Ontogenic Sex Ratio Variation in Nazca Boobies Ends in Male-Biased Adult Sex Ratio

TERRI J. MANESS[1], MARK A. WESTBROCK AND DAVID J. ANDERSON

Dept. of Biology, Wake Forest University, Winston-Salem NC USA 27109

[1]Corresponding author; tel 336 758 5573; fax 336 758 6008, e-mail manetj2@wfu.edu

Abstract.—Knowledge of the ontogeny of the sex ratio is required for proper framing of evolutionary hypotheses regarding adaptive parental sex allocation, competition for mates, evolution of mating systems, and endangered species management. We traced the development of a male-biased adult sex ratio in Nazca Boobies (*Sula granti*) by determination of the sex ratio at hatching, fledging, and at returning to join the adult population. The sex ratio at hatching and fledging did not differ from unity, while the return sex ratio was significantly male-biased. Therefore, the observed adult sex ratio bias arises after the period of parental care ends, during the subadult/juvenile stage, with important implications for mate competition. *Received 19 July 2006, accepted 23 October 2006.*

Key words.—Nazca Booby, *Sula granti*, fledgling survival, operational sex ratio, population sex ratio, sex allocation, sex-specific mortality.

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Biased adult sex ratios (proportion of males in the population; Wilson and Hardy 2002) in animal populations provide valuable opportunities to test hypotheses in several areas, including sex allocation (Fisher 1930; Trivers and Willard 1973; Clark 1978; Bull 1981; Charnov 1982), mating systems (Emlen and Oring 1977; Andersson 1994; Kvarnemo and Ahnesjö 2002; Shuster and Wade 2003), and endangered species management (Clout *et al.* 2002). Knowledge of the ontogeny of the bias provides critical context that allows proper framing of these hypotheses. For example, a bias attributable to sex-specific mortality early in the adult lifespan disturbs the operational sex ratio (OSR; proportion of sexually receptive males in the total population of sexually receptive individuals; Kvarnemo and Ahnesjö 1996, 2002) and thus can have a strong effect on the mating system via competition for mates (Emlen and Oring 1977; Andersson 1994; Shuster and Wade 2003). Conversely, a bias arising late in the reproductive lifespan may affect the adult sex ratio but exert little selective influence on mating dynamics (Weimerskirch *et al.* 2005). Regarding sex allocation, a bias in the adult sex ratio due to mortality before the end of parental care should induce frequency-dependent selection on parents to over-produce the rare sex; a bias arising after the end of parental care should not induce such selection (Fisher 1930; Charnov 1982). The ontogeny of sex ratio bias is thus a significant point of interest.

Tracing the sex ratio through the lifespan of a bird species can be difficult and is seldom attempted, in part because the possibility of sex-specific dispersal frequently interferes with comprehensive estimates of the sex ratio at demographic mileposts, and because non-invasive sex determination of nestlings (Griffiths *et al.* 1998; Sheldon 1998; Fridolfsson and Ellegren 1999) has only recently become available. To evaluate hypotheses regarding sex allocation, sex ratio at birth/hatching and at the end of the parental investment period/fledging have been measured for a number of species of mammals and birds (reviewed in Clutton-Brock 1986; Clutton-Brock and Iason 1986; Gowaty 1993) but only a few studies of birds (Rufous Vangas (*Schetba rufa*), Asai *et al.* 2003; Roseate Terns (*Sterna dougallii*), Szczys *et al.* 2005; Wandering Albatrosses (*Diomedea exulans*), Weimerskirch *et al.* 2005) have also documented the sex ratio after this offspring rearing period into adulthood. A biased (or balanced) sex ratio early in ontogeny may not persist into adulthood, so the sex ratio of young at the end of the parental care period may not predict the sex ratio of the adult population, highlighting the value of a comprehensive tracking of the sex ratio across the lifespan.

Townsend and Anderson (2007) documented a consistently male-biased adult sex ratio (0.589, 95% CI 0.589-0.589) in a 19 yr study of Nazca Boobies (*Sula granti*) in the Galápagos Islands, suggesting more intense male-male competition for mates. Adults showed no sex-specific mortality, but age-specific mortality was not examined because the age of many of the adults was not known. Nazca Boobies have a post-reproductive lifespan (PRLS; Anderson and Apanius 2003), during which sex-specific mortality would bias the adult sex ratio but not the OSR, similar to the result for Wandering Albatrosses (Weimerskirsh *et al.* 2005). If a bias arose during the PRLS, then evolution of the mating system should be independent of the excess of adult males. To inform hypotheses regarding competition for mates given the adult sex ratio bias, identification of the timing of the appearance of the bias is required. In this paper, we use our long-term database on this population and molecular sexing of two large cohorts of chicks to trace the ontogeny of this bias in the adult sex ratio and to determine the stage at which the male bias arises. We measured the sex ratio at hatching (secondary sex ratio), fledging (tertiary sex ratio), and early adulthood (return sex ratio, measured upon return into the colony-based adult population after several subadult years at sea).

Nazca Boobies are long-lived (Anderson and Apanius 2003) predatory birds with a low reproductive rate, raising, at most, only a single offspring per year (Humphries *et al.* 2006) from a clutch of one or two eggs (Anderson 1990). The second egg in two-egg clutches ("B-egg") is laid several days after the "A-egg" (Anderson 1989a), and if both eggs hatch, only one chick (usually the product of the A-egg) survives siblicidal interactions shortly after hatching (Humphries *et al.* 2006). Our long-term study of the reproductive life history of Nazca Boobies has revealed several strengths of this species as a model for research on sex ratio evolution. Colonial breeding (Anderson 1993) permits collection of large sample sizes, providing substantial statistical power. Adults and nestlings have been banded in most years since 1984-85, giving a total of 1960 birds banded as adults and 8,822 as nestlings (many of whom survived to adulthood). Unlike many seabirds, adults are sexually dimorphic (in voice) and can be easily sexed (Nelson 1978). The colony attendance patterns of banded adults yield high encounter probabilities (ranging from 0.82 to 0.90 for males and 0.76 to 0.86 for females, not significantly different; Townsend and Anderson 2007) during our annual band-resight surveys (Huyvaert and Anderson 2004), giving estimates of sex-specific survival with low error. Finally and of particular importance, both natal philopatry and adult nest site fidelity are essentially 100%, so a permanent absence from the breeding colony reliably indicates death (Huyvaert and Anderson 2004). We know of no studies that have traced the ontogeny of the sex ratio in a highly philopatric species which lacks the confounding influence of dispersal. Of the few studies available, females disperse to breed in the Rufous Vanga (Asai *et al.* 2003), up to 42% of juvenile Roseate Terns are estimated emigrate to other sites (Lebreton *et al.* 2003), and 23% of Wandering Albatross juveniles disperse to breed in non-natal colonies (Inchausti and Weimerskirsh 2002).

METHODS

We calculated the secondary sex ratio of 918 and 1,236 hatchlings in the 2001-02 and 2002-03 breeding seasons, respectively, based on analyses of blood samples collected from hatchlings at our study site at Punta Cevallos, Isla Española, Galápagos Islands (details in Anderson and Ricklefs 1987 and Huyvaert and Anderson 2004). We also calculated the post-siblicide offspring sex ratio by excluding all hatchlings lost during brood reduction, leaving 692 and 915 hatchlings in the two seasons, respectively. In these two years, we monitored 1,410 and 1,582 nests, respectively, on a daily basis, marking A- and B-eggs on the day of laying. We took blood samples within 24 h of hatching from the brachial or femoral vein by venipuncture, collecting the blood on a filter paper tab, and preserving it in 70% ethanol. In 2001-02 we failed to collect blood samples from five hatchlings due to errors and from eight who disappeared before sampling. In 2002-03, the corresponding figures were five and three. In 2001-02 we arrived at the colony after the start of hatching, and the 18 chicks already present, plus an unknown (but small) number that had already died and disappeared, were excluded from all analyses. Genomic DNA was isolated from blood samples by phenol/chloroform extraction (Sambrook *et al.* 1989). Sex of the nestlings was determined by PCR amplification of an intron region of the CHD gene (Fridolfsson and Ellegren 1999). We validated this sexing technique with blind testing of 100 known-sex adult Nazca Boobies. Of the 2,259 sex determinations attempted, 55 (2.4%) failed to amplify due to DNA degradation or low DNA content of the sample (28, or 1.2% of the total) or for unknown reasons (27, or 1.2% of the total). Our study does not include the determination of the primary (at fertilization) sex ratio because molecular identification of embryonic sex is problematic (Arnold *et al.* 2003) and would require sacrificing hundreds of eggs within a national park.

We calculated the tertiary sex ratio in these same two years by monitoring the sexed offspring during the daily nest checks, determining either the date of death or the date of fledging. Nazca Booby offspring remain at or near the nest site until they can fly, and are usually seen at the nest site at lower frequency after becoming volant. Approximately 15 days before fledging, chicks finish replacing their original downy plumage with pennaceous feathers. Since 1992-93, we have used daily nest checks to note the age at which chicks reached the "1% down" developmental stage, at which only 1% of the original down still remained. Since little mortality occurs after the 1% down stage (Humphries *et al.* 2006), we estimated fledging success using the number of chicks reaching this stage. To assess the breeding conditions in 2001-02 and 2002-03, we compared the number of nests initiated and the number of offspring fledged in those years with those of the previous nine years in all nests in the "Study Area," a subsection of the breeding colony in which all nests are monitored in every year since 1992.

After fledging, Nazca Booby fledglings vacate the colony; band returns indicate that the juvenile/subadult period of several years is spent at sea off the Central American and Mexican Pacific coasts (Huyvaert and Anderson 2004). They return to Punta Cevallos as prebreeding adults and are first detected in the annual band resight survey, conducted at the beginning of each breeding season (detailed in Huyvaert and Anderson 2004). Thereafter, these adults are seen regularly at Punta Cevallos, and we refer to this switch from a pelagic existence to a colony-centered existence as "return." We estimated the return sex ratio as the representation of males (determined by voice; Nelson 1978) among all individuals that were observed as adults in the colony during either the annual band resight survey (Huyvaert and Anderson 2004) or during yearly nest monitoring of breeders (described in Anderson and Ricklefs 1987; Huyvaert and Anderson 2004), for the cohorts that fledged during the breeding seasons beginning in 1984-87 and 1992-95 (eight cohorts). Ongoing annual band resight surveys began in 1984 and comprehensive nest monitoring began in the 1992-93 breeding season. Adults rarely appear in the colony for the first time after reaching the age of eight or nine (T. Maness, unpublished data); therefore, most of the fledglings that survived the juvenile period had returned and were regular colony attendants when this study was conducted (the youngest cohort was ten years old).

Statistical Analyses

Empirically determined sex ratios were compared using G tests, and empirical and predicted sex ratios were compared using χ^2 Goodness of Fit tests.

We examined sex- and age-specific variability in chick survival probabilities (S) by developing "known fate" models implemented in Program MARK (White and Burnham 1999). Using daily nest check data, we constructed individual encounter histories for all chicks showing whether (a) the chick was alive at the beginning of a given interval, (b) the chick died during an interval, or (c) the chick fledged during an interval, after which time it was censored. All individuals entered the study upon hatching, which we set to be the first interval in all cases (an "even entry" design), although hatching occurred over periods of 128 and 175 days, in 2001-02 and 2002-03, respectively. We developed an *a priori* set of four models incorporating the effects of chick sex (g: male or female), 10-d age group (a), and their interaction.

We based model selection and ranking on relative differences of the Akaike Information Criterion (AIC) following Burnham and Anderson (2002). We used adjusted AIC values (AIC_C) to account for small sample sizes, although the ratio of n to K (number of model parameters) was sufficiently large in most cases (>40; Burnham and Anderson 2002) to justify use of AIC. In such cases, inferences using AIC and AIC_C strongly tend to converge (Burnham and Anderson 2002, p. 66). Also following Burnham and Anderson (2002), any competing models with AIC_C differences ($DAIC_C$) <2 were considered to have similar explanatory power. In 2001-02, monitored nestlings were followed until they had not been seen for 21 days after apparently fledging, but in 2002-03 only until fledging. Elsewhere we have shown that little mortality occurs after fledging and before vacating the colony (Humphries *et al.* 2006). As a further test of the assumption that sex-specific mortality is not important between fledging and vacating the colony, we used the longer encounter histories from 2001-02 in two separate analyses: one for the period hatching to fledging (matching that of 2002-03 in extent), and another for the period hatching to vacating the colony.

All statistical tests except mark-recapture modeling were performed with Statistica software (kernel release 5.5; Statsoft Inc. 1999).

RESULTS

Molecular Sexing

Of known-sex adults, all 50 male and 50 female adults were correctly sexed from their blood samples.

The secondary sex ratio (all hatchlings) was not different from 0.50 in either 2001-02 (0.488, 95% C.I. 0.456-0.520; $\chi^2_1 = 0.53$, n.s.) or 2002-03 (0.474, 95% C.I. 0.446-0.502; $\chi^2_1 = 3.31$, n.s.). Similarly, the post-siblicide sex ratio (hatchlings, excluding brood reduction victims) was not different from 0.50 in either 2001-02 (0.490, 95% C.I. 0.453-0.527; $\chi^2_1 = 0.28$, n.s.) or 2002-03 (0.474, 95% C.I. 0.442-0.507; $\chi^2_1 = 2.41$, n.s.). The post-siblicide sex ratio was not different from the secondary sex ratio in 2001-02 ($G_1 < 0.001$, n.s.) or in 2002-03 ($G_1 < 0.001$, n.s.). In 2001-02, the tertiary sex ratio (0.490, 95% C.I. 0.428-0.552;

N = 245) was not different from the post-siblicide sex ratio ($G_1 = 0.00$, n.s.), or from 0.50 ($\chi^2_1 = 0.10$, n.s.). In 2002-03, the tertiary sex ratio (0.482, 95% C.I. 0.447-0.517, N=788) was also not different from the post-siblicide sex ratio ($G_1 = 0.100$, n.s.), or from 0.50 ($\chi^2_1 = 0.971$, n.s.).

Nestling Survival

In the Study Area (see Methods), the 2001-02 and 2002-03 breeding seasons were years of below (245 fledglings; 35% post-siblicide survival rate) and above average (788 fledglings; 86% post-siblicide survival rate) breeding productivity, respectively, compared to the previous nine years (Fig. 1).

Model ranking using AIC_C in both years gave little support for an influence of nestling sex on survival to fledging (Table 1). The model likelihood of the best model that included a nestling sex effect (g) in 2001-02 (S(g*a)) indicated that it received essentially no support relative to the best model overall, which included no sex effect (S(a); Table 1). The model likelihood of the best model including a sex effect in 2002-03 (also S(g*a)) indicated that the data supported the best model (S(a)) approximately 11.1 times (= 0.0897^{-1}; Table 1) more. Given the low support for the second ranked models (those including sex effects), use of "real parameter estimates" from those models for visual representation of the survival schedules of males compared to females was not advised (Burnham and Anderson 2002). Instead, we used the ratio of the actual number of nestlings surviving (or fledging during) a 10-d age class to the number entering the class to show survival schedules (Fig. 2).

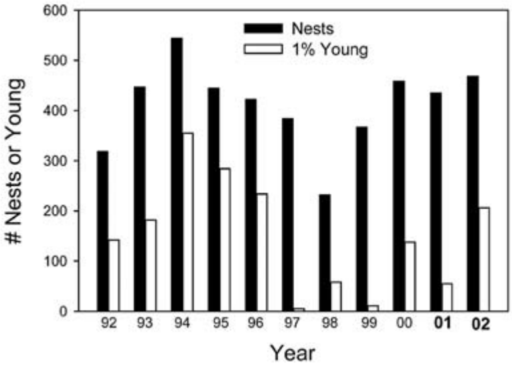

Figure 1. Number of nests initiated, and number of chicks reaching the 1% down developmental stage (see text), in the Study Area (a representative area of the Punta Cevallos Nazca Booby colony) over an eleven-year period. The two years in which secondary and tertiary sex ratios were estimated are indicated in bold. "92" refers to 1992-93 breeding season, etc.

Return Sex Ratio

The return sex ratio of four of the eight cohorts was significantly male biased ($\chi^2_1 \geq 5.35$, $P < 0.02$ for the 1986-87, 1987-88, 1992-93, and 1994-95 cohorts), and did not differ from a balanced sex ratio for the other four cohorts (Fig. 3). The overall return sex ratio was 0.575 (95% C.I. 0.551-0.598), and was significantly male biased (Fig. 3; $\chi^2_1 = 36.06$, $P < 0.001$).

DISCUSSION

We have shown that the male-biased adult sex ratio in our study population cannot be accounted for by male-biased hatching and/or fledging sex ratios in our study population and that no sex-specific mortality occurred during the nestling period (Fig. 2, Table 1). The two breeding seasons in which these parameters were measured were of below average (first year) and above average (second year) reproductive performance (Fig. 1). Parents might adaptively alter the sex of their offspring according to current environmental conditions, or sex-specific mortality might occur in poor food years; the fact that the sex ratio was balanced at hatching and fledging in both of these contrasting years provides evidence that the sex ratio at these stages is not sensitive to inter-annual environmental variation in Nazca Boobies. The overall return sex ratio, from eight cohorts, was significantly male-biased at a value similar to the overall adult sex ratio (Townsend and Anderson 2007), due to detectable deficits of females in four of the cohorts. These data indicate that the male biased adult sex ratio in our study population arises after the period of parental care ends, during the juvenile/subadult stage between fledging and return

Table 1. AIC$_C$ rankings of known fate models developed in Program MARK. Survival probabilities (S) were modeled as constant (.) over age intervals, as a function of age (a), and as a function of sex (g), incorporating interactions of these factors. The two sets of models fit for 2001-02 test the assumption that truncation of the encounter history at the fledging stage does not affect model selection and ranking.

Model	AIC$_C$	ΔAIC$_C$	AIC$_C$ weight	Model likelihood	Number of parameters
2001-02, hatching until fledging					
S(a)	1213.0	0	1.00000	1	15
S(g*a)	1243.7	30.7	0.00000	0.0000	30
S(.)	1271.7	58.8	0.00000	0.0000	1
S(g)	1273.7	60.8	0.00000	0.0000	2
2001-02, hatching until last seen					
S(a)	2690.0	0	0.99960	1	20
S(g*a)	2705.7	15.6	0.00040	0.0004	40
S(.)	2925.2	235.4	0.00000	0.0000	1
S(g)	2927.2	237.1	0.00000	0.0000	2
2002-03, hatching until fledging					
S(a)	1303.0	0	0.91771	1	13
S(g*a)	1307.5	4.8	0.08229	0.0897	26
S(.)	1387.4	84.7	0.0	0.0	1
S(g)	1389.0	86.3	0.0	0.0	2

to the colony. This bias cannot be attributed to sex-specific emigration (Huyvaert and Anderson 2004). Instead, the deficit of female recruits is apparently a consequence of sex-specific post-fledging mortality.

Sex differences in mortality of newly independent animals could have a variety of causes. In many bird and mammal species, males exhibit higher juvenile mortality, presumably because their larger body size leads to higher energy requirements, which they fail to satisfy while they are learning to become independent (Clutton-Brock *et al.* 1985). Adult female Nazca Boobies are 16% heavier than males (Nelson 1978), indicating the possibility of higher energy requirements, which could lead to higher mortality rates while learning to forage. If this were true, then the general quality of environmental conditions early in life should predict mortality based on this cause, but only partial correspondence exists between the indicators of breeding conditions in Fig. 1 and the eventual return sex ratios from those cohorts shown in Fig. 3. El Niño-Southern Oscillation (ENSO) conditions affect food supply around our study colony and depress breeding performance (Anderson 1989b), and three of the four cohorts with a male bias at return experienced conditions of the 1987-88 or 1992-93 ENSO events within a year of fledging (Fig. 3). Sub-adult females might have experienced more food stress

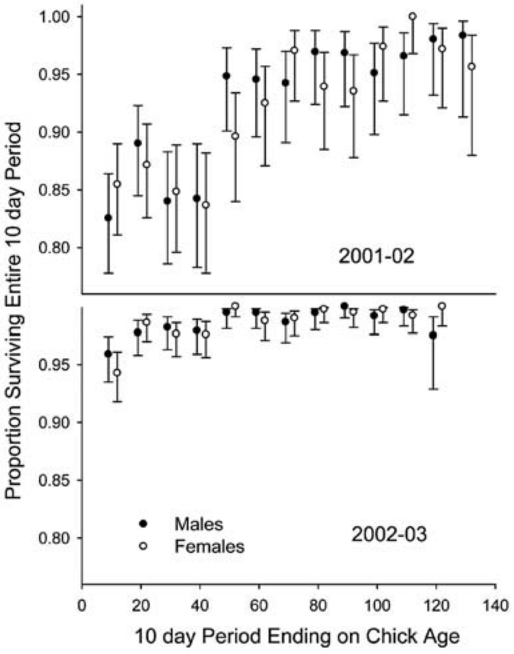

Figure 2. Proportion (± binomial 95% C.I.) of male and female offspring that enter a 10-d age class and also survive that age class in 2001-02 (A) and 2002-03 (B).

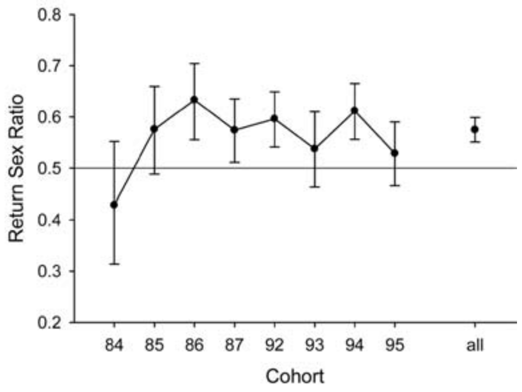

Figure 3. Return sex ratio (± binomial 95% C.I.) of all birds in selected cohorts that returned to join the adult, colony-based population. "84" refers to 1984-85 breeding season, etc. "All" is the overall return sex ratio determined from all eight cohorts.

than males did during these events, accounting for the deficit of females at return in these cohorts, but the strongly male-biased 1994-95 cohort, which did not experience ENSO conditions, departs from this pattern.

Alternatively, members of the larger sex may fledge at a disadvantage if parents meet their requirements less well than those of the smaller sex, which would exacerbate problems associated with post-independence inexperience. Townsend (2004) found that the asymptotic mass of Nazca Booby male nestlings was 105.8% that of mean adult male mass found by Anderson (1993), but the asymptotic mass of female nestlings was only 99.4% of typical adult female mass in the 2000-01 breeding season. In addition, asymptotic mass of females was more variable than that of males. This result suggests that female, but not male, nestlings were food-stressed to a degree that their growth was compromised. Hylton *et al.* (2006) found no correlation between body condition and subsequent post-fledgling mortality in the slightly size dimorphic Wood Stork (*Mycteria americana*), although they observed excess mortality of the larger sex (males) after fledging. The authors acknowledge, however, that their results may have been confounded by their inability to monitor body condition late in the nestling period; condition was assessed 3-4 weeks prior to fledging. Assessment of the condition of offspring just prior to independence and comparative survival analyses are needed to fully assess the influence of fledging condition on sex-specific mortality. Dispersal has also been linked to increased mortality risk in mammals and birds (Gaines and McClenaghan 1980; Clarke *et al.* 1997; Yoder *et al.* 2004), but is unlikely to account for higher mortality of juvenile females in Nazca Boobies given their virtually complete natal philopatry (Huyvaert and Anderson 2004).

The male bias in our population's sex ratio arises before the age of breeding, and so is expected to affect the OSR. If true, then mating system theory predicts more competition for mates among males than among females, a higher opportunity for selection on males, and a higher variance in male reproductive success (Emlen and Oring 1977; Andersson 1994; Shuster and Wade 2003). Our results provide the critical context in which to frame hypotheses regarding parental sex allocation and mate choice in this species and insight into the causes of bias sex ratios in birds. To our knowledge, our study is the most complete documentation of the ontogeny of the sex ratio across the lifespan for any highly philopatric wild bird species.

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