Secondary Sex Ratio in Anatinae

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Most waterfowl have highly skewed tertiary (adult) sex ratios in favor of males (Bellrose et al. 1961, Aldrich 1973, Bellrose 1980, Owen and Dix 1986). Sex ratios of diving ducks generally are more distorted than those of dabbling ducks (Mendall 1958, Aldrich 1973, Bellrose 1980). Perhaps the greatest disparity has been recorded for Canvasbacks (*Aythya valisineria*), and Common Pochards (*Aythya ferina*), with two to three or more males for every female in some major wintering areas (Haramis et al. 1985, Owen and Dix 1986). The skewed sex ratio among Temperate Zone ducks is of particular interest because most of these species show seasonal monogamy (reviewed by Rohwer and Anderson 1988, Oring and Sayler 1992). Thus, many males have little opportunity for reproduction, especially because the secondary reproductive tactic of forced copulation appears to be confined to successfully paired individuals (McKinney et al. 1983, McKinney 1985, Gauthier 1988). However, it is important to realize that male-biased sex ratios in adult ducks are the product, not the cause, of seasonal monogamy (Oring and Sayler 1992). The strong and consistent skew in tertiary sex ratios raises the question of when and how skewed sex ratios develop, and suggests that females may manipulate sex ratios. If females can control the sex ratio of her progeny to increase survival of one sex, parental fitness will increase too (Leblanc 1987).

Surprisingly little information has been published on secondary (at hatching) sex ratios of ducks. Most data come from ducklings hatched in an incubator from eggs collected from wild free-ranging females and provide no evidence that sex ratios at hatching differ from unity (Sowls 1955, Mendall 1958, Bellrose et al. 1961, Swennen et al. 1979). Dubovsky (1990) hatched captive wild-strain and game-farm female Mallard (*Anas platyrhynchos*) eggs in an incubator and found no evidence that sex ratio in this species varies with laying order, egg mass, and clutch sequence within a breeding season.

More complete information is available for other bird taxa, but the evidence for adaptive control of offspring sex is scant and controversial (reviewed by Clutton-Brock 1986, Ligon and Ligon 1990). For example, some studies report variation in sex ratios at hatching as a function of laying or hatching sequence

(Howe 1977, Fiala 1981, Davies and Payne 1982, Weatherhead 1985), parental age (Blank and Nolan 1983), egg size (Howe 1976, Fiala 1981, Mead et al. 1987), or season (Howe 1977, Patterson et al. 1980, Fiala 1981, Ligon and Ligon 1990). A potential bias in studies of variation in sex ratios is that only those showing significant effects are likely to be reported (Leblanc 1987).

Here we present data on secondary sex ratios at the population and individual levels, as well as investigate the relationship between sex ratios at hatching and date of hatching, clutch size, duckling mass, and the age and mass of female parent for three species of wild ground-nesting and over-water-nesting ducks. Further, we examined if parental allocation of resources, as determined by newly hatched duckling mass, was similar in the two sexes. In addition, we review the published information on secondary sex ratios in Anatinae and other bird taxa.

Methods.—We determined the sex for newly hatched ducklings of Northern Shovelers (*Anas clypeata*), Common Pochards, and Tufted Ducks (*Aythya fuligula*) by cloacal examination (Hochbaum 1942) as part of a long-term population study conducted on Engure Marsh, Latvia (57°15′N, 23°07′E) over a 16-year period from 1978 through 1993. The accuracy of sex determination was enhanced because about 95% of all ducklings were sexed by the junior author. Incubating females were captured on the nests using drop-door traps (Blums et al. 1983) or dip nets during the last week of incubation and fitted with conventional leg bands.

We obtained a sample of known-age females using two methods. First, more than 65,000 day-old ducklings were individually marked using plasticine-filled leg bands (Blums et al. 1994). Subsequent recaptures of these birds as breeding females allowed us to assign them an exact age. Second, unmarked incubating females were aged as either yearlings (one year old) or adults (two or more years old) using wing-feather characteristics (Blums et al. 1996). There were relatively few unmarked birds (no plasticine-filled or conventional bands) in the sample of incubating females whose progeny were sexed (21, 24, and 33% of Tufted Ducks, Northern Shovelers, and Common Pochards, respectively).

Conspecific brood parasitism was common in the diving ducks, but exceptionally rare in the Northern Shoveler. Widely differing initiation dates, differences in egg coloration and shape, appearance of two or more eggs per day, records of one or more eggs

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TABLE 1. Sex ratios at hatching of Northern Shoveler ducklings in 117 clutches in which all eggs hatched and sex was determined for all ducklings (Engure Marsh, Latvia, 1978–1993). Sex ratio within clutches did not deviate from expected binomial distribution ($P > 0.05$).

♂:♀	No. clutches
9 eggs	
2:7	2
3:6	8
4:5	7
5:4	3
6:3	6
7:2	2
8:1	1
10 eggs	
2:8	2
3:7	7
4:6	13
5:5	16
6:4	6
7:3	4
8:2	3
11 eggs	
3:8	2
4:7	5
5:6	7
6:5	9
7:4	10
8:3	4

TABLE 2. Sex ratio of one-day-old ducklings in relation to their hatching time and mass, and in relation to clutch size, mass and age of female parent. Data from Engure Marsh, Latvia, 1978–1993. For individual species, the sex ratio in each subdivision of independent variable did not differ from 50:50 distribution (z-test, all $P > 0.11$); all combined G-tests for sex ratio differences between two subdivisions also were not significant (all $P > 0.05$).

Type of partition	Northern Shoveler		Common Pochard		Tufted Duck	
	M	F	M	F	M	F
Hatching time[a] ($G = 0.11, 0.80, 0.50$)						
Early	779	777	276	289	830	842
Late	439	426	229	214	639	683
Mass of ducklings[b] ($G = 0.04, 3.74, 1.66$)						
Light	586	575	278	246	823	817
Heavy	617	615	188	215	584	639
Clutch size[c] ($G = 0.03, 0.10, 1.02$)						
Small	622	615	149	151	558	612
Large	574	576	164	158	541	545
Mass of female parent[b] ($G = 0.03, 1.41, 0.26$)						
Light	567	540	160	149	515	522
Heavy	556	537	125	142	525	556
Age of female parent ($G = 0.01, 1.11, 0.26$)						
Yearling	486	484	102	89	192	193
Adult	705	696	206	216	896	954

[a] (Early) hatched before the yearly $\bar{x}$ hatching date; (late) hatched after the yearly $\bar{x}$ hatching date.

[b] (Light) < yearly $\bar{x}$; (heavy) > yearly $\bar{x}$.

[c] Small and large clutches were negative and positive deviations from yearly predicted decline in clutch size (see Methods).

being found outside the nest bowl, and excessive sizes of clutches (>13 eggs for Northern Shoveler and Common Pochard; >14 eggs for Tufted Duck) provided evidence of brood parasitism. Hatching date was defined as the date when at least several eggs in a clutch were externally double-star pipping. We weighed ducklings (±1 g) and incubating females (±10 g) using Pesola spring scales.

Our initial analyses were based on numerous arbitrarily selected subdivisions of the continuous variables (i.e. female age and mass, clutch size, etc.) in order to maximize possible differences in the sex ratios. After not finding significant deviations from 50:50 sex ratios in any of these comparisons, we based most of our analyses presented here on positive or negative deviations from yearly means of independent variable. The two subdivisions were approximately equal as suggested by Clutton-Brock (1986), and this procedure allowed also to control for possible annual variation.

We used several statistical tests to evaluate the null hypotheses that: (1) duckling sex frequencies within clutches follow a binomial distribution (chi-square goodness-of-fit test; Sokal and Rohlf 1995); (2) the sex ratio in each subdivision of the independent variable does not differ from a 50:50 distribution (two-tailed

z-test; Snedecor and Cochran 1980); and (3) the sex ratio of ducklings does dot differ from a 50:50 distribution during the lifetime of an individual female (chi-square test of homogeneity; Sokal and Rohlf 1995). We used SAS (SAS Institute 1987) for other analyses: G-test for independence to test the null hypothesis that sex ratios do not differ between two subdivisions of the independent variable; and Student's t-test to compare the hatching mass of the two sexes. We based our clutch-size analyses on deviations from predicted seasonal declines in clutch size. Before application of the G-test, we regressed clutch size on time of nesting (nest initiation date) and then estimated sex ratios for positive and negative residuals. All positive deviations from the yearly predicted values were defined as large clutches and negative deviations as small clutches.

Results.—We determined the sex of 2,425 Northern Shovelers, 3,035 Tufted Ducks, and 1,035 Common Pochards immediately after hatching. Data from clutches with and without egg mortality were combined after we determined that there were no significant differences in sex ratios for these two classes

TABLE 3. Sex ratio of one-day-old ducklings for an individual female[a] Northern Shoveler over five years of breeding history at Engure Marsh, Latvia. There was no evidence (chi-square test of homogeneity, $P > 0.75$) against consistency in 50:50 sex ratio.

Year	Female age (years)	Offspring sex		Duck-lings sexed	Com-plete clutch size
		Male	Female		
1982	2	7	4	11	12
1983	3	5	6	11	11
1984	4	4	7	11	11
1985	5	6	5	11	11
1987	7	5	4	9	10
Total	—	27	26	53	—

[a] No signs of conspecific brood parasitism recorded for this female.

of broods (G-test, $P > 0.27$). Sex ratios of ducklings from 216 nests of Northern Shovelers and Tufted Ducks, in which all ducklings hatched and were sexed, did not differ from the expected binomial distribution (see example for Northern Shoveler in Table 1). For the Common Pochard, too few data were available for statistical analysis.

We did not find significant differences in the sex ratio at hatching among broods produced by females of different ages, or among those hatched at different times during the breeding season (Table 2). The sex ratio also was independent of clutch size, duckling mass, and female parent mass (Table 2). None of the sex ratios in Table 2 were significantly different from unity ($P > 0.11$). Although there were no significant differences in the sex ratio of ducklings between broods with and without signs of conspecific brood parasitism (G-test, $P > 0.56$), we excluded nests with mixed clutches from some analyses (female age, mass, and clutch size). Few females were monitored for more than four breeding seasons and none of these successfully hatched all eggs that were produced during their lifetimes. There was no evidence (chi-square test of homogeneity, $X^2 = 1.91$, df = 4, $P > 0.75$) against consistency in 50:50 sex ratio of ducklings for a highly successful individual female during five breeding seasons (Table 3). We did not find significant variation in the sex ratios among years over the entire study period for all three species (G-test, df = 15, $P >$

0.33). In addition, we found no difference in mass between one-day-old females and males (Table 4).

Discussion.—Published information on secondary sex ratios in ducks is scarce and deals mainly with incubator-hatched ducklings (Table 5). Although eggs hatched in an incubator were collected from free-ranging females, an incubator effect cannot be dismissed (Hochbaum 1959:51). This possibility has not yet been tested formally. Analyses of our data and evaluation of published sources do not indicate the presence of any nonrandom process operating on sex distribution in 10 Anatinae species (Table 5). Surprisingly, however, a significant ($z = 2.41$, $P = 0.02$) female bias occurred at the population level in a large sample of Common Eider (*Somateria mollissima*) ducklings at Kandalaksha Nature Reserve, White Sea, Russia (Shklarevitch and Nikulin 1979). In that study, 3,470 eider ducklings were sexed by cloacal examination under natural conditions, but authors did not provide any evidence regarding the accuracy of their sex determination. We suspect Russian biologists may have had a systematic bias toward females at the beginning of their five-year study. The percentage of females were much higher in the first two years (52.5 and 56.0%) of the study and decreased thereafter (51.4, 50.0, and 48.6%). In contrast, duckling sex ratios of Common Eiders in The Netherlands (Swennen et al. 1979), approximately 2,200 km southwest of the Russian study site, did not differ from a 50:50 distribution (Table 5).

We found no seasonal variation in sex ratio with hatching date. This is consistent with results obtained by Sayce and Hunt (1987) on the Western Gulls (*Larus occidentalis*), but contradicts studies on several species of passerines (Howe 1977, Patterson et al. 1980, Fiala 1981, Weatherhead 1983, Ligon and Ligon 1990). Our results provide no evidence that females invest more energy in eggs that will produce a particular sex (judged by newly hatched duckling mass). Similarly, no correlation between sex and hatching mass was found in two species of geese (Harmsen and Cooke 1983, Leblanc 1987) or the Common Eider (Swennen et al. 1979). These data suggest that for most, if not all, species of ducks and geese there may not be an advantage to allocating more resources to one sex.

It is not known how offspring sex ratios vary over the lifespan of an individual female, and it will be very difficult to obtain this information for any species, especially for free-ranging ducks. The maximum

TABLE 4. Mean ± SE (with n in parentheses) of duckling mass (g) by sex for three duck species at Engure Marsh, Latvia, 1978–1993.

Species	Male	Female	t[a]
Northern Shoveler	27.2 ± 0.06 (1,198)	27.3 ± 0.06 (1,188)	1.48
Common Pochard	43.6 ± 0.16 (478)	43.9 ± 0.16 (472)	1.27
Tufted Duck	38.3 ± 0.07 (1,425)	38.4 ± 0.07 (1,468)	1.17

[a] Student's t-test (two-tailed). All $P > 0.05$.

TABLE 5. Secondary sex ratios in Anatinae.

Species	Males (M)	Females (F)	M/F	z^a	P	C^b	Location	Source
Wood Duck (*Aix sponsa*)	548	564	0.97	0.48	0.63	I	Illinois, USA	Bellrose et al. 1961
Mallard (*Anas platyrhynchos*)	394	369	1.07	−0.91	0.36	I	Manitoba, Canada	Sowls 1955
Northern Pintail (*A. acuta*)	424	405	1.05	−0.66	0.51	I	Manitoba, Canada	Sowls 1955
Northern Shoveler (*A. clypeata*)	1,218	1,207	1.01	−0.22	0.83	W	Latvia	This study
Canvasback (*Aythya valisineria*)	315	307	1.03	−0.32	0.75	I	Manitoba, Canada	Sowls 1955
Common Pochard (*A. ferina*)	519	516	1.01	−0.09	0.93	W	Latvia	This study
Redhead (*A. americana*)	342	294	1.16	−1.91	0.06	I	Manitoba, Canada	Sowls 1955
Ring-necked Duck (*A. collaris*)	42	40	1.05	−0.22	0.83	I	Maine, USA	Mendall 1958
Tufted Duck (*A. fuligula*)	1,494	1,541	0.97	0.85	0.40	W	Latvia	This study
Common Eider (*Somateria mollissima*)	1,604	1,613	0.99	0.16	0.87	W	The Netherlands	Swennen et al. 1979

[a] Two-tailed z-test that sex ratio did not differ from 50:50.
[b] Conditions when sexed: (I) hatched in an incubator from eggs collected from wild free-ranging females; and (W) hatched in wild.

longevity of breeding females recorded in this study was at least 14 years (Common Pochard and Tufted Duck); however, few birds were monitored over more than four breeding seasons. A highly successful female Northern Shoveler was monitored for five years and hatched 53 ducklings, which accounted for 96.4% of eggs laid during this period. Offspring sex ratio for this individual did not deviate from a 50:50 distribution (Table 3).

The causes of disparate sex ratios in adult ducks are not well understood. Hunting mortality rates differ between the sexes in many species and may influence the sex ratios among adults (Johnson and Sargeant 1977); however, there is no consensus concerning the importance of hunting effects on sex ratios (e.g. Bellrose et al. 1961, Olson 1965, Aldrich 1973, Owen and Dix 1986, Haramis et al. 1994).

Intersexual competition, more specifically male dominance, may contribute to higher overwinter mortality of adult females in several duck species (e.g. Nichols and Haramis 1980, Owen and Dix 1986, Alexander 1987). Studies on social dominance in wintering waterfowl have shown that paired females were more dominant than unpaired females, and males dominated females when their pair status was identical (Hepp and Hair 1984, Heitmeyer 1985). Moreover, females of late-pairing species remained subordinate for longer periods and were more likely to be excluded from preferred feeding sites, particularly during times of limited resources. Consequently, these species appear to have more disparate sex ratios during the nonbreeding period than species that pair early (Hepp and Hair 1984). Indeed, diving ducks generally do pair later (Weller 1965, Paulus 1983, Hepp and Hair 1984) and have more distorted sex ratios (Mendall 1958, Aldrich 1973, Bellrose 1980) than dabbling ducks. The Common Pochards probably pair latest among the temperate duck species (Bezzel 1969) and have one of the most disparate adult sex ratios both in wintering and breeding areas (Bezzel 1969, Owen and Dix 1986, Blums et al. 1990:60).

Research on the breeding ecology of waterfowl during the last three decades has led to a belief that high mortality of females during the breeding season is a major cause of disparate sex ratios among adult ducks, at least in North America (e.g. Sargeant et al. 1984, Johnson et al. 1992, Sargeant and Raveling 1992, Greenwood et al. 1995, Reynolds et al. 1995; but see Owen and Black 1990:128).

The question of adaptive control of offspring sex in wild birds is controversial. Many studies, including those based on relatively large sample sizes, indicate that there is no convincing evidence of parental control over sex determination (e.g. Zwickel and Bendell 1967, Newton and Marquiss 1979, Harmsen and Cooke 1983, Leblanc 1987, Ryder and Termaat 1987, Sayce and Hunt 1987; see also Table 5). Evidence of some nonrandom patterns of sex allocation (e.g. Howe 1977, Patterson et al. 1980, Blank and Nolan 1983, Gowaty

and Lennartz 1985, Weatherhead 1985, Breitwisch 1989, Ligon and Ligon 1990) may represent an artifact of annual variations caused by factors other than natural selection (Weatherhead 1985, Leblanc 1987), or cases where the null hypothesis has been wrongly rejected by chance (Clutton-Brock 1986). We are aware of at least two studies (Lesser Snow Goose, *Chen caerulescens* [Ankney 1982]; Ring-billed Gull, *Larus delawarensis* [Ryder 1983]) that may have suffered from a type I error when small sample sizes gave statistical significance to a nonexistent phenomenon (Ryder and Termaat 1987). Collection of additional data in each case (Cooke and Harmsen 1983, Meathrel and Ryder 1987) provided no evidence for laying-order effects on sex ratios at hatching.

Ligon and Ligon (1990) have suggested that adaptive manipulation of the hatching sex ratio possibly may occur under certain ecological conditions in some sexually size-dimorphic altricial species that share certain important features (e.g. exhibit strong sexual dimorphism at nestling stage, experience seasonal or temporal variation in food abundance, and characteristically vary in the amount of provisioning assistance the female breeder will receive). However, most studies that suggest some kind of secondary sex-ratio adjustment in birds have been short-term (two to five years) and provide little or no evidence that sex ratio is biased at the population level. The results of our study do not support theoretical predictions of the Trivers-Willard hypothesis on how selection favors facultative manipulation of sex ratios among vertebrates of polygynous species (most ducks are seasonally monogamous) under varying environmental circumstances (Trivers and Willard 1973). We believe more long-term studies on secondary sex ratios in birds, including waterfowl, are needed and, as pointed out by Cooke and Harmsen (1983), large sample sizes are necessary and sampling techniques that exclude possible biases should be used.

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DNA Fingerprinting Reveals Monogamy in the Bushtit, a Cooperatively Breeding Species

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Cooperative breeding systems, which are characterized by individuals contributing parental care to offspring that are not their own direct descendants, have received much attention in the past three decades (Hamilton 1964, Brown 1978, 1987, Emlen 1982). The aid-givers may be nonbreeding adults, in which case they are usually called "helpers," or they may be cobreeders that share reproduction with the other group members of the same sex.

The Bushtit (*Psaltriparus minimus*) is one of the first species of cooperative breeders ever described (Skutch 1935). Bushtits breeding in the Chiricahua Mountains of Arizona display notable variation with respect to breeding-group composition. On average one-third of the nests have more than two attending adults (Sloane in press). The helpers are predominantly un-

mated males, or birds of both sexes that have failed in earlier breeding attempts (Sloane 1992).

In approximately 19% of nests, helpers have been observed to join prior to or during the egg-laying stage, thereby providing the opportunity for genetic contributions via extrapair fertilizations or intraspecific brood parasitism (Sloane in press). In addition, the relatively high incidence of double brooding in these birds (Sloane unpubl. data) may give additional reproductive options to helpers, if those joining a nest after the first clutch later become breeders or cobreeders for the second brood. Molecular-genetic studies are required to investigate the parentage contributions made by helpers.

The development of DNA probes (e.g. Jeffreys et al. 1985) that detect high levels of genetic variation has greatly simplified parentage determinations and also permitted the assignment of pairs of animals to relatedness categories (e.g. Wetton et al. 1987, Burke et al. 1989, Westneat 1990, Piper and Rabenold 1992, Quinn et al. 1994, Jamieson et al. 1994). Overall, studies

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