



## OFFSPRING SEX RATIO IS RELATED WITH LAYING DATE AND HATCHING SEQUENCE IN THE MAGELLANIC PENGUIN *SPHENISCUS MAGELLANICUS*

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**Abstract** · We analyzed the variation in the secondary sex ratio of Magellanic Penguin *Spheniscus magellanicus* breeding in six colonies on the Patagonian coast of Argentina. We tested the effects of laying date and hatching sequence on the probability of producing sons and daughters. The global secondary sex ratio did not differ from equality, and there were no differences among the colonies. However, regardless of the colony, laying date, and hatching sequence, there was a significant effect on the proportion of males and females reared. Pairs that were laid early in the breeding season were more likely to raise a male. In addition, offspring that hatched first were more likely to be male than those that hatched second. Our results are consistent with the adaptive importance of producing males, likely the costliest sex, early in the breeding season or early in the brood when food resources are still abundant.

**Resumen** · La proporción sexual de las crías está relacionada con la fecha de postura y el orden de eclosión en el pingüino de Magallanes *Spheniscus magellanicus*

Analizamos la variación en la proporción de sexos, al momento de la eclosión, en el pingüino de Magallanes *Spheniscus magellanicus*, que se reproduce en seis colonias en la costa patagónica de Argentina. Probamos los efectos de la fecha de puesta y la secuencia de eclosión sobre la probabilidad de producir hijos e hijas. La proporción global de sexos al momento de la eclosión no difirió de la igualdad y no hubo diferencias entre colonias. Sin embargo, independientemente de la colonia, la fecha de puesta y la secuencia de eclosión de las crías tuvieron un efecto significativo en la proporción de machos y hembras criados. Las parejas que pusieron huevos temprano en la temporada reproductiva tenían más probabilidades de criar un macho. Además, las crías que nacieron primero tenían más probabilidades de ser machos que las que nacieron en segundo lugar. Nuestros resultados son consistentes con la importancia adaptativa de producir machos, probablemente el sexo más costoso, al comienzo de la temporada de reproducción o al comienzo de la cría, cuando los recursos alimentarios aún son abundantes.

**Key words:** *breeding · brood · Patagonia*

### INTRODUCTION

Sex ratio Fisher's theory (1958) predicts similar investment in male and female offspring, and thus, an equal sex ratio at the end of parental care. The sex ratio can be different at fertilization (the time at which the sperm fertilizes the eggs, primary sex ratio), at the time of hatching at different ages of the young (secondary sex ratio), or when individuals reach sexual maturity (tertiary sex ratio). In species where male and female offspring differ in size, the larger sex may require more energy for growth, and it is costlier to rise to independence (Fiala and Congdon 1983, Velando et al. 2002, Kalmbach et al. 2005). Thus, equal investment by parents in offspring of different sexes may result in smaller sex producing more at the end of parental care (Kolman 1960). However, variation in the sex ratio of offspring should be favored by natural selection if the relative fitness of daughters and sons varies in the population (Trivers & Willard 1973, Charnov 1982). For example, in species in which the breeding success of males is more strongly influenced by body size and early growth than that of females, the sex ratio of males is skewed (Trivers & Willard 1973, Clutton-Brock 1985). In birds, a skewed sex ratio can result from the female's facultative influence on the sex of the offspring, since the female is the heterogametic sex and so non-Mendelian segregation of the sex chromosomes could conceivably be under maternal control. Another possibility is that follicles that ultimately give rise to males and females grow at different rates. Alternatively, the female might selectively abort embryos or 'dump lay' eggs of a particular sex, deny certain ova a chance of ovulation, fertilization, or zygote formation, or selectively provision eggs so that there is sex-specific embryonic mortality (Krackow 1995, Blanco et al. 2002, Pike & Petrie 2003).

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In size-dimorphic bird species, the larger sex is generally more susceptible to food shortages and has a higher mortality rate than the smaller sex (Torres & Drummond 1997, 1999a, 1999b, Kalmbach et al. 2005). When facultative brood reduction occurs, progenitors can minimize the loss of the more expensive sex by producing it at the time of the breeding season when food resources are more abundant (Olsen & Cockburn 1991, Velando et al. 2002), which would increase the probability of survival of a given sex. Skewed sex ratios depending on different environmental or parental conditions have been reported less frequently in birds than in mammals (Krackow 1995, Fargallo et al. 2004, 2006). However, several authors have reported changes in the direction of the sex ratio as a function of the egg sequence (Ankey 1982, Ryder 1983, Clutton-Brock 1985, Dzus et al. 1996, Blanco et al. 2002, Fargallo et al. 2006), and laying date (Dijkstra et al. 1990, Tella et al. 1996, Velando et al. 2002).

The Magellanic Penguin *Spheniscus magellanicus* is a monogamous, long-lived seabird that is widely distributed along the Atlantic and Pacific coasts of South America (Yorio et al. 1998, Tella et al. 2001, Forero et al. 2002, Bertellotti et al. 2006). Adults fast during the settlement and laying period (Boersma et al. 1990). They lay two eggs of almost equal size, usually 3–4 days apart, and the laying period lasts approximately a month (Boersma et al. 1990). It is a dimorphic species in which adult males are approximately 20% heavier and 10% larger than the females (Scolaro et al. 1983, Forero et al. 2001, Bertellotti et al. 2002). Size dimorphism is evident even in young birds (Scolaro 1987). During the breeding season, both sexes defend their nesting sites, incubate the eggs, and feed the chicks. Several studies have shown that a lack of food and extreme weather conditions in a high proportion of nests can lead to a reduction in brood size, with the loss of second-hatched chicks (Boersma et al. 1990, Boersma & Stokes 1995, Frere et al. 1998). Forero et al. (2001, 2002) showed that the lack of food in the vicinity of colonies strongly influences breeding success and the body condition of the offspring.

In this study, we investigated the sex-ratio of secondary offspring in six Magellanic Penguin colonies on the Patagonian coast in relation to different ecological conditions, including colony characteristics, geographical location, population density, and nest characteristics. We specifically focused on the effects of laying date and possible control of sex ratio by females by

determining the hatching sequence of eggs with embryos of different sexes.

## METHODS

The study was conducted in the province of Chubut (Patagonia, Argentina) between January and February 1999. In this area, we selected six breeding colonies distributed along 500 km of coastline, varying in size from 483 to 175000 breeding pairs (for more details on colony characteristics and distribution of colony size, see Yorio et al. 1998, Tella et al. 2001, Forero et al. 2002, Bertellotti et al. 2006). We captured 70–90-day old chicks in their nests just before they are mixed with other chicks in crèches. Since Magellanic Penguin defend their nests against all types of intruders, we assumed that the chicks in the nest are siblings, although we did not mark the chicks at hatching. We considered the largest chick to be the first chick, as in this species, the chicks that are fed soon after birth show a size difference between siblings (Gownaris & Boersma 2021). We recorded the size of the brood (one or two chicks) and the hatching order in the brood as a function of their size and stage of development (Boersma & Stokes 1995). To estimate chick age, we used beak length and data from Boersma et al. (1990) and performed a model II regression using standard principal axis regression (Legendre 2000). The age of the chicks was derived from the following equation: Chick age (days) =  $2.89 * \text{beak length} - 56.87$  ( $r^2 = 0.998$ ,  $P < 0.0001$ ,  $n = 21$ ). The laying date was estimated as the day of visit – (chick age + incubation period) from January 1, 1998, assuming an incubation period of 40 days (Boersma et al. 1990). The sex of the chicks was determined by molecular tools using a drop of blood from the brachial vein (Bertellotti et al. 2002).

First, we determined the sex ratio at hatching of 45 broods of two chicks from four colonies before brood reduction to assess parental female control over sex in the brood. To test the effects of ecological conditions on offspring sex ratio, we selected additional nests and measured nest sites, nesting habitats, and colony characteristics (Table 1). When selecting nests, we attempted to achieve a balance between the location in the colony, nesting habitat, and brood density. We included “nest” and “colony” as explanatory variables because some unmeasured characteristics could explain some of the variation in sex ratio. Nest site characteristics were assessed using three

**Table 1.** Variables used to analyze the sex ratio in nestling Magellanic Penguins.

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### INDIVIDUAL CHARACTERISTICS

SEX: Determined by molecular methods using the cellular fraction of blood as the source of DNA.

BROOD SIZE: Number of chicks in a brood: (1) one chick and (2) two chicks.

HATCHING ORDER: (1) single chicks, (2) older chick in a brood of two chicks, and (3) younger chick in a brood of two chicks.

DATE OF BROOD: Date of the egg (analysis by chick) and date of the first egg (analysis by nest).

### NEST-SITE CHARACTERISTICS

NEST OF ORIGIN: Code for each nest from which nestlings were sampled.

TYPE OF NEST: (1) nest under bushes, (2) nest in burrows, and (3) nest in burrows under bushes.

NEST COVER: Side and roof cover of the nest estimated visually to the nearest 5% from a position directly above the nest.

NEST DEPTH: Measured in cm with a self-retracting metal tape measure, as the distance between the nest entrance and nest-cup chamber.

### NESTING HABITAT CHARACTERISTICS

DISTANCE TO THE SEA: Measured in m using a portable telemeter as the distance between the nest entrance and the seaside.

COVER OF BUSHES: Estimated visually to the nearest 5% from several positions around the nest in a circular plot of 100 m<sup>2</sup> centered in each nest from where chicks were sampled.

NUMBER OF BUSH PATCHES: Counted in 100-m<sup>2</sup> circular plots around each nest from where chicks were sampled.

BREEDING DENSITY: Number of nests counted in 100 m<sup>2</sup> around each nest from where the chicks were sampled.

CHICK DENSITY: Number of penguin chicks in 100 m<sup>2</sup> around each nest from where the chicks were sampled.

DENSITY OF CRECHES: Number of associations of several chicks, usually between 5 and 50, in 100 m<sup>2</sup> around each nest from where the chicks were sampled.

NUMBER OF NESTS TO THE SEA: Counted in a band of one-meter width at each side of the observer, in a walked line transect from the nest entrance to the sea.

### COLONY CHARACTERISTICS

COLONY: Codes for each colony.

LATITUDE: Calculated in minutes south of the equator.

COLONY SIZE: Number of breeding pairs obtained from Yorio et al. (1998).

POPULATION DENSITY: Number of breeding pairs around 100 km obtained from Yorio et al. (1998).

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**Table 2.** Global sex ratio in Magellanic Penguin colonies in Patagonia, Argentina.

Colony	Colony size (pairs)	Population density	Chick sexed (number of nest)	Sex ratio
(1) Asentamiento W	483	43908	33 (22)	0.52
(2) Isla de la Caleta	13780	43908	34 (24)	0.41
(3) San Lorenzo	17034	43908	51 (34)	0.57
(4) Caleta Interna	1553	43908	52 (36)	0.46
(5) Punta Tombo	175000	252286	89 (66)	0.51
(6) Cabo Dos Bahías	9067	413555	49 (37)	0.51
Total			308 (219)	0.50

variables that could influence the breeding success of this species through warmth and avian predation (Table 1) (Stokes & Boersma 1998). Nest location in the colony was measured as the distance from the nest to the sea. Similarly, we counted the number of nests on a line transect from the nest site to the sea. Several variables described the characteristics of the colony in which individual chicks were sampled (Table 1). Forero et al. (2002) have shown that both colony size and conspecific density in the vicinity of the colony strongly influence the body condition of chicks and determine population structure through intraspecific foraging competence. Therefore, we tested the effects of both variables on the secondary sex ratio (Table 1).

**Statistical analysis** · We used generalized linear mixed models (GLMMs; Littell et al. 1996) to simultaneously assess the effects of explanatory variables and their interactions on the sex ratio of offspring in the Magellanic Penguin. GLMMs are a useful extension of traditional GLMs (see McCullagh & Nelder 1983) because they allow the inclusion of independent random variables and nested effects in the models. Thus, we included colony and nest identities nested within the colony as random variables using the SAS macro program GLIMMIX (Littell et al. 1996). The GLIMMIX macro automatically adjusts the extradispersion using scaled deviation. Finally, the kappa statistic (Titus, Mosher & Williams 1984) was applied to assess whether model discrimination between groups significantly improved random classifications.

We conducted two different approaches to analyze the offspring sex ratio by using two different response variables. First, we analyzed the secondary sex ratio by chick, using the individual sex of the offspring (male = 1, female = 0) as the response variable and all variables listed in Table 1 as explanatory variables, with a binomial distribution (denominator = 1) and a logistic relationship. Second, we considered the sex ratio of chicks in double broods, as brood reduction could introduce disturbances into the models.

## RESULTS

**Sex ratio at hatching** · The sex ratio at hatching was examined in 45 broods with two chicks from four colonies before brood reduction. The sex ratio did not differ between the four colonies (G-test,  $G = 6.38$ ,  $P = 0.094$ ,  $df = 3$ ; Table 2). The sex ratio in these nests did not vary significantly from parity when considering either all colonies together or each colony individually (binomial test, all  $P > 0.1$ ).

In double broods, 58.5% of the first chicks and 36.0% of the second chicks were male. 42.9% of the nests contained one male and one female, 35.2% of the nests contained no male, while 21.9% of the nests contained two male chicks.

**Sex ratio of 70–90-day old chicks** · The GLMM for secondary sex ratio using the sex of fledglings as the response variable showed that it was influenced by laying date, hatching sequence, and population density within 100 km of the colony (Table 3, all  $P < 0.002$ ). The probability of being a male decreased with increasing laying date in the breeding season and was higher for chicks hatched in the first sequence than in the second. The probability of being male in single and double broods was also higher at high population brood densities. This model explained 27.0% of the initial variation, correctly classified 66.6% of the cases, and significantly improved the random classifications (kappa test:  $Z = 5.78$ ,  $P < 0.001$ ; Figure 2).

For broods without nestling mortality (double broods), the model only considered laying date and hatching order (Table 4). Thus, the probability of producing a male was higher in the early broods and in the first hatching positions within the brood (Figure 1). This model explained 21% of the initial variation and 53.6% of the cases were correctly classified, which significantly improved the classification by chance (kappa test:  $Z = 3.63$ ,  $P < 0.001$ ).

## DISCUSSION

From the perspective of Fisher's theory (1958), the sex ratio is expected to vary inversely with relative parental investment in male and female offspring. Thus, given that males are heavier and larger than females at the end of parental care (Scolaro 1987) and assuming that males are more expensive to rear (Fiala and Congdon 1983), we expected a female-biased sex ratio. In contrast, we found a male-biased sex ratio in the Magellanic Penguin, but only at the beginning of the breeding season. Similar results have been found in several raptor species, where, although females are larger than males, a female-biased sex ratio was found despite the obvious costs associated with producing females early in the breeding season (Bortolotti 1986, Olsen & Cockburn 1991). Other studies on seabirds showed that the risk of death of offspring of the larger sex increased with hatching sequence and laying date, suggesting that the larger sex is more susceptible to food-related stress (Torres & Drummond 1997, 1999a, Kalmbach et al. 2005). The male-biased sex ratio early in the breeding season

**Table 3.** Generalized Linear Model (GLMMIX) for sex ratio in Magellanic Penguin chicks, using binomial error and logistic link (deviance initial = 425.6).

Variable	Parameter estimated	Standard error	P-value
Intercept	38.87	7.38	0.006
Laying date	-0.15	0.03	0.0001
Laying order (first)	1.34	0.26	0.0001
Population density	4.40	1.40	0.0018
Deviance residual	310.7		

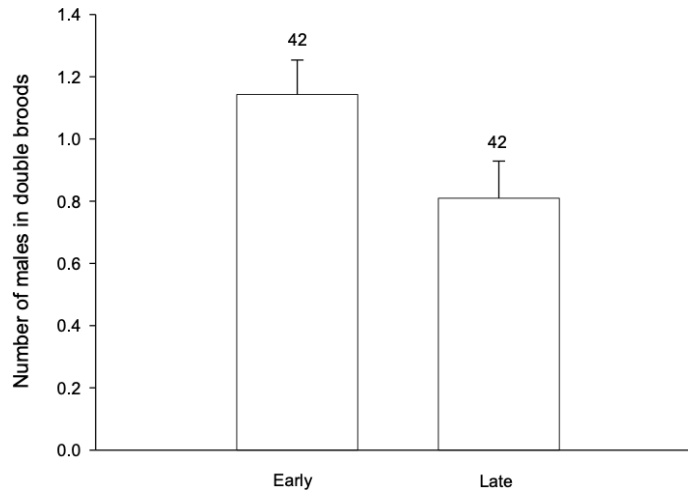
and early within the brood could be an adaptation to balance the survival probability in double broods by increasing the survival probability of the larger sex with higher nutritional requirements for growth.

Nest quality is an important feature that influences breeding success in Magellanic Penguin (Stokes & Boersma 1998, Villanueva et al. 2011). Fights between breeding males for better nests are very common at the beginning of the breeding season, with the largest males usually winning the fights before eggs are laid (Renison et al. 2002). Therefore, producing first and early males could be a strategy to improve their growth, which could have important effects on fitness. Facultative manipulation of the sex ratio should be beneficial if the costs and benefits of producing a particular sex vary over time (Wiebe & Bortolotti 1992).

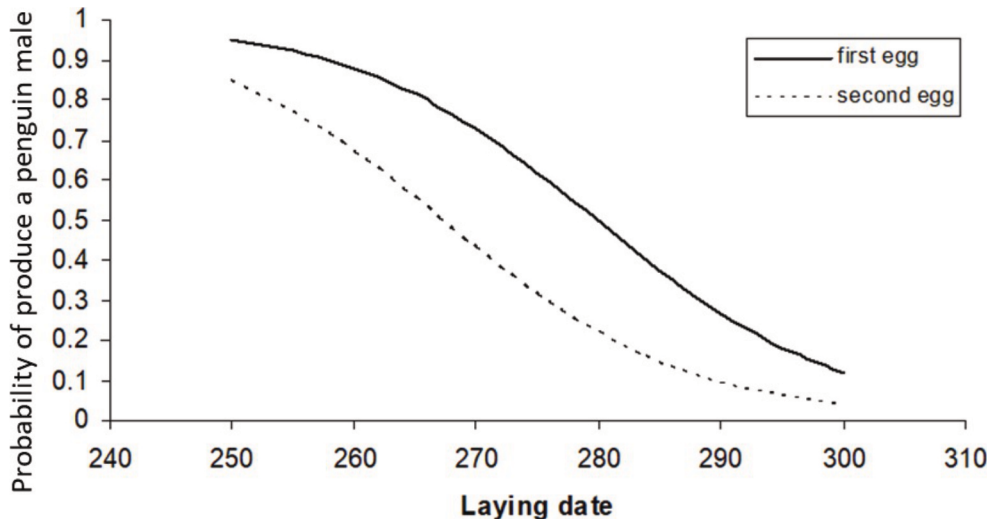
The probability of Magellanic Penguin producing males increased with the density of the breeding population near the colonies (100 km). However, this effect was not significant when double broods were analyzed, suggesting a large effect in low-quality pairs that exhibit brood reduction. Boersma & Stokes (1995) suggest for the same species that even in good years, starvation is the main cause of nestling mortality, with the second chick being more likely to die before fledging than the

first. In dense colonies, brood reduction may increase because of higher food competence (Forero et al. 2002). The body condition of Magellanic penguin chicks was worse at high breeding densities, and T-cell mediated immunity was inversely related to colony size (Tella et al. 2001). The increasing density of conspecifics can lead to a shortage of food and, consequently, to a density-dependent reduction in breeding performance (Sutherland 1996, Forero et al. 2002), which affects the population sex ratio.

However, the trend of producing offspring males early in the breeding season may be a consequence of a female's body condition. The growth of the second chicks depends not only on the asynchrony of hatching and the size difference of the eggs, but also on the maternal effect and body condition of the father. Females in good condition in the period before egg laying might invest more in second eggs than in first eggs, while foster fathers in good condition might invest more in rearing the second chicks. Thus, females breeding early in the season may have better conditions than those that breed later. Fargallo et al. (2004) have shown the relationship between parental quality and the sex ratio of offspring, suggesting that organisms such as birds can adjust the sex ratio of their offspring to increase their fitness in terms of sex-specific mortality and mating success.



**Figure 1.** Mean number of males in double broods of Magellanic Penguin nests (+ SE). Early and late broods were considered before and after the median laying date (October, 3) respectively.



**Figure 2.** Probability of producing a male offspring Magellanic Penguin in relation to laying date and hatching order. Single and first-hatched chicks of double broods were represented separately from second-hatched chicks.



**Table 4.** Generalized Linear Model (GLM) for sex ratio in double broods of the Magellanic Penguin, using binomial error and logistic link (deviance initial = 425.6).

Variable	Parameter estimated	Standard error	P-value
Intercept	26.47	8.05	0.021
Laying date	-0.10	0.03	0.0011
Laying order (first)	1.26	0.29	0.0001
Deviance residual	210.8		

Despite our findings, there is a need for future theoretical models to better incorporate the complexity of avian life histories and interactions among competing selective pressures that influence sex allocation (Merkling et al. 2019).

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