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Sex Ratio among Fledglings of Blakiston's Fish Owls.

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The sex ratio of 137 fledglings, from 91 broods, of Blakiston's Fish Owls *Ketupa blakistoni* raised in Hokkaido, Japan, over the period 1985-99, was analyzed. The sex ratio of fledglings was significantly male-biased (81 males and 56 females; $P = 0.04$) although no significant difference was detected when it was compared to the expected value (50% males) for each brood size (one or two). Logistic regression analysis did not reveal any significant effects of the locations of breeding sites on the sex ratio of fledglings. Young male owls suffered higher mortality than females. It is suggested that the male-biased sex ratio at fledging is moderated toward parity during the post-fledging stage. Factors considered to attribute to the skewed sex ratio at fledging of Blakiston's Fish Owl were: sexual dimorphism, local resource competition (LRC) and demographic stochasticity resulting from the small population size. Sexual dimorphism suggested that the male-biased sex ratio of fledglings was qualitatively consistent with Fisher's theory. However, sexual dimorphism alone does not quantitatively explain the male-biased sex ratio in Blakiston's Fish Owls. Differential natal philopatry between the sexes suggests that LRC is occurring. The small population size of the Hokkaido population is considered to be the most alarming factor from a conservation point of view.

Key Words: Blakiston's Fish Owl, *Ketupa blakistoni*, Local resource competition, Sex ratio, Sexual dimorphism, Small population size

Recently, facultative sex ratio manipulation, due to differential parental sex allocation in birds, has been studied intensively at the level of the individual family (reviews in Sheldon 1997; Eguchi 1999; Nishiumi 1999). Meanwhile, changing patterns in the avian sex ratio at the population level have not received much attention recently despite the development of molecular genetic techniques that allow swift sex identification from various DNA samples.

The first notable review of the avian sex ratio at the population level was presented by Clutton-Brock (1986). He concluded that the evidence for differential mortality between hatching and fledging was stronger and more consistent than the evidence of sex ratio variation at hatching. Furthermore, a female-biased sex ratio among the nestlings of some raptors exhibiting sexual dimorphism was interpreted as evidence of male-biased mortality caused by the larger females' superiority in competition for food brought by the parents (see Newton 1979). Thereafter, more male-biased and fewer female-biased sex ratios among fledglings were reported in many sexually dimorphic raptor species (reviews in Eguchi 1999;

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Nishiumi 1999).

The energetic costs of rearing offspring have been widely presumed to differ between sons and daughters due to sexual dimorphism; the male-biased sex ratio of fledgling raptors is consistent with Fisher's equilibrium sex ratio theory (Fisher 1930). Weatherhead & Teather (1991), however, concluded that the biased sex ratio among fledglings before independence was better explained as a nonadaptive consequence of greater vulnerability to starvation in the larger sex.

Modifications of Fisher's assumption, reveal that it is adaptive to bias investment in offspring in favor of one or other sex under some circumstances (Ellegren *et al.* 1996). The local resource competition (LRC) hypothesis, which was defined in relation to a prosimian primate (Clark 1978), was adapted to birds by Gowaty (1993). This hypothesis suggests that, when critical resources for breeding are scarce and when offspring of different sexes have different dispersal tendencies (one stays while the other leaves), the costs to parents of producing the non-dispersing sex can be high. In fact, sex ratios of nestlings or fledglings biased in favour of the dispersing sex occur in some species of passerines and anseriforms although evidence from raptors does not support the hypothesis (Gowaty 1993).

Other important investigations of raptors have demonstrated biased sex allocation with respect to laying date (Dijkstra *et al.* 1990; Olsen & Cockburn 1991; Zijlstra *et al.* 1992; Daan *et al.* 1996), laying sequences within broods (Bortolotti 1986; Edwards *et al.* 1988; Bednarz & Hayden 1991; Leroux & Bretagnolle 1996) and maternal condition (Wiebe & Bortolotti 1992). Although these studies explained adaptive sex ratio manipulation at the individual level, they also reported overall male-biased sex ratios of nestlings or fledglings at the population level, with the except of one study (Dijkstra *et al.* 1990). Consequently, parental manipulation of offspring sex ratio must affect sex ratios at the population level.

Furthermore, largely as a result of human activities, small population sizes have to be considered when sex ratios in populations are examined. As populations become smaller, demographic stochasticity increases, and the sex ratio is more likely to become skewed (Durant 1998). Skewed sex ratios are a powerful indicator of impending extinction (Durant 1998), because an imbalanced sex ratio reduces effective population size (Caughley 1994).

Blakiston's Fish Owl *Ketupa blakistoni*, one of the largest owls in the world, is monogamous, sexually dimorphic, and has a limited clutch size of just one or two eggs. In Japan, the species was widely distributed throughout Hokkaido until the 1950s (Hayashi 1999), destruction of its habitat has caused its population to decline. It now occurs only in very restricted areas of eastern and central Hokkaido and the present population is estimated at no more than 30 breeding pairs (Takenaka 1998). It was listed as a "Critically Endangered" species in Japan's Red Data list (Environment Agency, Japan 1998).

A long-term field study revealed that female offspring stayed longer than males in the natal area (Hayashi 1997). If the sex ratio of young is skewed in this small population, then a shortage of encounters with receptive mates increase the risk of extinction.

In this paper, we present data on the sex ratio among fledgling Blakiston's Fish Owls in Hokkaido, Japan, over the period 1985-1999, and examine the factors influencing it.

MATERIALS AND METHODS

1) Study population and general fieldwork

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LS AND METHODS

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Our data on the Hokkaido population of Blakiston's Fish Owl has come from the banding records of the Blakiston's Fish Owl conservation programs over the period 1985-1999. These programs have been undertaken by a group of professionals organized by the Environment Agency, Japan since 1984. The principal activities of these programs consist of three elements: artificial provision of their staple food of fish in some habitats in order to improve the food-supply, provision of nest boxes to supply nest sites, and ringing fledglings so as to be able to identify individuals. In the beginning, banding only took place in a small number of territories in the area of certain artificial feeding sites. As conservation efforts have increased, the number of study sites has also increased and most of the breeding sites in Hokkaido are now thought to have been detected. Accordingly, the number of fledglings ringed has increased as a direct result of increased efforts by researchers to locate active nests.

Most known nest sites, involving either nest boxes or natural cavities, were checked at least once during each breeding season. At active nest sites, the young were ringed, weighed and measured shortly before or after fledging, when they were about 45-60 days-old (in this paper they are referred to as fledglings). A specimen of skin or blood was taken for sex determination.

Frequent visits to nests were avoided so as not to disturb the owls' breeding activities. As a result, the primary sex ratio could not be determined because many of the nests were visited only when the fledglings were banded.

A total of 141 fledglings were banded in 23 breeding territories during the period 1985-1999. The breeding sites were located in central and eastern parts of Hokkaido. Twelve were on the Shiretoko Peninsula, four on the Nemuro Peninsula and nearby, two were in the vicinity of Lake Mashuh, four were in the Tokachi district and one was in central Hokkaido. These breeding sites were grouped into local assemblies based on distances between neighboring territories (Takenaka 1998). These groups were used to compare the sex ratio of fledglings (see RESULTS).

To measure the body weights of adult owls, a scale was set as a perch in an artificial fish-supplied pond in one breeding site. The owls' weights were read using binoculars. Data were obtained from the resident birds continuously during 1994 and supplemented with measurements taken when they were captured for other studies.

2) Sexing techniques

Chromosomal sexing

To determine the sex of fledglings, we used chromosomal analysis (1985-1996). Once chromosome preparations were obtained from cultured fibroblasts of skin, the sexes were determined by karyotypes because there are remarkable morphological differences of sex-chromosomes in Blakiston's Fish Owl (Sasaki *et al.* 1994). The reliability of this chromosomal method was ensured by use of the C-banding method (Rebholz *et al.* 1993).

Molecular sexing

With the advance of molecular genetic markers for determining sex, it has become possible to identify sexes using minute samples of blood relying on the polymerase chain reaction (PCR) amplification. Since 1997, a 50-μl blood sample was obtained from the brachial vein that runs along the humerus of all fledglings, by licensed veterinarians. Blood samples were stored in 500-μl STE buffer (NaCl 100 mM, Tris-HCl 10 mM, and 1mM EDTA, pH 8.0) which was kept cool (approximately 4℃) in the field. Once the samples were brought indoors, 25-

μl 10% SDS and 25-μl proteinase K (50 mg /ml) were added and the samples were incubated at 37℃ overnight for four days. DNA was extracted three or four times with a mixture of 500-μl of phenol and 250-μl of 24:1 chloroform : isoamyl alcohol. Subsequently, DNA was precipitated using ethanol, dried in air, and dissolved in TE (10 mM Tris-HCl and 1mM EDTA, pH 7.5).

Molecular sexing relies on polymerase chain reaction (PCR) amplification of the sex-linked CHD-W and CHD-Z genes, which map to the avian W and Z chromosomes, respectively (Ellegren 1996; Griffiths *et al.* 1996). All reactions were performed in 20-μl volumes containing 50 mM KCl, 1.5 mM $MgCl_2$, 10 mM Tris-HCl (pH 8.3), 0.2 mM each dNTP, 20 pM each primer (P2 and P3; Griffiths *et al.* 1996) and 0.15 units of *Taq* DNA polymerase (TaKaRa). Approximately 20 ng of genomic DNA was used for each reaction. After denaturation at 94℃ for 1 min, PCR amplifications were performed for 40 cycles of 94℃ for 30 sec, 55℃ for 15 sec, 72℃ for 15 sec with a finish of 72℃ for 5 minutes.

PCR products were restricted with two types of restriction enzymes: *Hae III* and *Mae II*, to cut the CHD-Z and the CHD-W fragments respectively. The fragments were separated in 4% agarose gels and detected using ethidium bromide staining. Females were characterized by displaying a CHD-W specific fragment with *Mae II* treatments, while males showed a CHD-Z fragment with *Hae III* treatments.

3) Data analyses

Sex ratio was calculated as the proportion of males out of the total number of fledglings. Deviation from parity was tested with the binomial distribution using the two-sided binomial probabilities for the given sex ratios (SPSS version 7.5). Logistic regression analysis was used to test whether brood size affected the fledgling sex ratio of the total population. In the analysis, the sex ratio of the fledglings was considered as the dependent variable, while the explanatory variable was brood size. Wald's test was used to determine the significance of the model, based on chi-squared goodness-of fit values. A significant Wald's value indicates that the explanatory variable accounts for a significant amount of variation in the dependent variable. The logistic regression models were run with Stat View (version 5.0-J). The model was also used to examine whether the sex ratio of fledglings was related to the distribution of the breeding sites.

RESULTS

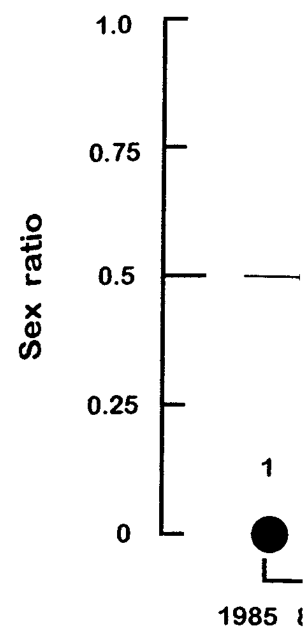
1) Sexual dimorphism

As in many species of raptors, Blakiston's Fish Owl females are larger than males. The adult female in one continuous study site had 16% greater mass than her mate in autumn though the magnitude of this dimorphism was lower during other seasons (the female ranged from 2,950-4,150 g, based on 14 measurements over nine months, whereas the male ranged from 2,950-3,600 g, based on 38 measurements over nine months).

Observed mean body weights for fledglings, which were measured at banding, were 1,961.2 g ($\pm$255.2SD, n=30) for daughters, and 1,855.2 g ($\pm$171.0SD, n=52) for sons. The weight difference between the sexes was significant (t=2.25, df=80, $0.01 < P < 0.05$). The magnitude of dimorphism among fledglings was apparent but slightly less than among adults, with daughters weighing just 6% more than sons.

2) Sex ratio of fledglings in the Hokkaido population

The total number of fledglings whose sex was identified during 1985-1999 included 81



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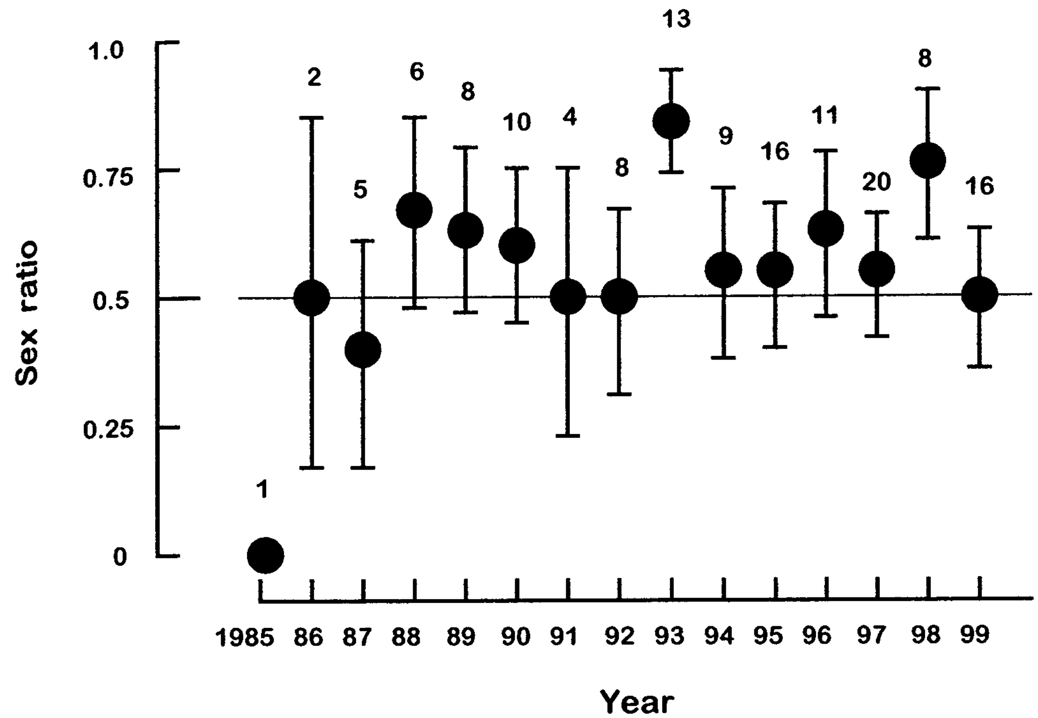

Fig. 1. Sex ratio among fledglings of Blakiston's Fish Owls defined as proportion of males from 1985-1999, Hokkaido, Japan. Error bars represent standard deviations in a binomial distribution. Numbers denote total number of sexed fledglings for each year. Sex ratio was calculated as the proportion of males out of the total number of fledglings.

(59.1%) males and 56 (40.9%) females. Only individuals that were found dead or in a debilitated condition, or captured before fledging though they had already been ringed and sexed, were excluded (Fig. 1).

Fledgling sex ratios ranged from a low of 0.40 in 1987 to a high of 0.85 in 1993 (years in which fewer than five individuals were ringed, i.e. 1985, 1986 and 1991 were excluded). Females outnumbered males in only two of the 15 years. The overall sex ratio among 137 fledglings from a total of 91 nests was significantly male biased ($P=0.04$, two-sided binomial test).

If the costs of rearing sons and daughters are proportional to the energy demands of each sex throughout the nestling period, and if the energy demands are in proportion to the offspring's body sizes, sexual dimorphism would affect the sex ratio of offspring. Using the original values of fledgling body weights, we calculated the expected sex ratio for Blakiston's Fish Owls to be 0.51. The observed sex ratio of fledglings was still higher than the expected value ($P=0.04$, two-sided binomial test).

3) Brood composition

Blakiston's Fish Owls produce clutches of either one or two eggs. There were no significant differences between the observed and expected sex ratios (50% sons) in either brood sizes (two-sided binomial test: brood size=1: $P=0.17$; brood size=2: P

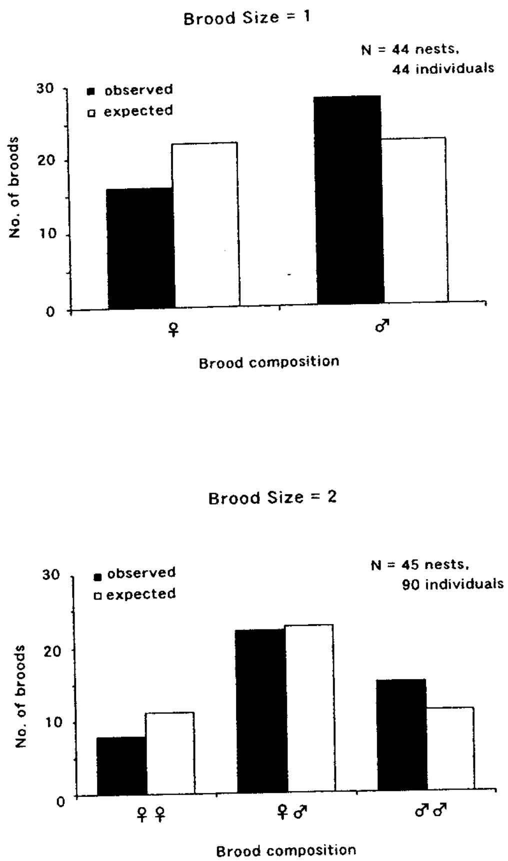

Fig. 2. Frequency distributions of sex compositions of broods of one offspring (above) and of two (below). Brood size=1 (above): n=44 broods, 44 chicks; brood size=2 (below): n=45 broods, 90 chicks. Expected values of sex ratio was 50% males in both brood sizes. In this analysis, a different data set from the previous analysis was used: we included those the broods in which one member was not be able to fledge safely after sex identification (two broods) and excluded the broods (five) one member of unknown sex died before the sex was identified to analyze the near birth composition.

=0.10; Fig. 2). Frequency distributions of observed compositions of broods of two offspring were also tested against the expected frequencies (♀♀:♀♂:♂♂=1:2:1). No significant difference was found in this analysis again (chi-square test for goodness of fit, $\chi^2=2.184$, $P=0.336$, n=90 fledglings). The lack of statistically significant differences, despite a male-biased sex ratio being detected in the total fledgling population, must be partially due to small sample sizes.

Assuming that sex-biased nestling mortality or sex-specific laying (hatching) sequences occur, fledgling sex ratios are expected to be more biased in one chick broods than in two chick broods. The results of the logistic regression analysis showed no evidence that brood size significantly influenced the sex ratio of the fledglings (goodness-of fit chi-square=0.278, $P=0.598$, n=134 fledglings) (Table 1). Tested against the logistic regression model, a model specifying constant expected frequencies was not rejected (likelihood ratio chi-square=0.280, $P=0.597$).

4) Local variations

If offspring sex ratios fluctuate with maternal conditions related to environmental factors such as food abundance, then the offspring sex ratio might vary among breeding sites. We examined the possibility that fledgling sex ratio variations were different between breeding sites (one breeding site was occupied by one pair). Eleven breeding sites, situated in four different local groups were used in the analysis (see METHODS).

The sex ratio of fledglings varied between breeding sites within the same breeding site groups (i.e. Shiretoko, Nemuro, Mashuh and Tokachi) and also varied between the four breeding site groups. Moreover, each group had its own trend around the expected value (50% male) (Fig. 3). On the Shiretoko Peninsula, various sex ratios were

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Table 1. Results of the logistic regression model, with sex ratio as the response variable and brood size as the explanatory variable (n=134 fledglings).

	χ^2	P	Log-odds ratios
Constant	1.316	0.251	0.468
Brood size	0.278	0.598	1.222

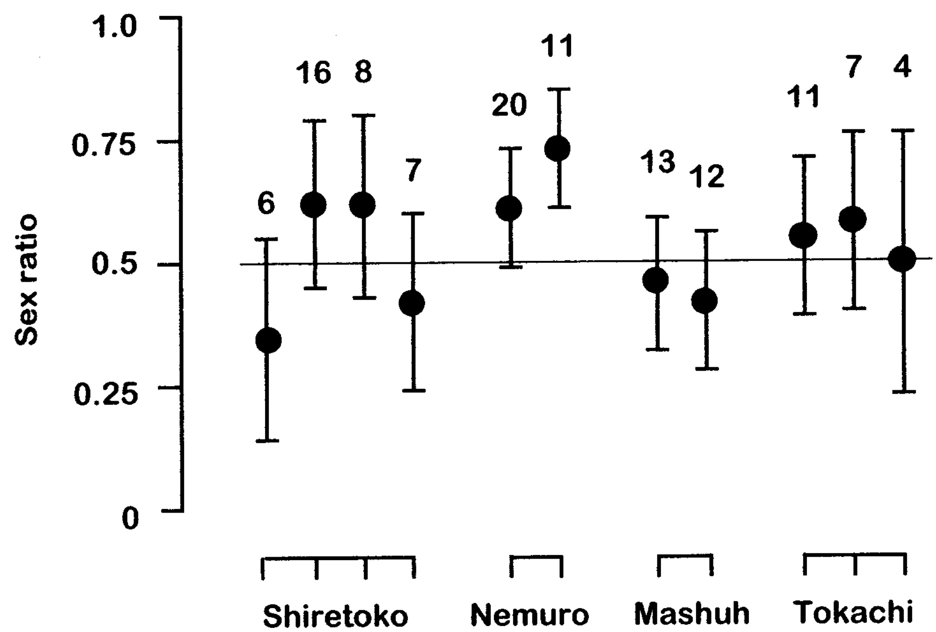

Fig. 3. Local variation in sex ratio of Blakiston's Fish Owl's fledglings. Only the habitats where offspring fledged successfully more than three years between 1985 and 1999 were chosen. The shortest distances between the categories of habitats are; 80.0 km: Shiretoko-Nemuro, 61.5 km: Nemuro-Mashuh, 106.0 km: Mashuh-Tokachi, respectively. Each plot shows sex ratio of each habitat. Error bars represent standard deviations in a binomial distribution. Numbers denote total number of sexed fledglings for each habitat.

recognized (33.3-66.7% male). Surplus males were produced in two breeding sites on the Nemuro Peninsula. Conversely, female-bias (41.7 & 46.2% male) occurred at two sites in the Mashuh area and near parity occurred in Tokachi.

However, logistic regression analyses showed neither breeding sites nor local groups of breeding sites affected the sex ratio of fledglings (Table 2).

5) Sex differences in post-fledging survival

Blakiston's Fish Owl has a long postfledging period of four to seven months during which the parents provide at least part of their food supply, furthermore the young stay within their natal area for some months or years after nutritional independence (Hayashi 1997).

Some information, on mortality during the period from fledging to dispersal is available

Table 2. Results of the logistic regression models to test hypotheses that breeding sites and /or the local groups of breeding sites effected sex ratio of fledglings (n=115 fledglings).

	χ^2	P	Log-odds ratios
Constant	0.104	0.748	1.382
Local groups	2.137	0.144	0.777
Breeding sites	2.217	0.137	0.919
Local groups + Breeding sites	0.082	0.775	0.929
Local groups + Breeding sites + Local groups × Breeding sites	0	0.992	0.999

(Hayashi 1999, and unpublished sources of the Environment Agency, Japan). Twenty young owls were found dead within their natal areas before they had dispersed. Known causes of death were accidents at fish farms (n=3), traffic accidents (n=2), and predation (n=2). Mortality showed a strong male bias (70.0%, 14/20 males), although there was no statistical difference from parity (two sided binomial test, $P=0.12$). The trend in male-biased mortality was not significant, perhaps simply caused by the small sample sizes.

DISCUSSION

In conclusion, the sex ratio of Blakiston's Fish Owl is male-biased at fledging, however the bias seems to be moderated toward parity during the post-fledging stage because young male owls seem to suffer higher mortalities than do females. Unfortunately, insufficient data is available on male and female survival during the nestling and post-fledging periods. Regional data were also considered too few for statistical comparison and further studies are needed to detect trends in the sex ratio of fledglings among habitats.

Three major factors are attributable to the skewed sex ratio at fledging stage of Blakiston's Fish Owl. These factors are not necessarily alternative nor exclusive. We suppose that the skewed fledgling sex ratio in Blakiston's Fish Owl has been achieved via some combination of differential factors.

1) Sexual dimorphism

In many raptor species, females are larger than males (Newton 1979). If the costs of raising sons and daughters differ due to sexual dimorphism, then the offspring sex ratio is expected to be biased according to Fisher's theory (1930). Actually, some studies have shown there to be a male-biased sex ratio in certain raptor species when they fledged (Golden Eagles *Aquila chrysaetos*: Edwards *et al.* 1988, Harris's Hawks *Parabuteo unicinctus*: Bednarz & Hayden 1991, Montagu's Harriers *Circus pygargus*: Leroux & Bretagnolle 1996, American Kestrels *Falco sparverius*: Wiebe & Bortolotti 1992, and Marsh Harriers *Circus aeruginosus*: Zijlstra *et al.* 1992) while others have found female-biased sex ratios (Hen Harriers *Circus cyaneus* and American Kestrels: Olsen & Cockburn 1991, reevaluated by Krackow 1993). Many species however showed no significant deviation from parity (Newton 1979; Krackow 1993). Even for the European Sparrowhawks *Accipiter nisus*, whose dimorphism is extreme, with females twice as heavy as males, the fledgling sex ratio was not significantly different from unity (Newton & Marquiss 1979). The extent of sexual dimorphism usually showed

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As for Blakiston's Fish Owls, the male-biased sex ratio of fledglings is qualitatively consistent with Fisher's theory. Here, we have noticed that the observed sex ratio (male: female=1.45:1) was higher than the body mass ratio (male: female=1:1.06), which is not common in other raptor species (Eguchi 1999). Our results, of testing the quantitative prediction from Fisher's theory against the observed fledglings sex ratio, suggest that sexual dimorphism alone is not always enough to explain the male-biased sex ratio in Blakiston's Fish Owls. Hereafter, we will try to find other factors that may cause the skewed fledgling sex ratio.

2) Local resource competition

On the basis of field studies, Blakiston's Fish Owl exhibits female-biased delayed dispersal. Male offspring first left their natal area in their second spring of life and wandered around the parental home range returning subsequently in winter, whereas female offspring remained within their natal range for their first two years of life (Hayashi 1997). All offspring dispersed from the natal area in their third spring but some females returned repeatedly to the parental territory (Hayashi 1997). This differential timing of dispersal and the intensive natal philopatry of daughters may lead to local resource competition (LRC, Clark 1978) because philopatric offspring may be potential competitors to their parents for food resources.

Weatherhead & Montgomerie (1995) emphasized that LRC was unlikely to contribute to biased fledgling sex ratio in birds because the rate of returns to natal areas was extremely low and unlikely to induce competition between offspring and parents for resources on the breeding grounds. In Blakiston's Fish Owls, however, extensive relationships between female offspring and natal areas were detected. It seems reasonable therefore to conclude that LRC also influences the fledgling sex ratio in this species.

3) Small population size

Small population size might be the most important factor leading to the observed skewed sex ratio in Blakiston's Fish Owl. It is generally agreed that the magnitude of demographic fluctuations, such as random variation in adult sex ratios, is inversely proportional to population size (Lande 1998). However, as far as we know, there have been few studies examining sex ratio changes in declining populations.

The case of the rare New Zealand Kakapo *Strigops habroptilus*, provides one such rare example. The Kakapo, the world's largest, flightless parrot declined to near extinction during the 1980s.

Conservation efforts, hindered by low net productivity, are further hampered by the relative scarcity of females in the surviving population (Trewick 1997). Although the subfossil data also show a scarcity of females indicating that this is not a recent aberration (Trewick 1997), effects of demographic stochasticity must be added to the very small population. A shortage of fertilization caused by there being insufficient females in the population combined with a male-biased birth ratio under a recent breeding program would increase the likelihood of the Kakapo becoming extinct (Courchamp *et al.* 1999).

Blakiston's Fish Owl likely may perhaps face a similar problem due to the male-biased sex ratio at fledging in the small population. We can not estimate the effects of population decline caused by anthropogenic factors on the present sex ratio because we have no data on the sex ratio before the artificial destruction of habitats occurred. Nevertheless, we should be more concerned about the current skewed sex ratio in the Hokkaido population because such a skewed ratio is typically a powerful indicator of impending extinction (Durant 1998) because on imbalanced sex ratio reduces the effective population size (Caughley 1994).

Whatever the mechanisms leading to the skewed sex ratio in fledgling Blakiston's Fish Owls, long-term monitoring of the breeding population to watch for fluctuations in the sex ratio should be continued given the conservation needs of this endangered species. Additional studies of the mortality of both sexes at different stages in the life-cycle, and of the dispersal patterns of the young are especially needed.

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