accordance with local resource competition or Fisherian theory.

ACKNOWLEDGMENTS

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