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Does breeding population trajectory and age of nesting females influence disparate nestling sex ratios in two populations of Cooper's hawks?

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Abstract

Offspring sex ratios at the termination of parental care should theoretically be skewed toward the less expensive sex, which in most avian species would be females, the smaller gender. Among birds, however, raptors offer an unusual dynamic because they exhibit reversed size dimorphism with females being larger than males. And thus theory would predict a preponderance of male offspring. Results for raptors and birds in general have been varied although population-level estimates of sex ratios in avian offspring are generally at unity. Adaptive adjustment of sex ratios in avian offspring is difficult to predict perhaps in part due to a lack of life-history details and short-term investigations that cannot account for precision or repeatability of sex ratios across time. We conducted a novel comparative study of sex ratios in nestling Cooper's hawks (*Accipiter cooperii*) in two study populations across breeding generations during 11 years in Wisconsin, 2001–2011. One breeding population recently colonized metropolitan Milwaukee and exhibited rapidly increasing population growth, while the ex-Milwaukee breeding population was stable. Following life-history trade-off theory and our prediction regarding this socially monogamous species in which reversed sexual size dimorphism is extreme, first-time breeding one-year-old, second-year females in both study populations produced a preponderance of the smaller and cheaper sex, males, whereas ASY (after-second-year), ≥2-year-old females in Milwaukee produced a nestling sex ratio near unity and predictably therefore a greater proportion of females compared to ASY females in ex-Milwaukee who produced a preponderance of males. Adjustment of sex ratios in both study populations occurred at conception. Life histories and selective pressures related to breeding population trajectory in two age cohorts of nesting female Cooper's hawk likely vary, and it is possible that these differences influenced the sex ratios we documented for two age cohorts of female Cooper's hawks in Wisconsin.

Introduction

The selective forces touted to influence the heterogeneity of sex ratios in nestling birds vary widely across avian taxa and include, for example, brood parasitism (Zanette et al. 2005), hatching date (Griggio et al. 2002), the presence or contribution of nest helpers (Griffin et al. 2005), sexual attractiveness of bill shape (Graham et al. 2011), resource competition between parents and their offspring (Gowaty 1993), and diet (Rutz 2012). Variation in selective pressures that lead to skewing perhaps is unsurprising given that sex ratios of offspring can affect a diverse suite of phenomena, including parental energy expenditure and fitness, adult sex ratios, and population growth rate (Engen et al. 2003; Donald 2007). One evolutionary theory predicts that parents should adjust the sex of their offspring when the relative fitness of male and female offspring varies with environmental conditions (Trivers and

Willard 1973). That said, population-level estimates of offspring sex ratio in birds do not generally differ from unity (Donald 2007). There is, however, a growing body of evidence to support expected adaptive adjustment of sex ratios in avian offspring, but empirical support for this prediction is lacking in many taxa and explaining the heterogeneity of sex ratios in avian offspring in the fit of sex ratio theory remains both challenging and controversial (West and Sheldon 2002; Ewen et al. 2004; Donald 2007).

Fisher (1930) was one of the first to offer a theoretical basis toward an attempt to understand sex ratios in populations of animals by suggesting that selection should favor equal parental expenditure in offspring in both sexes. Thus, offspring sex ratios at the termination of parental care should be skewed toward the less expensive sex (Howe 1977; Blank and Nolan 1983). Fisher's population model is controversial for several reasons and one, for example, is that its outcome of a sex ratio of unity is indistinguishable from that which is expected from random Mendelian (meiotic) sex allocation, but the model is oft-cited in sex ratio studies and is recognized as having explanatory power (Rosenfield et al. 1996a; Ranta et al. 2000; Donald 2007; Perlut et al. 2014). Among birds raptors offer an unusual dynamic because, unlike most other birds, they exhibit reversed size dimorphism with females being larger than males. And thus Fisher's equilibrium hypothesis would in raptors predict a preponderance of male offspring, the apparent cheaper sex (Rutz 2012), such as we earlier reported as occurring at conception and in broods for highly dimorphic Cooper's hawk offspring in Wisconsin exclusive of Milwaukee (Rosenfield et al. 1996a).

That said, several authors have specified that congruence between theory and empiricism regarding sex ratios in animals would benefit from more data across species and across populations of species (Donald 2007; Perlut et al. 2014). Moreover, West and Sheldon (2002) specified that there is a general lack of life-history details requisite to predicting sex ratio variation in birds and other animals. Aggravating this theme is that most studies of nestling sex ratios are relatively short-term investigations of 1–5 years (e.g., Bednarz and Hayden 1991; Gowaty 1993; Leroux and Bretagnolle 1996; Whittingham and Dunn 2000; Zanette et al. 2005; Rutz 2012). Relatively short-term studies on sex ratios can lack adequate sample sizes for statistical power (Rosenfield et al. 1996a; West and Sheldon 2002) and particularly fail to account for the influence of interannual selective pressures and repeatability, or precision, of sex ratios (Whittingham and Dunn 2000; West and Sheldon 2002). Short-term and many long-term studies generally do not provide information on population growth trajectory across generations. We

note that Fisher's equilibrium hypothesis predicts population sex ratios both within and across generations (Rosenfield et al. 1996a). The aforementioned short comings plague the majority of previous investigations of sex ratios in birds and consequentially inhibit understanding of (and especially predictive) selective pressures that influence possible adaptive adjustment of sex ratios (West and Sheldon 2002; Rosenfield et al. 2009, 2013).

We conducted long-term, cross-generational research on various aspects of the ecology and life histories of two breeding populations of Cooper's hawks in Wisconsin. One population colonized metropolitan Milwaukee and exhibited rapidly increasing population growth (number of nesting attempts tripled), whereas a breeding population on our ex-Milwaukee population study site was stable and likely territorially saturated during that colonization period in Milwaukee (Stout et al. 2007; Stout and Rosenfield 2010; Rosenfield et al. 2009, 2013; RNR, unpubl.). Both populations exhibit high breeding densities compared to other North American populations, similar annual survivorship and longevity of breeding adults, and consistently high productivity indices across years that are among the highest in North America for this socially monogamous species (Bielefeldt et al. 1998; Rosenfield et al. 2007a,b; Stout et al. 2007; Stout and Rosenfield 2010; R.N. Rosenfield and W.E. Stout, unpubl.). Cooper's hawks on both study areas also exhibit long-term and consistent annual reuse of nest sites and, related, we did not detect a significant temporal difference in annual survivorship of breeding adult males and females in urban and rural landscapes in ex-Milwaukee across 32 years (Rosenfield and Bielefeldt 1993, 1996; Stout et al. 2007; Rosenfield et al. 1995, 1996b, 2009; RNR, unpubl.). As in many North American populations of breeding Cooper's hawks, two age cohorts of females (brown yearling [second-year, or SY birds] and gray ≥2-year-old [after-second-year, or ASY] hens) are present each year in Wisconsin, although yearling females occur in much lower numbers outside of Milwaukee (Rosenfield and Bielefeldt 1993; Rosenfield et al. 2007a,b, 2013; Stout et al. 2007). Yearling females are relatively more common in colonizing and growing raptor populations such as our Milwaukee site (Newton 1979; Stout and Rosenfield 2010; Rosenfield et al. 2013). Yearling males, as in most other studies of raptors, are nonexistent to rare breeders in both our study populations (Stout et al. 2007; Rosenfield et al. 2013).

Both our study populations produce intrasite recruits of both sexes, but we have not detected intersite recruitment nor movement of marked breeding adults between our two Wisconsin study areas across 35 years, nor do we have any data indicating that fledglings or breeding adults in our study sites disperse to nests outside Wisconsin

(Rosenfield et al. 1996a, 2013; Stout et al. 2007; RNR, unpubl.). We assume that *nonyearling* recruits and surviving, breeding adults on both study sites have the potential and experience to collect information on the adult sex ratios of past years and current year, creating an environment where they could adjust their sex ratio output accordingly (Perlut et al. 2014). The two populations are not genetically different statistically, and they are morphologically similar, likely because they use the same type of prey, mostly small-to-medium-sized passerine birds and small mammals (Bielefeldt et al. 1992; Rosenfield et al. 2010; Sonsthagen et al. 2012, RNR and WES, personal observation).

Several studies have demonstrated that one-year-old breeding raptors of both sexes, including Wisconsin Cooper's hawks, are under different selective pressures than older, experienced birds in part because life-history trade-offs render yearlings competitively inferior to older breeders in several aspects of reproduction (e.g., Boal 2001; Lieske et al. 1997; Koons et al. 2008; Rosenfield et al. 2013). It is believed that yearling males and females typically produce fewer young than older birds in part because energetic costs of production are greater for inexperienced birds (e.g., Moore and Henny 1984; Boal 2001; Koons et al. 2008; Rosenfield et al. 2013). Moreover, some researchers have suggested that the trade-off in resource allocation to molt vs. reproduction is a mechanism by which the cost of reproduction is aggravated in yearling birds more than in older individuals (Dawson et al. 2000; Rosenfield et al. 2013). Indeed, breeding SY male and female Cooper's hawks in Wisconsin are molting to a greater extent than are ASY birds (Rosenfield et al. 2013; RNR and WES, unpubl.). In raptors, we speculate that such costs would be aggravated in production of females by yearlings in those species where reversed dimorphism is extreme such as the Cooper's hawk (Rosenfield and Bielefeldt 1993). Similarly, Ferrer et al. (2009) documented younger breeders producing male-biased broods in the Spanish imperial eagle (*Aquila adalberti*). We note that age structure is a major element in key theories about population biology (Lack 1968), but the role and mechanisms of maternal age as a factor in influencing avian sex ratios are poorly studied and need more investigation to further enhance our understanding of avian sex ratios.

We here provide a novel, long-term comparison of nestling sex ratios in two Cooper's hawk breeding populations that exhibited different population trajectories during concurrent study years (Rosenfield et al. 1995, 2013). We predicted that compared to the territorially saturated ex-Milwaukee population, more females would be produced by ASY females in the Milwaukee population because a preponderant production of male offspring, such as occurs in our ex-Milwaukee study site across 32 years (Rosenfield et al. 1996a; RNR, unpubl.), could render females the rarer sex in the adult Milwaukee population where breeding sites are more available. Hence, it would be adaptive for a breeding ASY female in Milwaukee to facultatively produce more females *compared* to breeding ASY females in the stable, ex-Milwaukee population because females would more likely become recruits in the Milwaukee population (Trivers and Willard 1973; Dawkins 1989; Lummaa et al. 1998; Engen et al. 2003). We highlight that we are *not* predicting that breeding females in Milwaukee necessarily produce a skewed sex ratio favoring females rather that comparatively more female young will occur in broods of Milwaukee vs. those of ex-Milwaukee ASY female Cooper's hawks. And because of possible trade-off costs between maternal age and production of females, the assumed costlier sex (Rosenfield et al. 1996a), we also predicted that inexperienced, one-year-old females in both study sites would produce a preponderance of males (Blank and Nolan 1983; Weimerskirch et al. 2000; Rosenfield et al. 2013). We note that our predictions of sex ratios are based on assumed presence of across-year selection pressures, and thus, the direction of predicted sex ratios should be interannually consistent.

We conducted this study to document, model, and understand patterns of variation in breeding female ages and nestling sex ratios across time between growing and stable populations of breeding Cooper's hawks, respectively. We highlight that our study may be particularly instructive compared to many previous studies on sex ratios in birds as our long-term work has provided strong documentation across generations of many fitness, life-history, and reproductive events, including evolutionary, adaptive trade-offs that are age and population trajectory related (e.g., Rosenfield and Bielefeldt 1997, 1999; Rosenfield et al. 2000, 2009, 2013; Stout and Rosenfield 2010). We reiterate that West and Sheldon (2002) specified that the expected sex ratio shift in most studies on sex ratios in birds depends on life-history details that are not known, and thus, sex ratios cannot be predicted a priori. A further strength of our study is that we assess long-term variation and thus the precision of heterogeneity (or lack thereof) of nestling sex ratios across years between populations under different growth demographics using a study species in which theoretical trade-offs in resource allocation to offspring of markedly different sizes by gender may be more readily manifested in nestling sex ratios. We note that population trajectory, long-term, annual variation in sex ratios and the effects of maternal age on nestling sex ratios have scarcely been examined (Wiebe and Bortolotti 1992; Ewen et al. 2004). Lastly, we will discuss life-history bases for a tenable suggestion that offspring sex ratios in Milwaukee were adjusted at conception.

Methods

Study areas and field methods

We investigated breeding Cooper's hawks during 1980–2011 in central and southeastern Wisconsin, as described by Murphy et al. (1988), Rosenfield and Bielefeldt (1996), and Rosenfield et al. (1995, 2010). Our central Wisconsin study area included rural landscapes and the abutting municipalities of Stevens Point, Whiting, and Plover (hereafter Stevens Point) with a predominately urban human population density of ~600 people per km^2. Our southeastern Wisconsin area primarily included rural environs of the Kettle Moraine State Forest, South Unit, which is about 60 km west of the Milwaukee study area. Numbers of breeding Cooper's hawks in these ex-Milwaukee areas likely were slowly increasing during the 1980s, but stabilized by the early-to-mid-1990s as breeding territories were likely saturated in this latter period (Rosenfield et al. 1995, 2013; RNR, unpubl.). The number of study nests was divided about equally between central and southeastern Wisconsin. We regard the ex-Milwaukee locales as one study area (Rosenfield et al. 2010, 2013).

We also studied nesting Cooper's hawks in the metropolitan city of Milwaukee and some surrounding municipalities in southeastern Wisconsin during 1995–2011 as described by Stout et al. (2007). The human population density in this study area is ~2400 people per km^2. Cooper's hawks colonized this study area about 14 years after the start of our research in the ex-Milwaukee study site in 1980 and grew rapidly through the late 1990s and into the early 2000s. Saturation of breeding territories was not extant as the hawk population in Milwaukee was still growing as of 2011 (Stout et al. 2007; Stout and Rosenfield 2010; RNR and WES, unpubl.)

The ex-Milwaukee and Milwaukee study areas were chosen without preconceptions about their suitability for nesting Cooper's hawks (Bielefeldt et al. 1998; Trexel et al. 1999; Rosenfield et al. 2007a,b; Stout et al. 2007; Stout and Rosenfield 2010). Each year nests in both study areas, whose populations exhibit identical nesting phenology (Bielefeldt et al. 1998; Rosenfield and Bielefeldt 2006), are found objectively at comparable times by intensive foot searches (ex-Milwaukee) or by vehicle (Milwaukee) during the pre-incubation or early incubation periods. Detailed descriptions of our nest finding techniques, including metrics and indices of breeding population trajectory on our two study sites, are presented by Rosenfield and Bielefeldt (1996), Rosenfield et al. (1995, 2013), and Stout and Rosenfield (2010).

Cooper's hawks are highly dimorphic, with males being two-thirds the mass of females at fledging; at ≥12 days of age, males are noticeably smaller and can be reliably sexed

(Rosenfield and Bielefeldt 1993; Rosenfield et al. 1996a). At both study sites we count, band, and sex nestlings when they are about 18 days of age (Rosenfield et al. 2007a,b, 2013; Stout and Rosenfield 2010). Sex ratios of nestlings were determined concurrently in both study sites in 2001–2011. We chose these study years because our field techniques, and especially efforts at aging breeding adults (see below), were most similar between study areas in these years, and we too were more likely assured that long-term population trajectories were different between these study sites (Stout and Rosenfield 2010; Rosenfield et al. 2013).

To facilitate an analysis of the possible role of maternal age on sex ratios in both intra- and intersite comparisons, we aged breeding females as either one-year-old, SY (second-year) birds in brown plumage or ≥2 years of age, ASY birds in gray plumage following Rosenfield and Bielefeldt (1997). We aged breeding females at capture or by noting plumage of uncaptured birds using binoculars and/or a spotting scope. We frequently obtained very close (1–5 m) and unobstructed views of breeding females who were near our traps (Rosenfield and Bielefeldt 1997; Stout et al. 2007; Rosenfield et al. 2013). We aged a minimum of 89% and 95% of all females on Milwaukee and ex-Milwaukee study sites, respectively, during study years of this investigation.

Statistical analysis

We used generalized linear mixed-effects models (Bolker et al. 2008) with binomial error distributions and logit link functions to estimate the influence of "Site" (ex-Milwaukee and Milwaukee) on proportion of breeding female age classes (SY and ASY). We used the Lme4 package (Bates and Maechler 2014) for R (R Development Core Team 2014) to fit two competing models, including a null model and a model with "Site" as a categorical fixed-effect variable. We specified "Year" (2001–2011) as a continuous random-effect variable in both models to account for potentially confounding variation arising from lack of independence among years (Gillies et al. 2006; Bolker et al. 2008).

We then used generalized linear models (no random-effect variable for "Year") with binomial error distributions and logit link functions to estimate temporal variation in annual proportion male nestlings from 2001 to 2011. We constructed five competing models, including (1) a null model, (2) a model with "Year" as a continuous fixed-effect variable, (3) a model with "Year" and "Site" interacting, (4) a model with "Year" and breeding female "Age" interacting, and (5) a model with "Year", "Site", and "Age" interacting.

We further examined variation in proportion male nestlings using generalized linear mixed-effects models (Bolker et al. 2008) with binomial error distributions, logit link functions, and "Year" as a random-effect variable to focus on the influence of "Site" and "Age" as

fixed-effect variables. We constructed a set of five competing models, including (1) a null model, (2) a model with "Site," (3) a model with "Age," (4) a model with "Site" and "Age" as additive variables, and (5) a model with "Site" and "Age" interacting (Bates and Maechler 2014; R Development Core Team 2014). We specified "Year" as a random-effect variable in all models to account for (1) temporal variation in proportion male nestlings, and (2) potentially confounding variation arising from lack of independence among years (Gillies et al. 2006; Bolker et al. 2008).

We used Akaike's information criteria with second-order bias correction for small sample sizes (AICc) and proportional model weights (*w*) to select and make inference from the most probable models (Burnham and Anderson 2002; Anderson 2008). We report model parameter estimates/effect sizes (β) and 85% CI (confidence intervals) (Arnold 2010) for predictor variables ("Site," "Year," and "Age"). We calculated estimates of proportion breeding female ages, proportion male nestlings, and 85% CI from generalized linear mixed-effects models with the AICcmodavg package (Mazerolle 2013) for R (R Development Core Team 2014). If model-selection uncertainty was high and AICc differences (ΔAICc) between the first and second most probable models were >2.0, we calculated model-averaged parameter estimates ($\bar{\beta}$) and predictions with 85% UCIs (unconditional confidence intervals) (Anderson 2008; Arnold 2010) with the AICcmodavg package (Mazerolle 2013) for R (R Development Core Team 2014). We considered predictor variables influential on response variables (proportion breeding female age classes and proportion male nestlings) if 85% CI/UCI for $\beta/\bar{\beta}$ did not overlap zero (Anderson 2008; Bolker 2008; Arnold 2010). We report and make inference from 85% CI/UCI, rather than conventional 95% CI/UCI, because AIC values are reduced by selecting model parameters with 85% CI/UCI excluding zero (i.e., $P < 0.15$), which is inconsistent with identifying influential parameters by assessing overlap of 95% CI/UCI with zero (i.e., $P < 0.05$ for influential parameters; Burnham and Anderson 2002; Arnold 2010).

Results

We sampled nestling sex ratios at 390 nests from 2001 through 2011, including 215 and 175 nests at Milwaukee and ex-Milwaukee sites, respectively (Table 1). Nests of ASY females accounted for 75% and 91% of all nests at Milwaukee and ex-Milwaukee study sites, respectively.

Annual range of proportion male nestlings for ASY females was 40–63% in Milwaukee and 47–74% in ex-Milwaukee (Table 1). Excluding 1 year (2001) when proportions of male nestlings were equal between the two study sites, proportions of male nestlings in broods of ASY females were lower (and therefore a greater number of female young were consistently produced) in 9 (90%) of 10 concurrent sets of study years in Milwaukee versus ex-Milwaukee. Overall, proportion male nestlings across 11 study years for ASY females was near unity or 49% in Milwaukee and 59% in ex-Milwaukee (Table 1).

Proportion of male nestlings in SY female broods annually ranged from 0% to 68% and from 30% to 80% in Milwaukee and ex-Milwaukee, respectively. Proportion of male nestlings in nests of SY females consistently exceeded 50% males in 8 (73%) of 11 years in Milwaukee and in 6 (86%) of 7 years when SY females were detected as breeders in both study areas (Table 1). Overall proportions of male nestlings among all study years were 55% in Milwaukee and 70% in ex-Milwaukee (Table 1). Overall proportion male nestlings for combined breeding female ages across all study years was 51% and 60% for Milwaukee and ex-Milwaukee study sites, respectively (Table 1).

The most probable generalized linear mixed-effects model for predicting proportion breeding female ages included the "Site" variable ($w = 1.00$; ΔAICc = 15.2 with null model). Model-predicted proportion of SY breeding females was greater in the Milwaukee site (0.23, 85% CI = 0.18–0.30) compared to the ex-Milwaukee site (0.08, 85% CI = 0.05–0.12) ($\beta_{Mil} = 1.23$, 85% CI = 0.78–1.69).

The most probable generalized linear model for predicting temporal variation in annual proportion male nestlings from 2001 through 2011 included interacting variables for "Year" and "Site" (Table 2). Model-predicted annual proportion male nestlings increased at the ex-Milwaukee site ($\beta_{Year*Ex-Mil} = 0.10$, 85% CI = 0.05–0.15) but was stable at the Milwaukee site ($\beta_{Year*Mil} = 0.16$, 85% CI = -0.09 to 0.40) (Fig. 1).

The most probable generalized linear mixed-effects model for predicting overall proportion male nestlings for 2001 through 2011 included additive variables for "Site" and "Age," but we report model-averaged parameter estimates ($\bar{\beta}$) and predictions with 85% UCIs because of model-selection uncertainty (Table 3). Influence on proportion male nestlings was positive for the ex-Milwaukee site ($\bar{\beta}_{Ex-Mil} = 0.39$, 85% UCI = 0.23–0.55) and SY age ($\bar{\beta}_{SY} = 0.28$, 85% UCI = 0.06–0.50) compared to the Milwaukee site ($\bar{\beta}_{Mil} = -0.39$, 85% UCI = -0.55 to -0.23) and ASY age ($\bar{\beta}_{ASY} = -0.28$, 85% UCI = -0.50 to -0.06). Proportion male nestlings for Milwaukee ASY females (0.50, 85% UCI = 0.47–0.53) were lesser than those for ex-Milwaukee SY (0.65, 85% UCI = 0.56–0.74) and ASY females (0.59, 85% UCI = 0.56–0.62). Proportion male nestlings for Milwaukee SY females (0.55, 85% UCI = 0.49–0.60) tended toward being lesser than those for ex-Milwaukee SY females (0.65, 85% UCI = 0.56–0.74) but UCIs slightly overlapped.

Table 1. Number of Cooper's hawk nests, male (♂) and female (♀) nestlings, total nestlings, and proportion male nestlings for ASY (after-second-year) and SY (second-year) breeding females at Milwaukee and ex-Milwaukee sites from 2001 to 2011, Wisconsin, USA.

	Milwaukee					Ex-Milwaukee				
	Nests	♂	♀	Total	% ♂	Nests	♂	♀	Total	% ♂
ASY Year										
2001	12	24	24	48	0.50	15	26	26	52	0.50
2002	13	24	21	45	0.53	10	22	17	39	0.56
2003	13	25	25	50	0.50	18	36	27	63	0.57
2004	17	33	19	52	0.63	14	21	24	45	0.47
2005	10	19	20	39	0.49	17	39	26	65	0.60
2006	15	22	33	55	0.40	16	32	27	59	0.54
2007	23	44	42	86	0.51	23	50	37	87	0.57
2008	19	30	32	62	0.48	18	38	24	62	0.61
2009	17	27	37	64	0.42	16	43	20	63	0.68
2010	11	25	21	46	0.54	6	18	7	25	0.72
2011	12	19	24	43	0.44	7	23	8	31	0.74
ASY Total	162	292	298	590	0.49	160	348	243	591	0.59
SY										
2001	1	3	1	4	0.75	0	0	0	0	0.00
2002	4	7	5	12	0.58	3	7	2	9	0.78
2003	5	10	9	19	0.53	1	1	2	3	0.33
2004	1	0	1	1	0.00	1	2	1	3	0.67
2005	6	11	9	20	0.55	0	0	0	0	0.00
2006	5	10	9	19	0.53	2	4	1	5	0.80
2007	2	3	2	5	0.60	0	0	0	0	0.00
2008	8	17	10	27	0.63	4	9	3	12	0.75
2009	9	15	15	30	0.50	0	0	0	0	0.00
2010	4	4	11	15	0.27	2	4	3	7	0.57
2011	8	19	9	28	0.68	2	4	1	5	0.80
SY Total	53	99	81	180	0.55	15	31	13	44	0.70
Grand Total	215	391	379	770	0.51	175	379	256	635	0.60

Table 2. Generalized linear (binomial) models predicting variation in annual ("Year") proportion male nestlings for second-year and after-second-year ("Age") breeding female Cooper's hawks at Milwaukee and ex-Milwaukee sites ("Site") for 2001–2011, Wisconsin, USA. K, number of model parameters; $Log_e(L)$, model log-likelihood; ΔAIC_c, relative differences in Akaike's information criteria with second-order bias correction for small sample sizes; and w, relative model weights. Year * Site AIC_c = 1022.8.

Models	K	$Log_e(L)$	ΔAIC_c	w
Year * Site	4	−507.3	0.0	0.86
Year * Site * Age	8	−505.0	3.7	0.14
Null	1	−517.3	13.8	0.00
Year	2	−516.9	15.0	0.00
Year * Age	4	−516.3	17.9	0.00

Discussion

We conducted a novel comparative study of sex ratios in nestling Cooper's hawks in two study populations across 11 concurrent years in Wisconsin, 2001–2011. One breeding population recently colonized metropolitan Milwaukee and exhibited increasing population growth, while the ex-Milwaukee breeding population was stable during this study. Both populations exhibit some of the highest nesting densities and consistently high, interannual reproductive indices for the species. As we predicted, and *compared* to the ex-Milwaukee population of ASY breeding females, our model demonstrated that a greater proportion of female offspring were produced in Milwaukee by ≥2-year-old, ASY females. Also in accord with our presupposition, modeling showed that SY females produced a preponderance of males on both study sites, and thus, our analyses demonstrated age differences in sex ratios, particularly in SY females in ex-Milwaukee vs. ASY females in Milwaukee.

Our overall skewed sex ratio in ex-Milwaukee for both ASY and SY females of 60% males is in accord with Fisher's equilibrium hypothesis (1930), which posits that selection should favor equal parental expenditure in offspring of both sexes. Thus, offspring, population sex ratios should be skewed toward the less expensive sex (Howe 1977). Cooper's hawks are strongly dimorphic such that females are about one-third larger than males at
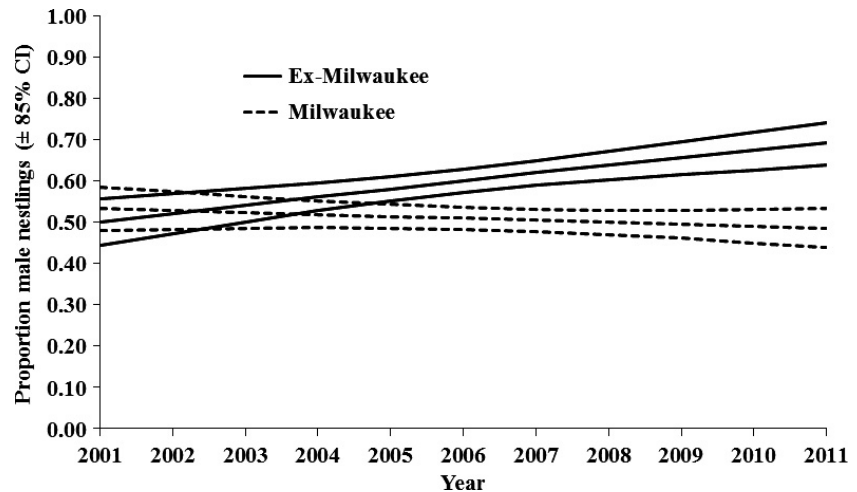
Figure 1. Model-predicted estimates of proportion male nestlings for breeding female Cooper's hawks at Milwaukee and ex-Milwaukee sites from 2001 to 2011, Wisconsin, USA.

Table 3. Generalized linear mixed-effects models predicting proportion male nestlings for second-year and after-second-year ("Age") breeding female Cooper's hawks at Milwaukee and ex-Milwaukee sites ("Site") for 2001–2011, Wisconsin, USA. K, number of model parameters; $Log_e(L)$, model log-likelihood; ΔAIC_c, relative differences in Akaike's information criteria with second-order bias correction for small sample sizes; and w, relative model weights. All models include parameters for intercept and "Year" random-effect variable. Site + Age model $AIC_c = 1028.1$.

Models	K	$Log_e(L)$	ΔAIC_c	w
Site + Age	4	−510.0	0.0	0.50
Site	3	−511.7	1.4	0.25
Site * Age	5	−509.7	1.5	0.24
Null	2	−517.3	10.6	0.00
Age	3	−516.7	11.5	0.00

fledging (Meng 1951). Therefore, males are assumed to be the cheaper sex because they apparently require fewer resources during development than do females (Howe 1977; Rosenfield et al. 1996a; and see below). These findings extend similar results from an earlier, temporally exclusive 16-year study (1980–1995) in the same ex-Milwaukee study area wherein nestling sex ratio was somewhat lower (54%) but significantly skewed toward males across generations (but see below; Rosenfield et al. 1996a).

The sex ratio of nestling Cooper's hawks produced by ASY females was near unity in Milwaukee, and thus, the costlier sex was being produced to a greater extent compared to the ex-Milwaukee population. Moreover, excluding 1 year (2001) when sex ratios were the same in both study sites, in 9 (90%) of all other 10 concurrent sets of years, and in accord with our prediction, ASY females in Milwaukee consistently produced more females compared to ASY females in ex-Milwaukee across years (Table 1).

Time, variation in productivity, samples sizes of nests, and lack of precision (or repeatability) in estimates of nestling sex ratios cannot explain the disparity in sex ratios of ASY females between the two study areas as this long-term investigation was conducted in concurrent years and the total number of study nests is virtually identical (Table 1). Further, between-year productivity is high (highest in North America) and virtually identical on both study areas, suggesting in part that interannual availability of food is not limiting on either study area (Rosenfield et al. 2007a,b, 2009; Stout and Rosenfield 2010). We too note that other factors, such as age of breeding males, gender-skewed natal dispersal, nesting phenology, and survivorship of nestlings, fledglings, and adults, are similar and/or identical between the two study sites where genetically similar breeding birds use similar prey (Bielefeldt et al. 1998; Rosenfield et al. 2007a,b, 2009, 2010; Stout et al. 2007; Stout and Rosenfield 2010; Sonsthagen et al. 2012, RNR and WES, unpubl.).

It is possible that breeding Cooper's hawks are able to produce more females in cities where, compared to rural areas, higher densities and greater biomass of avian prey species likely occur (Marzluff et al. 1998; Rutz et al. 2006; Cava et al. 2012), and which prey conditions could thus support a comparatively greater production of the costlier sex in urban settings. However, it is unknown whether such a scenario regarding sex ratios is generally true of cities in Wisconsin (or elsewhere) because to our knowledge, no data on sex ratios of offspring have been published for urban Cooper's hawks. However, our research here does not support such a scenario, as the nestling sex ratio was also skewed toward males (59% male of 309 total nestlings [and skewing toward males in 7 of 11 years]) for ASY females breeding in the city of Stevens Point within our ex-Milwaukee study site during 2001–2011. Moreover, a greater ability to produce females in

urban versus rural settings is not necessarily adaptive. Contrary to Milwaukee's growing population of breeding Cooper's hawks where comparatively higher production of female offspring may be adaptive, Stevens Point is a stable and likely territorially saturated population since probably the mid-1990s (Rosenfield et al. 1995, 2013; Stout and Rosenfield 2010; RNR, unpubl.). We note that we did find Cooper's hawks breeding in Stevens Point in 1980, the first year of study in the ex-Milwaukee area, and thus, we do not know when Cooper's hawks first colonized (or recolonized) this city (Bielefeldt et al. 1998).

It is possible that the difference in breeding population trajectories may explain the disparate sex ratios between ASY females on our study sites. And that producing a higher proportion of females in this socially monogamous species is individually adaptive in the growing population in Milwaukee (Trivers and Willard 1973; Dawkins 1989; Nomura 2002; Engen et al. 2003; Lenz et al. 2007). Implicit in this conjecture is that the offspring sex ratio manifests itself similarly in the adult sex ratio of potentially breeding Cooper's hawks, a metric that we do not have for sexually mature adults in our study areas, and that females are comparatively more of the limiting sex in Milwaukee versus ex-Milwaukee.

In support of our breeding population trajectory hypothesis, we note that in only of 1 (9%) of 11 years was the sex ratio of nestlings for ASY females in ex-Milwaukee skewed toward females (Table 1), compared to skewing toward females in 4 (25%) of 16 years in the earlier study in ex-Milwaukee (Rosenfield et al. 1996a) where selection perhaps favored a females' fitness with such skewing. As aforementioned, females are the limiting sex in a growing breeding population of Cooper's hawks if the population produced a preponderance of males. Thus, a greater production of females would be adaptive for a breeding female in the slowly growing population from 1980 through perhaps the early-to-mid-1990s when the nestling sex ratio was 54% males (we reiterate that we demonstrated that the ex-Milwaukee population exhibited stability in the early-to-mid-1990s to present [Rosenfield et al. 2013]), whereas since population stabilization accordingly fewer females were being produced as the nestling sex ratio was 59% males. Indeed, unpublished data on nestling sex ratios from 1996 through 1999, along with results presented here and in Rosenfield et al. (1996a), reveal that skewing toward female nestlings was detected in only five of 32 years in ex-Milwaukee (1980–2011), and four of those five times occurred when the breeding population was growing (Rosenfield et al. 1996a, 2013).

Seemingly in accord with some of our findings, Ferrer et al. (2009) documented a long-term sex ratio favoring male offspring in a declining population of the size-di-morphic (males smaller than females) Spanish imperial eagle in Spain, and an offspring sex ratio of unity when the population grew to high densities (such as in our Milwaukee Cooper's hawks). However, their results are not directly comparable to ours in part (and we reiterate that SY male Cooper's hawks were nonexistent to rare breeders on both our study sites, and thus, virtually all ASY females were mated to ASY males, [i.e., adult pairs]) because they found that adult–adult pairs of eagles in both high and low nesting densities produced a sex ratio of unity, whereas adult–adult pairs of hawks on our high-density ex-Milwaukee site produced a significantly skewed sex ratio toward males. That said, younger-aged breeders in their population produced, in both low and high nesting densities, a preponderance of males in apparent accord with our results. However, younger-aged eagles in their study were 1–4 years of age and some of these birds could have bred more than once and are thus may not be strictly analogous as a cohort to the SY, one-year-old inexperienced breeding Cooper's hawks in our study.

Birds can adjust the offspring sex ratio either at the egg-laying stage (primary sex ratio adjustment) or during the period of provisioning for the nestlings (secondary sex ratio adjustment). In ex-Milwaukee, we annually obtain clutch counts and in some years opportunistically obtain counts of fledglings about 25–56 days of age (Rosenfield et al. 1996a). But we do not routinely conduct either of these counts in Milwaukee, and thus, we cannot analyze comparatively the primary and fledgling sex ratios between study sites for the study years reported here (see Rosenfield et al. 1996a). Published and unpublished clutch count data from populations on both study sites suggest that Cooper's hawks typically lay 4–5 eggs on our study sites (which are among the highest average clutch counts in North America for this species; Rosenfield et al. 1996a, 2000; Rosenfield and Bielefeldt 2006; Stout 2009) and that egg loss from completion of clutch to brood counts on both sites (and elsewhere for Cooper's hawks in North America) is typically one egg (Rosenfield et al. 2007a,b, T.G. Driscoll and RNR [North Dakota], A.C. Stewart [British Columbia]).

We have also demonstrated across generations in ex-Milwaukee that it is the primary sex ratio that is adjusted toward males (Rosenfield et al. 1996a), and this was true for ex-Milwaukee within the study years of this investigation (59% males at fertilization, RNR, unpubl.). We reiterate that nesting phenology is identical between the two study sites, and given that average brood counts on both study sites are almost identical, consistently high across years (breeding generations), and among the highest documented for the species, we believe it highly unlikely that secondary sex ratio adjustment occurs in Milwaukee such that the loss of apparently just one egg/young between

the time of clutch completion and our examination of broods produces with such precision the disparate sex ratios we found between study sites. Indeed, secondary sex ratio adjustment would seem to be requisite by nesting females when gender of very small young is morphologically virtually indistinguishable to us (<ca. 12 days of age [Rosenfield et al. 1996a]). Moreover, our observations in both Milwaukee and ex-Milwaukee study sites, and those of other researchers elsewhere in North America, to study diet, diseases, and developmental behavior of nestling and fledgling Cooper's hawks of all ages (e.g., Bielefeldt et al. 1992; Cava et al. 2012; Nicewander and Rosenfield 2006; Rosenfield and Sobolik 2014; Stout et al. 2005, A.C. Stewart [British Columbia], T. G. Driscoll [North Dakota], RNR, unpubl. data), reveal no discernable differences in interactions by adults with individual young of known or unknown gender.

We too have neither observations of partially eaten carcasses of nestlings, nor observations of sudden partial brood loss of some young at Cooper's hawk nests in Wisconsin that would suggest secondary sex ratio adjustment. We previously reported that sex ratios are significantly skewed toward males at conception with no differential mortality between the sexes through the fledgling stage in ex-Milwaukee (Rosenfield et al. 1996a). We too do not believe that secondary sex ratio adjustment could occur in Milwaukee beyond the time at which we counted nestlings (about 18 days of age [see Methods]), as we have no observations, band recovery data, or reports from the urban public (with whom we frequently interact) that would imply higher, gender-biased mortality of nestlings, fledglings, or yearling Cooper's hawks in and around Milwaukee relative to elsewhere in Wisconsin (Stout et al. 2007; WES and RNR, personal observation). Moreover, parental facultative adjustment of brood sizes in raptors typically occurs under conditions of food stress (e.g., Bortolotti 1986; Wiebe and Bortolotti 1992; Franke et al. 2013), whereas Stout and Rosenfield (2010) demonstrated that food was not a limiting factor for the rapid population growth of breeding Cooper's hawks in Milwaukee. We therefore conclude that manipulation of sex ratios in Milwaukee Cooper's hawks occurs at conception and that this adjustment persists at least into the fledging stage.

We note that the ilk and temporal extent of parents tending (e.g., feeding, defending) fledglings and especially postfledglings, and if such parental care is biased toward sibling gender in any manner (a requisite for secondary sex ratio adjustment), are mostly unknown as the behaviors of fledgling and postfledgling Cooper's hawks are generally poorly studied (Nicewander and Rosenfield 2006; Rosenfield and Sobolik 2014). That said, nonindependent movements and group behaviors (including mimicking) by fledged sibling Cooper's hawks of both sexes (up to 6 weeks postfledging in our study areas [Nicewander and Rosenfield 2006; Rosenfield and Sobolik 2014) seem to be common throughout urban and rural habitats of Wisconsin [and elsewhere in North America, Nicewander and Rosenfield 2006;]). Group behavior dynamics in fledged siblings, with an apparent similar exposure of grouped young to parental interactions and possible mortality factors (Nicewander and Rosenfield 2006), may in part account for our inability to document gender-biased mortality of offspring.

In accord with our prediction, nestling sex ratios of yearling females were skewed consistently toward males across years in both study areas, that is, in 8 (73%) of 11 and in 6 (86%) of 7 years when SY females breeders were detected in Milwaukee and ex-Milwaukee, respectively (Table 1). ASY females are likely experienced breeders who can energetically incur the costs of producing females more so than SY hens (Newton 1979; Boal 2001). Brood sizes in yearling raptors, including both male and female Cooper's hawks, are typically smaller than that of ASY birds, which is also true in Milwaukee (Newton 1979; Moore and Henny 1984; Boal 2001; Stout and Rosenfield 2010; Rosenfield et al. 2013). Boal (2001) suggested that despite the putative difference in quality of male mates, who are responsible for providing the bulk of food for himself, his mate, and his nestlings, brood size in Cooper's hawks, and hence associated energy dynamics of raising young of different genders (sizes), may be more closely related to reproductive condition or physiology of the female.

The inexperience of breeding by yearling females likely results in a trade-off manifest in reduced production in SY females versus ASY females, with the cost of reproduction in SY females perhaps being aggravated by a trade-off in resource allocation to molt versus reproduction because SY female Cooper's hawks are molting to a greater extent than are ASY females (Boal 2001; Dawson et al. 2000, RNR and WES, personal observation). Under this scenario, we suggest that compared to ASY females, it would be more difficult for yearling females to produce the costlier sex.

To our knowledge, literature on the possible effects of maternal age on sex ratios in avian offspring is rare (Bennett and Owens 2002). Blank and Nolan (1983) demonstrated in the red-winged blackbird (*Agelaius phoeniceus*) that young mothers produced almost twice as many females (the smaller and thus cheaper sex) as males compared to older females. Ferrer et al. (2009) documented that nesting pairs of imperial Spanish eagles with younger male and female breeders also produced a preponderance of males (the cheaper sex).

We emphasize that the long-term nature of our research, which we reiterate is lacking in the majority of studies of sex ratios in birds, was essential to many of our conclusions and inferences about Cooper's hawk biology

including breeding population trajectories and life-history trade-offs pertinent to this paper (see Rosenfield et al. 2013), and also for tenable predictions, precision, and inferences about sex ratios in our populations. Indeed, with our annual sample sizes, a study of 10 years previously was necessary to document that sex ratios deviated significantly from unity in ex-Milwaukee (Rosenfield et al. 1996a), while our long-term results on sex ratios in Milwaukee herein provide insight into the aforementioned selective pressure of population growth which may have influenced the comparatively greater number of female nestlings detected almost exclusively in years of population increase across 32 years in ex-Milwaukee. Similarly, it necessarily took 32 years in our ex-Milwaukee site to tenably identify some age-related life-history trade-offs in breeding male Cooper's hawks (Rosenfield et al. 2013). Our study thus underscores the call by several researchers for long-term data stemming from investigations that account for various life histories pertinent to predictive sex ratios in birds. Lastly, future long-term studies that document both the heterogeneity of offspring and adult sex ratios in a given population will better be able to identify the putative adaptive value of skewed sex ratios in nestling birds.

Acknowledgments

Conflict of Interest

None declared.

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