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SEX RATIOS OF PREFLEDGING WESTERN GULLS

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ABSTRACT.—Western Gull (*Larus occidentalis*) chicks on Santa Barbara Island, California, had a sex ratio at hatching of 1.12 M/F ($n = 609$); the sex ratio of chicks ≥ 35 days of age was 0.89 ($n = 189$). The sex ratio at hatching and fledging did not vary significantly from 1.0 or from each other, but the data suggest that male mortality before fledging exceeded that of females. Depressed growth rates of male chicks hatched third may be responsible for these higher male mortality rates. We found no evidence for seasonal or hatching-order effects on sex ratios at hatching. We suggest that postfledging differences in mortality between the sexes are in part responsible for the skewed sex ratio (0.67 males/female) observed in the adult breeding population. Received 4 October 1985, accepted 11 June 1986.

SEVERAL theorists have demonstrated that sex ratios of young should be biased such that parents invest equally in offspring of each sex (Fisher 1930, MacArthur 1965, Trivers and Willard 1973, Charnov 1975). Because the primary sex ratio may be fixed at 1.0, adjustments may be restricted to changes in the secondary (at birth) and tertiary (at end of parental care) sex ratios due to differential parental investment (Maynard Smith 1980). These theories predict, because of differential parental investment, biased sex ratios in species in which young are sexually dimorphic in size at the termination of parental care.

Numerous recent studies have investigated the hatching and fledging sex ratios of sexually dimorphic birds. Newton and Marquiss (1979), working with the Eurasian Sparrowhawk (*Accipiter nisus*), Fiala (1981) with Red-winged Blackbirds (*Agelaius phoeniceus*), Lombardo (1982) with Eastern Bluebirds (*Sialia sialis*), and Harmsen and Cooke (1983) with Lesser Snow Geese (*Chen caerulescens*) found no deviation from a 1:1 sex ratio at hatching or fledging. Others found variation in sex ratios at hatching as a function of hatching order (Ankney 1982, Lesser Snow Goose; Davies and Payne 1982, domestic fowl, *Gallus domesticus*; Ryder 1983, Ring-billed Gull, *Larus delawarensis*; Weatherhead 1985, Red-winged Blackbird) or season (Howe 1977, Common Grackle, *Quiscalus quiscula*). Differential chick mortality resulting in biased sex ratios at fledging were found for Common Grackles (Howe 1976), Common Capercaillie (*Tetrao urogallus*; Wegge 1980), Northern Harriers (*Circus cyaneus*; Picozzi 1980), and Red-winged Blackbirds (Blank and Nolan 1983).

In Western Gulls (*L. occidentalis*), males are larger than females. The breeding population of Western Gulls on Santa Barbara Island (SBI), California, has an estimated adult sex ratio of 0.67 (males/female) (Hunt et al. 1980). The female-biased sex ratio in the adult population could result from differential mortality after fledging. Alternatively, differential mortality of chicks could initiate sex-ratio bias at hatching, particularly if males required greater parental investment and an adjustment of the sex ratio before the termination of parental care resulted. We tested the hypothesis that a female bias in the sex ratio of chicks before fledging was responsible for the observed bias in the adult breeding population on SBI. Additionally, we sought evidence for mechanisms that might result in a biased prefledging sex ratio.

METHODS

We determined the sex of Western Gull chicks on SBI during the breeding seasons of 1979–1982 by unilateral laparoscopy (Fry and Toone 1981, Sayce 1983). Sex was determined for birds between 36 and 42 days of age in 1980–1982; in 1979 some chicks were 14 days old when laparoscopies were performed. We attempted to determine the sex of all chicks in a brood, including chicks that died. The sex of a dead chick could be determined only if the carcass was fresh.

We estimated sex ratios at fledging on the basis of all laparoscopies performed on chicks within 6 days of normal fledging age (42 days). This range in age was necessary to have sufficient time to find and examine chicks before they fledged. In 1979 we did not know the age of chicks, so chicks above 500 g (a threshold mass used as a criterion for survival; Hunt and Hunt 1975) were used to estimate the sex ratio at fledging. Little mortality takes place in these chicks

TABLE 1. The sex ratios at hatching of chicks in 185 clutches in which all eggs hatched and sex was determined for all chicks, 1979-1983. The sex ratio within clutches did not deviate from the expected binomial ratio ($P > 0.05$).

Clutch size	No. of males	No. of clutches
1 egg	0	3
	1	5
2 eggs	0	4
	1	20
	2	7
3 eggs	0	15
	1	53
	2	60
	3	18

just before fledging, and it is unlikely that there could be sufficient sex bias in this late mortality to alter our results.

Sex ratios at hatching were estimated from nests in which we could determine the sex of all chicks that hatched, although sex necessarily had to be determined at a later date. We could not determine the sex of newly hatched chicks without causing some chick mortality, so laparoscopies were delayed until chicks were older than 14 days. Our estimates of sex ratios at hatching may underestimate a bias toward males if males have higher post-hatching mortality than females. Such a bias would result if males die at an earlier age than females and if we failed to determine the sex of dead males. In this case broods in which males died would be underrepresented.

To determine the influence of laying order, egg mass, and growth rates on sex-biased mortality, we monitored nests from the time of hatching in 1980 and from the time of clutch initiation until chicks fledged in 1981 and 1982. During daily visits to nests we marked eggs on the large end with a felt pen so that laying and hatching order could be determined. We marked the egg tooth of each pipping chick, which allowed us to associate each chick with a marked egg.

We determined initial egg mass in a sample group of eggs within a day of laying with a 100-g capacity Pesola spring scale. We measured the length and breadth of these eggs with dial calipers to the nearest 0.05 mm, and we calculated a regression of mass vs. volume based on egg volumes determined by the equation of Barth (1967). We used this procedure to estimate initial egg masses from measurements gathered later in the season. To compare chick growth rates in relation to sex and hatching order, in 1982 chicks were weighed at 4-7-day intervals, beginning about the fifth day after hatching and continuing until the day that laparoscopies were performed. Small chicks were weighed with a 300-g capacity Pesola

TABLE 2. Egg mass ($\bar{x} \pm$ SD in grams) by sex.

Egg order	Male	Female	t^*	P
First	91.3 \pm 6.7 $n = 20$	89.8 \pm 4.8 $n = 26$	0.88	>0.40
Second	90.4 \pm 5.4 $n = 20$	92.6 \pm 5.3 $n = 26$	1.39	>0.20
Third	85.3 \pm 5.7 $n = 21$	85.3 \pm 4.1 $n = 16$	0.00	>0.90

* Student's t -test.

spring scale, and larger chicks with a 1,000-g capacity scale.

Growth-rate comparisons within sex and between hatching orders were based on an interval analysis [(mass at t_2 - mass at t_1)/($t_2 - t_1$); Ricklefs 1983] of the linear portion of the growth curves. The interval from t_1 to t_2 corresponds, approximately, to the time it takes Western Gull chicks to grow from 150 to 500 g.

RESULTS

We determined the sex of 1,291 Western Gull chicks over the period 1979-1983. For the 1,169 chicks that were living when we identified their sex, the sex ratio was 0.94 (M/F); for 122 chicks found dead before sex determination, the sex ratio was 1.19. Neither of these ratios is significantly different from 1.0, nor from each other (G -test, $P > 0.05$). We estimated a sex ratio at hatching of 1.12 M/F for 609 chicks from broods in which sex was determined for all chicks that hatched. The sex ratio in 185 sibships in which all chicks hatched and for which we determined the sex of all chicks did not differ from the expected binomial distribution (Table 1). Broods from clutches with and without egg mortality were combined after we determined that there were no significant differences in sex ratio for the two classes of broods. The sex ratio of chicks 25-35 days old was 1.01 ($n = 263$) and that of chicks more than 35 days old was 0.89 ($n = 189$). Neither of these sex ratios varied significantly from 1.0 (G -test, $P > 0.05$). There was an apparent shift from a predominance of males at hatching to a predominance of females among older chicks. We examined this shift in sex ratio by comparing the sex ratios of fledging-age chicks in broods in which all chicks survived (M/F = 1.12, $n = 599$) with the sex ratio in broods in which one or more chicks died (M/F = 0.80, $n = 162$) using a G -test ($G =$

TABLE 3. Growth rates (g/day) for Western Gull chicks on Santa Barbara Island (1980 and 1982) by sex and hatching order.

Hatching order	Males		Females	
	1980	1982	1980	1982
1	\bar{x}	32.5	25.3	
	SD	5.7	5.1	
	<i>n</i>	17	27	
2	\bar{x}	32.4	25.3	
	SD	6.9	4.9	
	<i>n</i>	18	28	
1 + 2	\bar{x}	29.6	24.8	25.3
	SD	3.2	2.3	5.0
	<i>n</i>	18	16	55
3	\bar{x}	23.7	24.7	23.9
	SD	3.2	5.8	3.2
	<i>n</i>	9	9	19
	<i>t</i> ^a	3.58	2.15	0.06
	<i>P</i>	<0.01	<0.05	>0.90
				>0.20

^a Student's *t*-test. Comparison of first- and second-hatched chicks with third-hatched chicks.

3.67, $P = 0.055$). This result suggests an excess male mortality before fledging that is marginally nonsignificant because of sample size.

We did not find significant seasonal differences in sex ratio at hatching among broods hatched at the beginning ($M/F = 1.01$, $n = 87$), middle ($M/F = 1.07$, $n = 467$), or end of the season ($M/F = 1.01$, $n = 185$). Likewise, in a subset of 73 three-egg clutches for which data on sex ratio and hatching order were available, we did not find statistically significant differences in the sex ratio of chicks hatched from first- ($M/F = 0.72$), second- ($M/F = 1.09$), or third-laid eggs ($M/F = 1.09$) (*G*-test, $P > 0.05$).

Male and female chicks hatched from eggs of similar mass (Table 2), but females grew at a slower rate than males (Table 3). Growth rates of first- and second-hatched males and females did not differ within sex (*t*-test, $P > 0.05$), and we therefore combined data within-sex for first- and second-hatched chicks. Growth rates for third-hatched males were less than those of first- and second-hatched males in both years for which data were available; third-hatched females did not exhibit significantly reduced growth in either year (Table 3).

Male chicks ≥ 36 days of age ($n = 91$) were heavier than females of a similar age ($n = 104$) (859 ± 68 vs. 705 ± 50 ; $t = 18.15$, $P < 0.001$). Although within broods there was no evidence

TABLE 4. Mean mass of broods of three near fledging (\bar{x} age = 39.1 ± 1.7 days, $n = 90$). There is a significant ($P < 0.001$) added variance among broods for combined sibling mass ($F = 15.85$).

Brood composition	Combined mass	No. of broods
3 females	$2,095 \pm 100^a$	5
2 females, 1 male	$2,247 \pm 133$	12
1 female, 2 males	$2,458 \pm 127$	10
3 males	$2,613 \pm 121$	3

^a Mean \pm SD.

for adjustment of parental investment such that equal masses of chicks of each sex are produced (Table 4), overall in the colony nearly equal masses of the two sexes fledged (1.09 gM/gF). Among males 35–40 days old, there were no statistically significant differences in mass between first- (A), second- (B), or third- (C) hatched chicks (A: 865 ± 55 g, B: 862 ± 55 g, C: 849 ± 63 g; $F = 0.5106$). Third-hatched chicks continued to grow after A and B chicks had completed growth; this allowed C chicks to achieve fledging masses similar to those of first- and second-hatched chicks, which reached asymptotic mass earlier.

DISCUSSION

Our results fail to support the hypothesis that the female bias in the sex ratio of breeding Western Gulls on SBI (0.67 M/F) can be accounted for solely by a similar bias in present-day sex ratios at fledging (0.89 M/F). It is also clear that the gulls are not adjusting the sex ratio of offspring at fledging to produce more of the rarer sex (Fisher 1930). Sex ratios in this population of Western Gulls did not vary with laying order, as has been found in other bird species (Ankney 1982, Davies and Payne 1982, Ryder 1983). There was no seasonal variation in sex ratio with date of initiation of hatching (Howe 1977, Weatherhead 1983).

There was a nonsignificant bias toward greater male mortality between hatching and fledging. Previous studies have associated chick mortality with hatching order, egg size, and reduced growth rates (Parsons 1970, 1975; Hunt and Hunt 1975, 1976; Lundberg and Väisänen 1979) and behavioral changes in hungry chicks (Hunt and McLoon 1975). The reduced growth rate of third-hatched males relative to first- and second-hatched males was the only mechanism

we could find for the excess male mortality (see also Howe 1976).

The apparent shift in sex ratio between hatching and fledging for the colony was in the same direction as that predicted by theories of equal parental investment in the two sexes (Fisher 1930, Trivers and Willard 1973, Charnov 1975), and was almost great enough to result in the production of an equal biomass of the two sexes at fledging. Although we did not detect a similar adjustment within broods, it is possible that a pair makes the appropriate adjustment of investment over a period of several breeding seasons. We have no evidence to test this hypothesis. Additional changes in sex ratio or parental investment may occur postfledging, as Western Gulls continue to care for their chicks for several weeks or months after departure from the colony (Briggs 1977).

We suggest that greater postfledging mortality of males than females must be primarily responsible for the biased sex ratio observed in the adult breeding population. Males are larger than females at fledging, and therefore may have greater difficulty in obtaining an adequate amount of food (Meyers 1978), particularly during the first months of independence when they are learning to forage (Verbeek 1977a, b; Searcy 1978). As adults, males also may suffer higher mortality rates than females because of stresses associated with territory establishment, as shown by Coulson and Wooler (1976) for the Black-legged Kittiwake (*Rissa tridactyla*).

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