



Variation in offspring sex ratio of a long-lived sexually dimorphic raptor, the Eastern Imperial Eagle *Aquila heliaca*

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Sex ratio theory attempts to explain observed variation in offspring sex ratio at both the population and the brood levels. In the context of low-fecundity organisms producing high-investment offspring, the drivers of adaptive variation in sex ratio are incompletely understood. For raptors that display reverse sexual dimorphism (RSD), preferential allocation of resources to the putatively cheaper sex (male) may be a response to environmental, social or demographic stressors. To assess the extent of skew in offspring sex ratios and to evaluate possible dietary, environmental and demographic correlates of such skew to long-lived RSD avian species, we evaluated the offspring sex ratio of 219 chicks from 119 broods in 30 territories of Eastern Imperial Eagles *Aquila heliaca* across 7 years and four regions at a nature reserve in Kazakhstan. Only in one region in 1 year of our study did the offspring sex ratio differ significantly from parity (10 males : 1 female in 11 territories). Whereas offspring sex ratios were independent of dietary diversity, precipitation, temperature and productivity, we found that year had a moderate effect on brood sex ratio within territories. Our results provide limited evidence of brood sex manipulation in these populations of Eastern Imperial Eagles, and no mechanistic insight into predictions associated with it. Stochastic variation is likely to explain much of the fluctuation we observed in sex ratios, but our observations are also consistent with the hypothesis that sex-ratio manipulation may occur irregularly, in concurrence with atypical environmental or demographic conditions that fluctuate at a time scale longer than that of our 7-year study.

Keywords: *Aquila heliaca*, brood sex ratio, eagle, irregular variation, stochastic variation.

Sex ratio theory attempts to explain observed variation in offspring sex ratio, often the proportion of male offspring produced, both at the population and at the brood or litter levels. Fisher (1930) first

recognized a role for frequency-dependent selection in the maintenance of sex ratio at the population level. He predicted that the relative profit of producing a given sex is dependent on a population's current sex ratio, assuming a linear relationship between the cost of producing each sex and its associated fitness returns. In the context of low-fecundity, high-investment organisms, however, this relationship is often non-linear (Frank 1990). In addition, natural selection predicts active primary (pre-laying or pre-birth) and secondary (post-laying or post-birth) brood or litter adjustments when

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possible. Both types of mechanisms are thought to occur in a complex response to environmental, individual and social conditions (Trivers & Willard 1973, Charnov 1982, Bednarz & Hayden 1991, Wiebe & Bortolotti 1992, Hardy 2002, Bowers *et al.* 2013, Wojczulanis-Jakubas *et al.* 2013) and both can interact with sibling competition, resulting in siblicide influencing offspring sex ratios (Bortolotti 1986, Edwards *et al.* 1988).

Although theory has been successful in predicting parental investment and associated sex ratio skews in invertebrates (Fisher 1930, Trivers & Willard 1973, Charnov 1982, Frank 1990), those successes have less frequently been replicated in vertebrate animal groups (Ewen *et al.* 2004, but see Cassey *et al.* 2006). Putative brood manipulation should be especially evident in sexually dimorphic species, in which the cost of producing an individual of the smaller sex should be less than that of producing an individual of the larger sex (Komdeur & Pen 2002, McDonald *et al.* 2005). However, the role of offspring size as a reliable indicator of cost to parents in sex ratio theory has been questioned (McDonald *et al.* 2005) and reports of non-linear relationships suggest complicated responses in offspring sex ratio to environmental variation (Millon & Bretagnolle 2005).

Avian species, especially those in which females are larger than males (i.e. those that exhibit reverse sexual dimorphism, or RSD), have been the focus of many sex ratio analyses (Albrecht 2000, Ramsay *et al.* 2003, Leech *et al.* 2006, Pike & Petrie 2006). Raptors, which are often highly sexually dimorphic, are known to manipulate their brood sex ratio facultatively at both the primary (pre-laying) and the secondary (post-laying) level. Yet collectively these reports are equivocal (Appleby *et al.* 1997, Arroyo 2002, Sasvari & Nishiumi 2005), variously reporting male-biased sex ratios (Rosenfield *et al.* 1996, Brommer *et al.* 2003, Sasvari & Nishiumi 2005), sex ratios at parity (Negro & Hiraldo 1992, Arroyo 2002), female-biased sex ratios (Tella *et al.* 1996, Appleby *et al.* 1997, Durell 2006) and occasional tightly constrained facultative primary sex ratio manipulation (Cassey *et al.* 2006). Such a diversity of outcomes is difficult to interpret in the context of predictions built around manipulation driven by sexual dimorphism. These empirical incongruities may be due to limitations of sex ratio theory when applied to complex life histories of most birds and mammals and the highly variable situations under which brood rearing may occur

(Bortolotti 1986, Frank 1990, Dzus *et al.* 1996, Komdeur & Pen 2002). Indeed, recent work has highlighted an important role of spatial and temporal correlates to offspring sex ratio manipulation (Byholm *et al.* 2002, Howe 2010). Identifying the environmental correlates of, and mechanisms behind, sex ratio variation is therefore a priority.

To assess the extent of skew in offspring sex ratios and to evaluate possible spatial and temporal correlates of those skews to a long-lived RSD avian species, we evaluated the sex ratio of offspring of Eastern Imperial Eagles *Aquila heliaca* over 7 years in north-central Kazakhstan. Our study area is spatially partitioned into ecological regions in which Eagles show temporal demographic and behavioural variability, particularly with respect to dietary diversity and reproductive output (Katzner 2003, Katzner *et al.* 2005). Preliminary work has shown some landscape-wide variability in sex ratios over time and across these ecological regions (Rudnick *et al.* 2005).

The aim of this study was to advance Rudnick *et al.*'s (2005) preliminary analyses by considering a longer-term dataset and by linking potential spatial, temporal and environmental correlates to offspring sex ratio variability. This work contributes to sex ratio theory by providing relatively long-term and population-wide analyses of variability in brood sex ratio of a long-lived species and by scaling that variation to trends in environmental parameters. The inconclusive nature of previous studies on this problem provides little predictive framework for this study. Nevertheless, as a heuristic null, we expected sex ratio parity; departures from parity could therefore suggest responses to environmental variation. We tested for deviations from parity in response to variation in breeding region, temperature, precipitation and dietary diversity.

METHODS

Study area

We conducted research during the summers of 1998–2004 at the Naurzum Zapovednik (Naurzum National Nature Reserve) in the Kostanay Oblast of north-central Kazakhstan (51°N, 64°E). The term Zapovednik refers to the reserve as a whole, within which three forested patches – Tersec (T), Sip-sin (S) and Naurzum – make up most of the land area. Because of ecological differences within the Naurzum forest, we further divide this

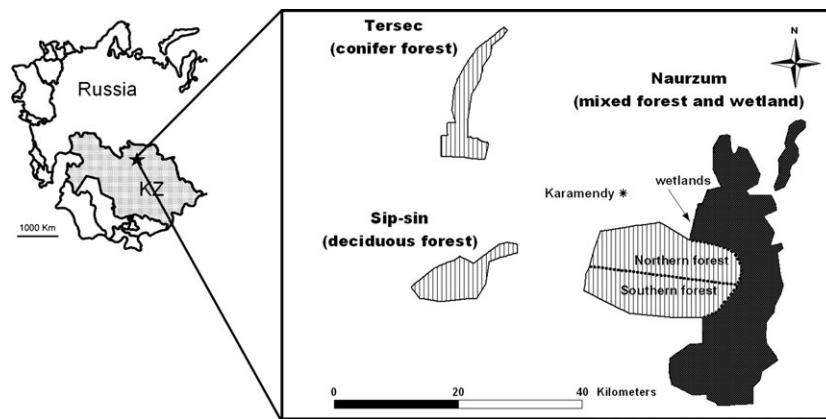


Figure 1. Map of the Naurzum Zapovednik, Kazakhstan, showing its location in the former Soviet Union and the three administrative and four biotic forest regions of the reserve. Adapted from Katzner *et al.* (2005).

woodland into two separate biotic regions – North and South Naurzum (NN and SN, respectively; Fig. 1). Regions differ in the distribution of prey species, differences in eagle dietary patterns (diversity and primary prey), differences in eagle nesting density (Katzner *et al.* 2005, 2006a) and previously described differences in habitat use by eagles (Katzner *et al.* 2003). The remainder of the Zapovednik is dry steppe interspersed with predominantly ephemeral saline and freshwater lakes (Katzner *et al.* 2005). The 87 700-ha study site and population have been described in detail elsewhere (Katzner 2003, Katzner *et al.* 2005). The study population comprised approximately 40 active Eastern Imperial Eagle breeding territories that were relatively stable over time and which coexist alongside breeding territories of White-tailed Eagles *Haliaeetus albicilla*, Steppe Eagles *Aquila nipalensis* and Golden Eagles *Aquila chrysaetos* (Katzner *et al.* 2005).

Eastern Imperial Eagle biology

The Eastern Imperial Eagle is a large monogamous raptor with a geographical range that extends from eastern Europe to Siberia (Rudnick *et al.* 2005). There are limited data on the morphometrics of adult Imperial Eagles but those that do exist suggest that the species is moderately sexually dimorphic. In northern Kazakhstan, females are generally 3–12% larger than males, depending on the particular measurements considered ($n = 1-6$; E. A. Bragin unpubl. data on weight, wing-chord, tail-length, tarsus-length and width, skull length,

beak height and depth, foot span and hallux length). Other authors from other parts of the former Soviet Union report similar trends (Dementiev 1951, Zubarovskyi 1977) and English-language sources report substantial morphometric overlap, with sex-specific maximum and minimum measurements differing by 1–25% (Ferguson-Lees & Christie 2006).

In northern Kazakhstan the species is migratory and initiates the on-territory component of its breeding cycle in March (Katzner 2003). Breeding territories are distributed throughout the reserve and breeding is attempted at 20–35 territories each year (Katzner *et al.* 2006b). Nests are built in pine, birch and occasionally aspen trees; conspecific nearest-neighbour distances among active nests average 2.1–2.7 km (SN and T) and 3.5–4.6 km (NN and S; Katzner *et al.* 2003). When breeding is successful, Eastern Imperial Eagles at the Zapovednik produce one to three chicks that fledge in early to mid-August, 71–80 days after hatching (Katzner 2003).

Eagles at the Zapovednik forage on a variety of primarily steppe-living prey and nesting density is correlated with diet (Katzner *et al.* 2005). Among the most important prey are Bobak Marmots *Marmota bobac*, susliks (i.e. Ground Squirrels *Spermophilus fulvus*, *Spermophilus major*, *Spermophilus pygmeus*), hares (*Lepus* spp.), small mammals (Muridae), and birds including corvids (Carrion Crow *Corvus corone*, Rook *Corvus frugilegus*, Eurasian Magpie *Pica pica*), Little Bustard *Tetrax tetrax*, and several species of waterfowl and raptors. There is a large suslik colony (diameter > 15 km;

primarily *S. fulvus*) south of Naurzum forest, and there is a large marmot colony (diameter > 20 km) west and south of Tersec.

Data collection

Each spring we surveyed established Eastern Imperial Eagle territories and new breeding sites. In July or August of each year we climbed to nests and plucked developing feathers from chicks that were close to fledging (generally *c.* 50–65 days). Feathers were immediately placed in lysis buffer (100 mM Tris-HCl pH 8.0, 100 mM EDTA, 10 mM NaCl, 2% SDS), and stored at room temperature for several months prior to -80°C storage (Rudnick *et al.* 2005). Genetic material in these plucked feathers was the source of DNA used for the genetic determination of sex. We sampled a total of 253 chicks, representing more than 90% of fledged offspring of all nesting territories occupied in the Zapovednik during each year. For the remaining 10% of cases, the sex of chicks was not identified because samples were not collected (nests could not be reached or were found too late) or genetic analyses were inconclusive. The data presented in this paper are from the 31 nests at which all chicks were sexed in at least 2 of the 7 years of our study. Only broods in which all chicks were successfully sexed were included in our analyses. We did not consider nests that only produced a single year of offspring because sample size over the long term for territory-level analysis was prohibitively small. DNA extraction and isolation was carried out as described in Rudnick *et al.* (2005). The sex of each individual was genetically determined by polymerase chain reaction (PCR) using primers 2550F and 2718R (Fridolfsson & Ellegren 1999, Rudnick *et al.* 2005).

In 1998, 1999 and 2000 we visited nests on a monthly basis from June to August. At each visit we collected regurgitated pellet castings and prey remains at nests and associated roosts. Pellet contents were identified and we quantified the number and frequency of occurrence of each prey species in pellets from each territory. We compiled dietary data for each territory separately, producing estimates of diet and of variability in diet within each territory and within each region, thereby allowing analysis of relationships between territory- and region-specific sex ratios and dietary correlates. We estimated dietary specialization in each Eagle territory with Levins' index of diet

breadth, using the 53 prey groups that we could identify accurately in pellets and prey remains (Levins 1968, Krebs 1989). Description and identification of pellet contents and prey remains, as well as statistical analyses of these data, are presented elsewhere (Katzner *et al.* 2005).

We sourced data on rainfall and temperature from a government-operated weather station at the town of Karamendi (formerly Dokuchaevka), Kazakhstan (Fig. 1). Rainfall data were collected with a standard rain gauge and temperature data with a mercury thermometer. Temperature data were collected from 1998 to 2003, precipitation data from 1998 to 2002.

Data analysis

To evaluate temporal variability in offspring sex ratio at territories, we used two generalized linear mixed models (GLMMs; PROC GLIMMIX; SAS v 9.3). Our models evaluated the number of male chicks as a proportion of total chicks, with a binomial response and a logit link function (Krackow & Tkadlec 2001, Wojczulanis-Jakubas *et al.* 2013). In both models we included a unique brood identifier as a random effect.

Our first GLMM tested for spatial and temporal population-level differences in offspring sex ratio, and included breeding region and year as categorical fixed effects. Territory density was not included directly in this model but as our analysis considers two relatively high-density areas (SN and T) and two relatively low-density areas (NN and S), comparison among the four should reveal density-driven effects.

Our second GLMM identified potential correlates of individual territory-level sex ratio variation, and included dietary diversity, weather and territory productivity variables as fixed effects. Weather variables included were average temperature (measured three times monthly) and precipitation for the months of February, March and April. Data from these months were chosen based on their perceived relevance to potential sex ratio manipulation during the breeding cycle (Katzner 2003). Values reported are means ± 1 sd.

To evaluate deviance from parity in broad-scale regional pooled data, we used a log-likelihood ratio goodness-of-fit test (G-statistic) with a Yates' correction (Zar 1999, McDonald 2009). In this context, the value of the G-statistic is a measure of skew of sex ratios, with high values indicating high

degrees of skew (either male or female skewed). In these analyses, following grouping schemes aimed at identifying broad patterns (e.g. Juola & Dearborn 2007), we did not use the territory as the sampling unit. In our initial characterization of sex ratio we summed the numbers of chicks of each sex produced reserve-wide (hereafter, reserve-wide sex ratios). In years where reserve-wide patterns suggested a significant deviation from parity, we then repeated this test, summing chicks within each of the four regions within the reserve (hereafter, regional sex ratios). This pooling approach allows inference about reserve- or regional-level patterns in sex ratios of offspring that is distinct from that provided by the GLMM (above), but it does not permit inference about the adaptive response of individual pairs of Eagles (Hurlbert 1984).

RESULTS

Of the 253 chicks sampled during the study period, we genetically determined the sexes of 239: 123 male and 116 female. Twenty chicks came from nests where not all chicks were successfully sampled or from territories with less than 2 years of data, and thus only 219 chicks (115 males, 104 females) from 119 broods at 30 territories were used for analyses.

We monitored between nine (2004) and 27 (2000) territories, and average sex ratio at all territories ranged from 0.31 (2004) to 0.77 (2001) (Table 1). There was no effect of region and by extension of territory density on territory-level

brood sex ratio (GLMM: $F_{3,108} = 0.59$, $P = 0.6256$) and year was significant only at the $\alpha = 0.10$ level (GLMM: $F_{6,108} = 1.89$, $P = 0.0894$).

Average sex ratio at territories was independent of the demographic, dietary and meteorological parameters we measured (Table 2). Specifically, there was no effect on brood sex ratio of within-territory productivity (GLMM: $F_{1,52} = 0.04$, $P = 0.8452$) or dietary breadth (GLMM: $F_{1,52} = 0.70$, $P = 0.4066$), or reserve-wide temperature (GLMM: $F_{1,52} = 0.05$, $P = 0.8306$) or precipitation (GLMM: $F_{1,52} = 0.73$, $P = 0.3954$).

Annual reserve-wide sex ratio averaged 0.52 ± 0.54 and ranged from 0.33 in 2004 to 0.76 in 2001 (Table 3a). The number of chicks considered ranged from 15 in 2004 to 55 in 2000. When data from all years were considered together, we found no significant deviation from parity in reserve-wide sex ratio (Table 3a; $n = 209$).

There was only 1 year (2001) in which reserve-wide sex ratio deviate significantly from parity (BSR = 0.76; Table 3a). In that year there was a general trend towards male-skew in chick sex ratios in three regions (Sip-sin (BSR = 0.8), Tersec (0.91), south Naurzum (0.83)), but the deviation from parity was statistically significant only in Tersec (Table 3b).

DISCUSSION

Theory predicts that under certain circumstances there will be a selective advantage for offspring sex ratios to become skewed. Few of the patterns we

Table 1. Annual observed sex ratios and modelled solutions for fixed effects (on a logit scale) and intercept value for spatial (region) and temporal (year) terms of a generalized linear mixed model for effects of year and region on brood sex ratio at territories of Eastern Imperial Eagles at the Naurzum Zapovednik, Kazakhstan, from 1998 to 2004.

Model term	<i>n</i>	Mean brood sex ratio (\pm sd/se)	Effect estimate (\pm se)	<i>t</i>	<i>P</i>
Intercept			-0.62 \pm 0.59	-1.05	0.2949
1998	13	0.65 \pm 0.47	1.42 \pm 0.76	1.88	0.0634
1999	18	0.47 \pm 0.41	0.71 \pm 0.65	1.10	0.2742
2000	27	0.57 \pm 0.36	0.92 \pm 0.61	1.50	0.1354
2001	16	0.77 \pm 0.35	1.89 \pm 0.70	2.68	0.0085
2002	21	0.44 \pm 0.39	0.58 \pm 0.65	0.90	0.3714
2003	14	0.43 \pm 0.42	0.44 \pm 0.67	0.65	0.5168
2004	9	0.31 \pm 0.43	0	-	-
S. Naurzum	7	0.51 \pm 0.28	-0.27 \pm 0.36	-0.76	0.4464
N. Naurzum	7	0.46 \pm 0.26	-0.35 \pm 0.39	-0.89	0.3736
Sip-spin	7	0.55 \pm 0.21	0.16 \pm 0.44	0.37	0.7113
Tersec	7	0.52 \pm 0.24	0	-	-

Values reported for regions are grand means ± 1 se, values reported for years are annual means ± 1 sd; $df = 108$ for all comparisons of effect estimates against the reference value; $n =$ number of broods (for year terms) or number of years (for regional terms).

Table 2. Potential reproductive (productivity), dietary (Levins' index) and meteorological correlates of brood sex ratio of Eastern Imperial Eagle chicks at the Naurzum Zapovednik, Kazakhstan, from 1998 to 2004. Average temperature and precipitation were measured at the start of the nesting cycle in February (F), March (M) and April (A) each year. Not all parameters were measured in all years.

Year	Mean territory productivity	Mean territory diet breadth	Mean F, M, A, temperature (°C)	Mean F, M, A, precipitation (mm)
1998	1.31 ± 0.48	8.81 ± 2.17	-7.68	14.07
1999	1.94 ± 0.54	7.29 ± 2.38	-6.67	18.67
2000	2.10 ± 0.77	7.61 ± 3.03	-2.66	15.67
2001	1.81 ± 0.75	-	-2.96	17.6
2002	1.81 ± 0.68	-	-0.72	26.3
2003	1.87 ± 0.52	-	-10.56	-
2004	1.67 ± 0.71	-	-	-

Table 3. (a) Reserve-wide sex ratio variation of Eastern Imperial Eagle chicks at the Naurzum Zapovednik, Kazakhstan. Data are pooled across nesting territories and regions. (b) Regional-level (NN, North Naurzum; C, Sip-sin; SN, South Naurzum; T, Tersec) sex ratios of Eastern Imperial Eagle chicks at the Naurzum Zapovednik, Kazakhstan, from 2001. Data are pooled across nesting territories within each region.

Year	Biotic scale	<i>n</i> chicks	Sex ratio	<i>G</i> (Yates' corrected)	<i>P</i> (2-tailed, <i>df</i> = 1)
(a)					
1998	Reserve-wide	17	0.65	0.95	0.3297
1999	Reserve-wide	35	0.49	0	1
2000	Reserve-wide	57	0.54	0.28	0.5961
2001	Reserve-wide	29	0.76	7.05	0.0078
2002	Reserve-wide	38	0.45	0.24	0.6263
2003	Reserve-wide	28	0.43	0.32	0.5703
2004	Reserve-wide	15	0.33	1.08	0.2988
1998-2004	Reserve-wide	219	0.53	0.46	0.4991
(b)					
2001	Regional - NN	7	0.43	0	1
2001	Regional - C	5	0.8	0.82	0.3644
2001	Regional - SN	6	0.83	1.57	0.2102
2001	Regional - T	11	0.91	6.49	0.0108

observed in offspring sex ratio of Eastern Imperial Eagles were linked to environmental variation in a way that either supported or undermined established theory. Furthermore, because we were not able to observe sex ratio at hatching, our data provide insight into the outcome of manipulations that may have occurred but limited information on potential mechanisms that resulted in that outcome (i.e. limited information to evaluate primary vs. secondary manipulation). Nevertheless, our data provide a more holistic picture of sex ratio variation in raptors, specifically in eagles of the genus *Aquila*.

We observed only one case where offspring sex ratios consistently varied significantly from parity (Tersec in 2001, 10 males : 1 female; Table 1). Although year was a statistically significant effect in

our GLMM (at $\alpha = 0.10$), the model suggests that 2001 was an exceptional year (Table 1). This result is consistent with the more broadly based aggregated data that are suggestive of trends towards producing males (Table 3). Although the skew we observed here is real, the lack of significance in other tests from the same year suggests that this result should be interpreted with caution because of our small sample size and the limited spatial extent of our study. These problems are difficult to resolve when studying eagles (Bortolotti 1986, Edwards *et al.* 1988, Dzus *et al.* 1996, Ferrer *et al.* 2009) and other apex predators that occur at low densities. Nevertheless, the importance of large-scale variation in offspring sex ratio reported for other birds (e.g. Byholm *et al.* 2002, Howe 2010) suggests that even though our sample size and

sampling scale were large relative to those of other eagle studies, they were still too small to capture the true variation in eagle offspring sex ratios.

Small sample size notwithstanding, we observed few regional differences in brood sex ratio. The lack of a significant regional effect on sex ratio variation may suggest that temperature and precipitation (as measured here and at the spatial and temporal scale for which we have data) have little effect on eagle brood sex ratios, regardless of differences in diet and productivity. Thus, if Eastern Imperial Eagles at Naurzum manipulate their offspring sex ratio, it is probably in response to other types or scales of environmental stimuli than those evaluated here. This prediction is more likely in the context of the substantial intra-regional and intra-annual variation we observed in chick sex ratio.

The general trends in our data did not provide evidence for manipulation of sex ratios and variation in dietary diversity, temperature or precipitation. This is inconsistent with studies of Bald Eagles *Haliaeetus leucocephalus* in North America (Dzus *et al.* 1996) but is consistent with a study of the closely related Spanish Imperial Eagle *Aquila adalberti* that showed no relationship between habitat quality and offspring sex ratio (Ferrer *et al.* 2009). Similar results have been observed for other vertebrate species (Aparicio & Cordero 2001, McDonald *et al.* 2005) and in some cases, RSD raptor sex ratio variation has been observed to be opposite that predicted by the Trivers–Willard hypothesis (Olsen & Cockburn 1991).

The cause of the single year of statistically significant sex-ratio variation we observed in Tersec in 2001 is difficult to discern. When sex ratio variation is not stochastic it is generally assumed that adults are manipulating the sex of their offspring (Dzus *et al.* 1996). Whether the adaptive value of sex ratio manipulation outweighs its costs is linked to a species' life history (Pen *et al.* 1999, cited in Hasselquist & Kempenaers 2002). Specifically, costs of reproduction and adaptive sex ratio manipulation should be scaled to the intensity of environmental signals causing the response. Furthermore, the costs of implementing mechanisms for facultative sex ratio manipulation may be significantly greater than those of failing to initiate breeding in any particular year.

For breeding pairs of the Eastern Imperial Eagle, our data provide little evidence for the

manipulation of offspring sex ratios in response to environmental conditions. This lack of variation in offspring sex ratio may simply be a reflection of the fact that long-lived species have many potential breeding opportunities over a lifetime. Instead of incurring costs associated with sex ratio manipulation in response to annual environmental variation (e.g. as in many short-lived Passerines), long-lived species may maximize overall lifetime reproductive success by producing equal sex ratios. Thus, eagles may produce dozens of clutches over their lifetime, and annual environmental 'noise' may not merit offspring sex ratio manipulation due to the energetic, physiological or other costs.

Alternatively, our data may be explained by an irregular sex-ratio response to extreme environmental variation. Irregular responses would allow a long-lived species to endure typical environmental variation but also enable individuals to respond to extreme instances in which the increased effort of sex ratio manipulation could confer reproductive benefit. In this way, the costs of reproduction would be accurately scaled to the longer-term patterns of environmental variation that a long-lived species encounters. Such a mechanism is consistent with the original Trivers and Willard (1973) hypothesis and with a recently proposed explanation for an irregularly skewed eagle offspring sex ratio (Ferrer *et al.* 2009). If correct, such a mechanism would be evident only at a time scale well beyond that of our 7-year study.

Sex ratio responses in other avian systems are consistent with irregular manipulation. For example, Sasvari and Nishiumi (2005) reported male-skewed broods following harsh winters that drastically reduced rodent prey availability. Likewise, Ingraldi (2005) linked the population-level (pooled) male-skewed offspring sex ratio of Northern Goshawk *Accipiter gentilis* to increased rainfall and limited prey availability and Dzus *et al.* (1996) reported a male skew in the brood sex ratio of Bald Eagles during bad years. If similar mechanisms operate for Kazakhstan's Eastern Imperial Eagles, we would predict that dietary specialization, which can be positively correlated with eagle productivity (Katzner *et al.* 2005), might influence brood sex ratio in years of extreme variability in prey availability. Those Eagles with relatively highly specialized diets would be relatively more susceptible to and encounter different patterns of resource availability. Interestingly, the significantly skewed sex ratio we observed

occurred in Tersec, a region in which diet is highly specialized (Katzner *et al.* 2005).

Our analyses provide little evidence that chick sex ratios of Imperial Eagles were skewed temporally or spatially in response to the dietary and environmental variables we measured. However, the one regional statistically significant deviation from sex ratio parity in our study (Tersec in 2001) hints at the possibility that irregular events may have consequences for eagle demography. In a large population, such irregularly skewed dynamics should have little impact on population sex ratios, while still have consequences for individual lifetime reproductive success. In a small population, however, irregular events should have dramatic consequences for demography and population viability (Brook *et al.* 2000).

The possibility of an irregular skew in offspring sex ratio suggests that expected lifespan is an important and often unconsidered variable in the avian sex ratio debate. Future research on long-lived vertebrates may find it useful to consider field studies that last several times the generation time of the species in question and across substantially larger spatial scales to address irregular deviations from sex ratio parity.

Steve Latta, Vincenzo Penteriani, Gary Bortolotti, Patrik Byholm, Beatriz Arroyo, Rauri Bowie and several anonymous reviewers provided insightful comments on the manuscripts. Adam Duerr assisted with analysis. This project was funded by the Wildlife Conservation Society, the National Birds of Prey Trust, the US National Science Foundation (INT-0301905), the US Environmental Protection Agency, the USGS Biological Resources Division, the Arizona State University Department of Biology, the Frank M. Chapman Memorial Fund, the Hawk Mountain-Zeiss Raptor Research Award, the Arizona State University Graduate Research Support Program, the International Osprey Foundation, the World Nature Association and the National Geographic Society. West Virginia University, the National Aviary, Purdue University, the Naurzum National Nature Reserve and the government of Kazakhstan provided critical logistical, permitting and institutional support.

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Received 4 September 2013;
 revision accepted 27 December 2013.
 Associate Editor: Beatriz Arroyo.