

Does sex-biased hatching order in bald eagles vary with food resources?¹

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Abstract: In birds that exhibit sexual size dimorphism, hatching asynchrony, and siblicide, the probability of nestling mortality and the cost of rearing young may vary with different combinations of sex and hatching sequence. When food abundance varies spatially and temporally, parents may maximize their fitness by manipulating their primary sex ratio. We examined the sex and hatching order of nestling bald eagles (*Haliaeetus leucocephalus*) over 17 years on one lake and 5 years on another. The lakes are approximately the same size, but differ dramatically in eagle density and prey abundance. In years when the number of eaglets fledged was high (suggesting higher food abundance), there was a significant bias in the first-hatched chick toward the larger sex (females), and broods with a first-hatched male and a second-hatched female (MF broods) were under-represented. In years with lower productivity, and on the lake with lower food abundance, there was a male-bias in the population sex ratio of nestlings and the first-hatched egg. Variation in sex ratio and hatching order may relate to the probability of siblicide associated with MF broods, or the differential cost of raising the sexes.

Keywords: bald eagle, facultative manipulation, sex ratio, hatching order, *Haliaeetus leucocephalus*.

Résumé: Chez les espèces d'oiseau ayant un dimorphisme sexuel marqué, la non-synchronisation de l'éclosion des oeufs, les cas de fratricide, la probabilité de mortalité au nid et les coûts associés à l'élevage des jeunes peuvent varier selon la combinaison des sexes et la séquence dans laquelle les sexes apparaissent lors de l'éclosion. Lorsque l'abondance de nourriture varie spatialement et temporellement, les parents peuvent maximiser leur succès reproducteur en manipulant le rapport des sexes de leurs rejetons. Nous avons examiné, chez les pygargues à tête blanche (*Haliaeetus leucocephalus*), le sexe des aiglons et la séquence dans laquelle les sexes apparaissent lors de l'éclosion des oeufs. L'étude s'est déroulée pendant 17 ans sur un lac et 5 ans sur un autre lac, ces derniers ayant à peu près la même taille, mais différant fortement en ce qui concerne la densité des aigles et l'abondance des proies. Durant les années où le nombre d'aiglons parvenant à maturité est élevé (suggérant ainsi une certaine abondance de nourriture), il y a un biais significatif envers la production d'une femelle de plus grande dimension chez les aigles) pour le premier oeuf. Les nichées avec un mâle pondu en premier lieu et une femelle en second lieu sont sous-représentées. Lors des années avec production faible d'aiglons, ainsi qu'au lac ayant une faible abondance de nourriture, il y a un biais envers les mâles dans les nichées, et plus particulièrement en ce qui concerne le premier oeuf pondu. Les variations dans le rapport des sexes et dans la séquence dans laquelle les sexes apparaissent lors de l'éclosion peuvent être reliées à une probabilité de fratricide plus élevée dans les nichées comportant les deux sexes, ou au coût différentiel d'élevage des sexes.

Mots-clés: pygargue à tête blanche, manipulation facultative, rapport des sexes, ordre d'éclosion, *Haliaeetus leucocephalus*.

Introduction

Most examinations of avian sex ratios at hatching or fledging have not shown significant differences from unity (Charnov, 1982; Clutton-Brock, 1986). However, despite methodological difficulties associated with detecting sex ratio variation (Charnov, 1982; Gowaty, 1991), recent studies have shown that the proportion of male and female nestlings varies with such diverse factors as maternal age (Blank & Nolan, 1983) helpers at the nest (Gowaty & Lennartz, 1985), attributes of the clutch (Ryder, 1983; Bortolotti, 1986a), attractiveness of mates (Burley, 1986), and laying date (Dijkstra, Daan & Buker, 1990; Zijlstra, Daan & Bruinenberg-Rinsma, 1992). In many such studies, population sex ratios are pooled among years or have a limited perspective on variation among years or populations. Consequently, it is often not possible to determine to

what degree biased sex ratios are genotypically fixed, or whether parents may choose the gender of their young in response to different ecological conditions.

Parents may manipulate offspring sex ratios conditional on circumstances at the time of breeding (Myers, 1978; Frank, 1990; Gowaty, 1991). Potential relationships between parental condition, environmental resources and the differential cost of rearing males and females for species that are sexually dimorphic in size have been of particular interest. The larger sex is more expensive to raise (Fiala & Congdon, 1983; Teather, 1987; Anderson *et al.*, 1993b). Parents may thus manipulate the number of sons and daughters in a brood to optimize the number and quality of offspring, and hence presumably maximize fitness (Williams, 1979). Various studies have suggested that the non-random distribution of the sexes in their samples (not associated with nestling mortality, Clutton-Brock, 1985) may be linked to maternal body condition, although that

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variable, or food supply, was not quantified (Fiala, 1981; Ankney, 1982; Ryder, 1983). Meathrel & Ryder (1987) found that ring-billed gulls (*Larus delawarensis*) produced more females (the cheaper sex) at hatching when mothers were in poor condition. Similarly, Wiebe & Bortolotti (1992) found a preponderance of the cheaper sex, in this case males, at hatching in American kestrels (*Falco sparverius*) in years of poor food availability, and when both male and female parents were in poor physical condition.

In this study we examine how nestling sex ratios of bald eagles (*Haliaeetus leucocephalus*) may vary with food resources. This species typically lays two eggs that hatch asynchronously (Gerrard & Bortolotti, 1988). Previously, Bortolotti (1986a) found that within a clutch, first-hatched eggs tended to produce females while second-hatched eggs usually produced males. He interpreted this finding as an adaptive strategy. Second-hatched eaglets may suffer from brood reduction, depressed growth, and delayed fledging, largely from the size differences created by hatching asynchrony (Bortolotti, 1984a; 1986a,b). The size differences between siblings in the critical early period are exacerbated in MF (first-hatched male, second-hatched female) broods. Parents may thus avoid that brood type to maximize the number or condition of fledglings, and ultimately the number of descendents. Bortolotti (1986a) was not able to determine whether sex ratios and hatching sequence were fixed, or a facultative response. Parents may manipulate hatching order and sex, *i.e.*, the competitive asymmetries of siblings, in response to the availability of resources (Anderson *et al.*, 1993a; Wiebe & Bortolotti, 1994; Stoleson & Beissinger, 1995). We investigate this possibility by examining temporal and spatial variation in sex ratios of nestling bald eagles. We use annual variation in population productivity as an index of resource availability (see below), and compare two lakes that are known to differ in prey abundance.

Study area

We determined the sex and hatching order of nestling bald eagles on Besnard (55° 20' N, 106° 00' W) and Nemeiben (55° 20' N, 105° 25' W) lakes, Saskatchewan, Canada. These lakes are approximately 40 km apart, similar in size, and both lie in the northern coniferous forest near the southern boundary of the Precambrian shield (see Dzus & Gerrard, 1993 for details). The number of breeding and non-breeding bald eagles on Besnard Lake is approximately three times that on Nemeiben Lake (Dzus & Gerrard, 1989).

A central premise behind our discussion of Besnard and Nemeiben lakes is that they differ in food abundance. Fish represent 99% of prey deliveries to eagle nests on Besnard Lake, with cisco (*Coregonus artedii*) and white sucker (*Catostomus commersonii*) being the two most common prey species (Gerrard & Bortolotti, 1988). Water chemistry and the biomass of benthic invertebrates, as well as fisheries data (commercial and angling), suggest that food was substantially more abundant in Besnard Lake than in Nemeiben Lake (Chen, 1974; Koshinsky, 1964). A difference in prey abundance was confirmed by test-netting (Dzus &

Gerrard, 1993); catch per unit effort of cisco was significantly lower on Nemeiben Lake relative to Besnard Lake. Eaglet growth was also slower on Nemeiben than Besnard Lake, further suggesting differences in habitat quality (Dzus, 1988; Bortolotti, 1989). Food abundance, as evidenced from various levels of the food chain (*i.e.*, benthic invertebrate and fish abundance), was the only ecological variable measured that differed between these two lakes (Dzus & Gerrard, 1993).

Methods

POPULATION LEVEL ANALYSES OF SEX RATIO

Sex ratio information for 1980-1982 on Besnard Lake is the same as Bortolotti (1986a). In 1987, the hatching order and sex of eaglets on Nemeiben Lake were determined while studying eaglet growth (Dzus, 1988). Data for all other years were collected by the authors during single nest visits to band the young when they were 45-60 days old. Hatching order was inferred from the length of the eighth primary (Bortolotti, 1984b; 1986a). For all nests with known hatching order and individually marked young ($n = 56$ on Besnard Lake, $n = 3$ on Nemeiben Lake) that were visited repeatedly from hatching to past 40-45 days, there were no changes in feather length that would cause us to err in assigning hatching order.

Bald eagles show marked sexual size dimorphism as adults (Bortolotti, 1984c) and nestlings (Bortolotti, 1984b). For a subsample of birds that were repeatedly measured ($n = 56$ on Besnard Lake, $n = 3$ on Nemeiben Lake), we know that eaglets are near full size for > 30 days prior to fledging (Bortolotti, 1984a; Dzus, 1988). At > 40 days after hatching there is no overlap in bill depth or length of the foot pad (Bortolotti, 1984b). Hence, eaglets in this study were accurately sexed using morphometric measurements. In a discussion of Bortolotti's (1986a) results, Drummond *et al.* (1991) expressed concern over the reliability of the methods used for sexing and ageing eaglets because young at some nests were measured when < 40 days. To ensure eaglets in our sample are old enough to be sexed correctly, young at 4 nests (3% of our sample) that had an estimated age of < 40 days were excluded from our analyses. Another concern regarding identification of the sexes is that birds may be misclassified as "males" in years or areas of low food abundance due to slow growth, or vice versa for "females" when food is more abundant. While it is true that growth rate and the mass of prey delivered were correlated, there was no correlation between asymptotic size and mass of prey delivered to the nest (Bortolotti, 1989). Since we measured birds near asymptotic size, there should be no misclassification due to differences in growth rate. Thus, we feel confident in our ability to accurately determine the sex and hatching order of young eagles in our sample.

ANNUAL PRODUCTIVITY

Assessment of annual reproductive success of a raptor population is usually represented by the mean number of fledged young per territorial pair or per occupied territory. Such an approach includes failure of territorial pairs to lay eggs, which is the most frequent cause of depressed productivity in many birds of prey (Brown, 1974; Postupalsky,

1974; Steenhof, 1987). Breeding areas (defined as one or more nests within the range of a mated pair) were checked annually and a productivity index was derived from the number of young fledged per occupied breeding area (OBA, one which is consistently used in a given year by a pair of adults) (Gerrard *et al.*, 1983; 1992). Because productivity of bald eagles, and other birds, is strongly and positively associated with food abundance (Gerrard & Bortolotti, 1988; Hansen, 1987; Martin, 1987; Newton, 1979; Stalmaster, 1987; Whitfield & Gerrard, 1985), we use the number of young fledged/OBA as an indicator of available food resources. The mean productivity on Besnard Lake from 1968-1994 was 1.12 young/OBA (Table I). We will refer to years on Besnard Lake with a value of young/OBA < 1.12 as "poor" and years with young/OBA \geq 1.12 as "good".

TABLE I. Number of bald eagle broods of different combinations of sex and hatching sequence on Besnard Lake, Saskatchewan (1975-1994)

| Year | Productivity ¹ | Two-chick broods (C1/C2) ² | | | | Single-chick broods | |
|---------------------------|---------------------------|---------------------------------------|-----------|-----|-----|---------------------|----|
| | | M/M | M/F | F/M | F/F | M | F |
| | | 1975 | 0.63-0.83 | 2 | 0 | 0 | 1 |
| 1976 | 1.14 | 1 | 0 | 5 | 1 | . | . |
| 1980 | 1.22 | 3 | 0 | 3 | 1 | 2 | 5 |
| 1981 | 1.19 | 3 | 0 | 3 | 4 | 2 | 1 |
| 1982 | 1.38 | 4 | 1 | 3 | 2 | 0 | 2 |
| 1983 | 1.56 | 1 | 0 | 2 | 1 | 1 | 2 |
| 1984 | 1.35 | 3 | 1 | 1 | 2 | 1 | 3 |
| 1985 | 0.95 | 2 | 0 | 2 | 1 | 0 | 1 |
| 1986 | 0.75-0.86 | 2 | 0 | 1 | 1 | 1 | 4 |
| 1987 | 1.11 | 2 | 0 | 3 | 1 | 3 | 1 |
| 1988 | 1.22 | 0 | 3 | 2 | 3 | 0 | 3 |
| 1989 | 1.23-1.28 | 2 | 1 | 2 | 1 | 1 | 4 |
| 1990 | 0.81 | 3 | 4 | 0 | 0 | 0 | 5 |
| 1991 | 0.92-0.96 | 1 | 3 | 1 | 2 | 1 | 0 |
| 1992 | 1.17 | 1 | 0 | 4 | 2 | 0 | 2 |
| 1993 | 1.14 | 1 | 0 | 3 | 0 | 2 | 1 |
| 1994 | 1.04 | 4 | 2 | 3 | 0 | 3 | 2 |
| Total observed | | 35 | 15 | 38 | 23 | 17 | 36 |
| "Good" years ³ | | 19 | 6 | 28 | 17 | 9 | 23 |
| "Poor" years | | 16 | 9 | 10 | 6 | 8 | 13 |

¹ Young per occupied breeding area.

² C1 indicates the first-hatched egg; C2, the second-hatched egg.

³ "Good" years have young/OBA \geq 1.12; "Poor" years have young/OBA < 1.12.

The number of young/OBA is useful as a measure of annual reproductive success within a population, but should not be used for comparisons between populations as it does not account for differences in density of breeding areas. Productivity indices on Besnard Lake were based on 18 to 29 OBA's/year, whereas Nemeiben Lake supported only 6 to 11 OBA/year. Thus, the mean productivity level from Besnard Lake was not used to classify years on Nemeiben Lake as good or poor. Productivity on Nemeiben Lake was considered poor in all years due to the low density of eagles (Dzus & Gerrard, 1989; 1993).

ASSESSMENT OF THE EFFECTS OF DIFFERENT HATCHING ORDERS

Differences in growth dynamics of male and female bald eagles may influence the probability of siblicide (as suggested by Bortolotti, 1986a) or mass of nestlings near

fledging. Nestling mass was recorded in most years. If the amount of food available to the nestlings is monopolized by the more dominant eaglet, greater differences in mass between siblings may result. Thus, examination of the magnitude of difference in mass of eaglets within a nest gives some information about the amount of food available to the nestlings.

Evidence for the potential of one eaglet to monopolize food items is found by assessing the amount of food an individual can consume in one meal, and presenting such data in light of average prey size. Twelve eagles, captured as part of a reintroduction program to Pennsylvania, were fed one evening and the next morning to determine the approximate maximum capacity of food they could consume in one meal. Eaglets ranging in age from 22 to 38 days (\bar{x} = 31, SD = 4, n = 12) were fed until their crop was fully distended. The eaglets were weighed immediately before and after feeding to determine the mass of each meal.

Results

SINGLE-CHICK NESTS

Fledging one young may be the result of laying one egg, hatching only one egg (infertility) or nestling mortality. One-egg clutches are rare (1 of 34 known-size clutches on Besnard Lake, Gerrard & Bortolotti, 1988). Of 11 known two-egg clutches that resulted in only one chick fledging, 7 were due to hatching failure and 4 to brood reduction. The number of known-sex, single-chick nests per year on Besnard Lake was similar in good (\bar{x} = 3.6, SD = 1.6, n = 9) and poor (\bar{x} = 3.5, SD = 2.0, n = 6) years.

The sex ratio (M/F) of single-chick nests on Besnard Lake did not differ between good and poor years (G = 0.26, df = 1, P = 0.61, Table I), and did not differ from unity in poor years (M/F = 0.62, G = 0.61, df = 1, P = 0.44). The sex ratio tended to be female biased in single-chick nests in good years (M/F = 0.39, G = 3.25, df = 1, P = 0.07). Five of 9 nests on Nemeiben Lake that fledged one young produced females.

SEX RATIO OF TWO-CHICK NESTS

The sex ratio of nestlings near fledging from two-chick nests on Besnard Lake was not significantly different from unity for all years combined (M/F = 1.24, G = 1.30, n = 111 nests, P = 0.25), nor in good years (M/F = 1.06, G = 0.06, n = 70 nests, P = 0.81) (Table I). The sex ratio was skewed toward males on Besnard Lake in poor years (M/F = 1.65, n = 41 nests), but this was not significant (G = 2.50, P = 0.11, Table I). A significant male bias existed for two-chick nests on Nemeiben Lake for all years (M/F = 3.8, G = 4.56, n = 12 nests, P = 0.03, Table II).

Consistent with Bortolotti's (1986a) results from a smaller data set, we found that sex was not independent of hatching order; however, the direction of the bias was dependent on type of year for Besnard Lake. For 70 nests in good years females represented 64% of first-hatched eggs and 33% of second-hatched eggs (G = 14.1, P = 0.001). In poor years, females comprised 39% and 37% of first- and second-hatched eggs respectively (G = 0.05, n = 41 nests, P = 0.82).

TABLE II. Number of bald eagle broods of different combinations of sex and hatching sequence on Nemeiben Lake, Saskatchewan

| Year | Productivity | Brood type (C1/C2) ¹ | | | |
|----------------|--------------|---------------------------------|-----|-----|-----|
| | | M/M | M/F | F/M | F/F |
| 1986 | > 0.9 | 1 | 1 | 0 | 0 |
| 1987 | > 0.9 | 0 | 2 | 1 | 0 |
| 1992 | 1.43 | 3 | 0 | 0 | 0 |
| 1993 | 1.43 | 2 | 0 | 1 | 0 |
| 1994 | 0.64 | 1 | 0 | 0 | 0 |
| Total observed | | 7 | 3 | 2 | 0 |

¹ C1 indicates the first-hatched egg; C2, the second-hatched egg.

Using Bonferoni confidence intervals we found that broods of male-first/female-second (MF) were found significantly less often than expected for all years combined on Besnard Lake (14%, $n = 111$ nests, $P < 0.01$) and in good years (9%, $n = 70$ nests, $P < 0.01$) (Table I). FM broods were found more often than expected in good years on Besnard Lake (40%, $n = 70$ nests, $P = 0.04$). MM broods were most common in poor years on Besnard Lake (39%, $n = 41$ nests, $P > 0.1$, Table I) and on Nemeiben Lake (years combined, 58%, $n = 12$ nests, $P < 0.08$, Table II).

CONSEQUENCES OF SEX AND HATCHING ORDER

The degree to which one nestling can monopolize food resources has important ramifications on sibling competition and siblicide (Mock, 1984). Monopolization of entire food items may result in subordinate chicks consuming less food than their dominant sibling and potentially affecting the probability of siblicide, body condition, and post-fledging survival. Prey deliveries to bald eagle nests were relatively infrequent events. The mean rate of prey delivery per nest ranged from 0.23 - 0.36 prey/hour, and the mean prey size among nests varied from 288 to 760 g ($\bar{x} = 461$ g, $SD = 150$, $n = 7$ nests) (see Bortolotti, 1989 for details). The average meal size for the captive eaglets we fed was 354 g ($SD = 75.5$, $n = 21$, three birds were excluded because their crops were not fully distended at the end of feeding). Under natural conditions, one eaglet (age > 30 days) typically feeds from a prey carcass at a time, and many fish are consumed entirely by one nestling (Bortolotti, unpubl. data).

In times of food shortage, the effects of dominance of the first-hatched chick may increase. We investigated this possibility by examining the relative difference in mass between siblings in good *versus* poor years on Besnard Lake, and for Nemeiben *versus* Besnard lakes. For MM and FM broods, the relative difference in mass between siblings appeared to be greater in poor than good years on Besnard Lake (Figure 1). Consistent with that observation, the values for the poor years on Besnard Lake resemble those for the poorer habitat of Nemeiben Lake (Figure 1). The consequences of dominance may be particularly severe in FM broods where sex and age may act additively in determining the size difference between siblings.

Discussion

In this paper we have demonstrated a bias in the sex and hatching order of two-chick nests of bald eagles. Females (the larger sex) were more likely to hatch first in years when the number of eaglets fledged was high

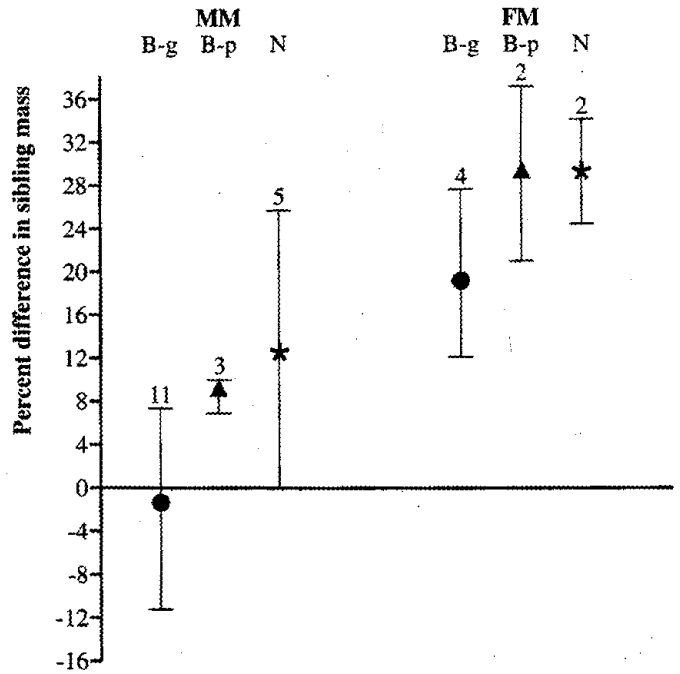


FIGURE 1. Difference in mass between first-hatched and second-hatched chicks in broods of different hatch orders on Besnard (B) and Nemeiben (N) lakes. "g" represents good years on Besnard Lake when productivity exceeded 1.12 young fledged per occupied breeding area; "p" represents poor years where productivity was less than 1.12. Symbols show the mean difference, bars are the range of values, and sample size is above each range. MM and FM refer to hatch order combinations of male and female nestlings.

(suggesting greater food abundance). Conversely, a male bias existed in years with poorer productivity and on a lake with lower food abundance. We focus our discussion of temporal and spatial variation in nestling sex ratios on two-chick broods. In most cases we were unable to determine if single chicks were the result of laying one egg, siblicide, or hatching problems. It seems unlikely that this could bias our results. Even if all single-chick nests were the result of siblicide, it would not account for the lack of MF nests in good years on Besnard Lake because there was a female bias in single-chick broods. One would expect a male bias if MF broods were being produced in equal proportion to other hatching orders and if the older chick dominates its younger sibling (Meyburg, 1974; Edwards & Collopy, 1983; Bortolotti, 1986a).

Bortolotti (1986a) suggested that MF broods were avoided to maximize the number of young that survive to fledge. Those results were based on 5 years of data, four of which were subsequently classified by us as good years. It was unknown in the original paper whether the sex bias was fixed, or if eagles could vary the probability of producing each sex in relation to hatching order. In a review of Bortolotti's (1986a) results, Gowaty (1991) hypothesized that "the failure of some populations of bald eagles to produce expected frequencies of MF broods is a regular facultative response to relatively low food abundance". While our results do suggest a facultative response, they are in the opposite direction of that predicted by Gowaty (1991). Analysis of long-term data from Besnard Lake and a comparison with the poorer habitat of Nemeiben Lake, are

consistent with Bortolotti's (1986a) original conclusions.

Under Bortolotti's (1986a) hypothesis, MF broods are the most likely, and FM broods the least likely, to experience siblicide. Hence, there should be a facultative response to produce MF broods under low, and FM broods under high, food abundance. If food is insufficient to produce two nestlings in good condition, the parents should produce MF broods, if there is a higher probability that the first-hatched male will kill the second-hatched female. It may be better to produce one surviving (M) nestling in good condition, than two (e.g., in a FM brood) in poorer condition. The second egg or offspring may serve as insurance against hatching failure or early nestling death (Meyburg, 1974; Mock & Forbes, 1995). In this way, the number of young surviving to fledging is maximized.

Survival to fledging is unlikely to be the only fitness variable of consequence to sibling competition in eagles. Birds in their first year of life typically incur food stress and associated mortality (Newton, Marquis & Village, 1983; Stalmaster & Gessaman, 1984; Martin, 1987), and thus any depression in condition that is attributable to being a subordinate nestling will likely exacerbate problems encountered after independence (Spear & Nur, 1994). Second-hatched bald eagles have suppressed growth rates and fledge at a later age (Bortolotti, 1984a; 1989). The consequences of condition to post-fledging survival are likely to be particularly important for top predators like bald eagles, given that predation is unlikely to be a significant cause of mortality (Stalmaster & Gessaman, 1984).

Our results are also consistent with the hypothesis that the differential cost of rearing the sexes may influence parental decisions to manipulate sex ratios (Meyers, 1978). Female bald eagles are heavier and structurally larger than males (Bortolotti, 1984a,b,c). In sexually dimorphic species, the larger sex requires more food and hence imparts greater cost of rearing to the parents (Teather, 1987; Wiebe & Bortolotti, 1992; Anderson *et al.*, 1993b). The cheapest brood for eagles, MM, predominates in poor years at Besnard Lake and all years in the poorer habitat of Nemeiben Lake. The higher cost of all other brood types would enhance the likelihood of brood reduction or fledging young in poor condition.

Given that resources vary from year to year, and among habitats, it is imperative that females be able to predict food abundance for their young prior to egg laying if facultative manipulation of sex ratio is to evolve. Bald eagles arrive on the breeding grounds in the boreal forest of northern Saskatchewan in late March or early April well before the lake ice thaws (Gerrard & Bortolotti, 1988). Eagles must survive and produce eggs on endogenous reserves, carrion, or fish captured in streams or other areas of open water. The importance of fish in our area is suggested by the fact that reproductive success is higher in breeding areas located close to streams (Gerrard *et al.*, 1975) and the breeding density of eagles is correlated with commercial fisheries catch (Whitfield & Gerrard, 1985). The abundance of fish in spring may provide a reliable cue about subsequent food abundance during the brood-rearing period. Fish, such as suckers and northern pike (*Esox lucius*), that are important in the eagle's summer diet (Gerrard & Bortolotti, 1988) are

early spring spawners (Scott & Crossman, 1973). We have observed eagles congregating at streams and feeding on spawning fish. In addition, fish show definite cohort effects resulting in annual variation in abundance of prey for eagles (Chen, 1974; Koonce *et al.*, 1977). Therefore, the numbers of fish moving into the streams to spawn in spring may provide female eagles with the information needed to adjust sex ratios facultatively. Alternatively, the proximate cue for adjusting sex ratios may involve a bird's physical condition. Weather, and a host of other factors, also potentially affect availability of food and the energetic cost of maintenance, and hence determine the body reserves of pre-laying birds. Condition at the time of laying may be indicative of the ability of parents to subsequently provide for their young.

It is clear that sex ratio variation may have to be examined over a period of years if temporal variation in resources is expected, particularly for species that are sexually dimorphic in size (Meathrel & Ryder, 1987; Wiebe & Bortolotti, 1992; this study). The long-term data set analyzed here contributed a much broader understanding of eagle sex ratios than previous work (Bortolotti, 1986a); however, we are unable to differentiate between the cost of rearing hypothesis (Meyers, 1978) and Bortolotti's (1986a) hypothesis relating to probability of siblicide. The two hypotheses are not incompatible and both may explain benefits to parents. Future challenges in avian research involve not only documenting patterns of sex ratio in relation to environmental and social parameters, but also identifying potential mechanisms (Krackow, 1995) by which parents can influence the sex of their eggs.

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