

Phenotypic assortative mating and within-pair sexual dimorphism and its influence on breeding success and offspring quality in Magellanic penguins

M.G. Forero, J.L. Tella, J.A. Donázar, G. Blanco, M. Bertellotti, and O. Ceballos

Abstract: We examined within-pair sexual dimorphism and phenotypic assortative mating in Magellanic penguins (*Spheniscus magellanicus*) breeding in six colonies located on the Patagonian coast (Argentina). All measured phenotypic traits except the number of pectoral spots differed between the sexes; bill depth and flipper length were the most and least dimorphic traits, respectively. We found assortative mating by bill depth and body mass. The similarity in body condition within pairs was close to significant. When we performed separate correlations for birds that bred successfully, i.e., raised one or two offsprings, and birds that did not attempt to breed or bred unsuccessfully, only the successful breeders showed assortative mating by body mass. In addition, we attempted to relate the body size of each member of the pair and the degree of sexual dimorphism within pairs to the breeding performance of individuals, which was measured as brood size, and body condition and immunocompetence of offspring. We found that pairs that were less dimorphic in flipper length raised more offspring. This effect was due to female flipper length per se and not to the relative difference in flipper length between members of the pair. Females with larger flippers had a higher probability of raising two chicks. No effects of body measurements or degree of sexual dimorphism on body condition or T-cell-mediated immune response of offspring were found. We discuss these results in the context of potential factors responsible for the maintenance of sexual size dimorphism in this species.

Résumé : Nous avons étudié le dimorphisme sexuel et le choix d'un partenaire en fonction du phénotype chez des couples de Manchots de Magellan (*Spheniscus magellanicus*) dans six colonies reproductrices de la côte de la Patagonie (Argentine). Tous les caractères phénotypiques mesurés différaient chez le mâle et la femelle d'un même couple, à l'exception du nombre de taches pectorales; la hauteur du bec était le caractère le plus dimorphe, la longueur des ailerons, le caractère le moins dimorphe. Le choix d'un partenaire se faisait en fonction de la profondeur du bec et de la masse corporelle. La similarité de la condition physique chez le mâle et la femelle d'un couple était presque significative. En faisant des corrélations séparées chez les oiseaux à reproduction réussie et chez les oiseaux non reproducteurs ou les oiseaux qui avaient raté leur reproduction, seuls les oiseaux à reproduction réussie (i.e., qui avaient élevé un ou deux petits) avaient choisi leur partenaire en fonction de sa masse corporelle. Nous avons également tenté de relier la taille de chaque partenaire du couple et l'importance du dimorphisme sexuel au sein du couple avec la performance reproductrice individuelle en mesurant la taille des couvées, la condition physique et la compétence immunitaire des rejetons. Ce sont les couples les moins dimorphes quant à la longueur des ailerons qui ont élevé le plus de petits. Cet effet est attribuable à la longueur per se des ailerons de la femelle et non pas à la différence relative de longueur des ailerons entre le mâle et la femelle d'un couple. Les femelles aux ailerons les plus grands sont celles qui avaient la plus grande probabilité d'élever deux poussins. Ni les mesures corporelles, ni l'importance du dimorphisme sexuel n'ont influencé la condition physique ou la réaction immunitaire reliée aux cellules T chez les rejetons. Nous examinons ces résultats à la lumière des facteurs potentiellement responsables du maintien du dimorphisme sexuel de la taille chez cette espèce.

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Introduction

Among birds and mammals, males are typically larger than females, although there appear to be some exceptions (reversed size dimorphism; RSD) in a number of avian groups such as raptors, owls, some shorebirds, and seabirds (Mueller and Meyer 1985; Jehl and Murray 1986; Paton et al. 1994; Catry et al. 1999; Figuerola 1999; Székely et al. 2000). Hypotheses concerning the evolution and maintenance of sexual size dimorphism in birds generally focus on sexual selection resulting from either female mate choice (intersexual selection) or intrasexual selection (Darwin 1871; Hedrick and Temeles 1989; Moore 1990; Olsen and Cockburn 1993; Andersson 1994). However, natural selection can also lead to morphological differences between the sexes (Shine 1989; Andersson 1994). In this sense the “intersexual food competition hypothesis” postulates that sexual dimorphism and differential use of ecological niches by males and females reduce intersexual competition in the exploitation of food resources (Selander 1972; Slatkin 1984; Hedrick and Temeles 1989; Andersson 1994; González-Solís et al. 2000). Sexual and natural selection could influence the evolution of the same traits to different degrees, and even sexual selection favoring dimorphism may be opposed to natural selection acting on the same traits (Olsen and Cockburn 1993).

Independently of the selective forces driving sexual dimorphism, the body size of each sex and (or) the relative differences in size among members of the same pair could have some effects on fitness. Despite the fact that in many studies, attempts have been made to demonstrate the mechanisms that could lead to the evolution of sexual dimorphism in several species (see the review in Hedrick and Temeles 1989), little work has been devoted to relating body size and different degrees of sexual dimorphism within pairs to the breeding performance of individuals (Teather and Nol 1997; Sandercock 1998; Catry et al. 1999; Massemin et al. 2000).

Studies on morphometry and body size also provide data to answer a second question related to sexual dimorphism: whether or not individuals mate assortatively according to some aspects of body size or phenotypic characteristics. Assortative mating is defined as nonrandom mating in relation to phenotypic characteristics and could be positive or negative (Burley 1983). Assortative mating has been studied both in terms of plumage characteristics or secondary sexual traits and in terms of body size in monomorphic and dimorphic species (Marti 1990; Stern and Jarvis 1991; Bortolotti and Iko 1992; Choudhury et al. 1992; Olsen et al. 1998; Catry et al. 1999; Wagner 1999; Wiebe 2000).

Penguin species seem to lack secondary sexual characteristics. However, most of them, including the Magellanic penguin (*Spheniscus magellanicus*), exhibit some degree of sexual size dimorphism, the males being generally heavier and structurally larger than the females (Scolaro et al. 1983; Scolaro 1987; Stern and Jarvis 1991; Gandini et al. 1992; Fairbairn and Shine 1993; Agnew and Kerry 1995; but see Catry et al. 1999). Although numerous studies have been carried out on body size and sex discrimination in several species of penguins (Agnew and Kerry 1995), assortative mating and within-pair sexual dimorphism in body size characteristics and its fitness consequences have been scarcely studied in this group of birds (see the review in Davis and

Speirs 1990). Furthermore, to our knowledge, the degree of dimorphism and assortative mating according to phenotypic characteristics other than body size have been not explored in penguins.

In this study, our first aim was to report the degree of within-pair sexual dimorphism for several body-size measurements and phenotypic traits, using individuals sexed on the basis of molecular procedures. Second, we determined whether male and female Magellanic penguins mate assortatively with respect to any body-size measurement or phenotypic trait. Finally, we explored whether phenotypic traits of males and females separately and the degree of sexual dimorphism within pairs had some effect on their breeding performance, measured as brood size and offspring quality, in terms of body condition and immunocompetence of fledglings.

Materials and methods

The Magellanic penguin is a monogamous and long-lived seabird with a wide distribution along Atlantic and Pacific coasts of South America (del Hoyo et al. 1992). Individuals return to breeding colonies after migration in late August or early September. Males usually arrive before females, and both sexes fast during the settlement and laying period (Boersma et al. 1990). Nests are placed in burrows and under bushes at variable local densities (Yorio et al. 1998). Adults lay two eggs nearly equal in size and both sexes defend the nest sites, incubate eggs, and feed the young (Boersma et al. 1990). They can raise up to two fledglings in late January and February. However, second-hatched chicks are lost from a high proportion of nests, mainly because of starvation and extreme weather conditions (Boersma et al. 1990; Boersma and Stokes 1995; Frere et al. 1998).

This study was carried out in the province of Chubut (Argentinean Patagonia) during January–February 1999. In this area we selected six breeding colonies distributed from Península Valdés (42°04'S, 63°21'W) to Cabo Dos Bahías (44°54'S, 65°32'W). We visited the colonies at the fledgling stage, a few days before the chicks acquired their independence. In selecting nests an attempt was made to balance brood size (one or two chicks) and other factors such as location within colony, conspecific breeding density around the nest, and characteristics of the nest and surrounding habitat. For each nest we captured the chicks while they were attended by one of their parents, and we captured the parent as well. We revisited all nests 24 h later to try to capture the second member of the pair. However, in some cases we were unable to sample both parents because they may spend more than 1 day at sea between successive food deliveries to the chicks (Scolaro 1984; Boersma et al. 1990). We recorded the body mass of the chicks during both visits. Additionally, we captured mated individuals that actively defended empty nests. We cannot discern whether these pairs did not attempt to breed or bred unsuccessfully. In chicks and adults we measured flipper length, bill length, and bill depth to the nearest 0.1 mm using a digital caliper. Individuals were weighed with a spring balance to the nearest 25 g. In adults we also measured the thickness of the black band on the breast (hereinafter referred to as the pectoral band) and counted the black spots on the breast (hereinafter referred to as pectoral spots). Before chicks and adults were released, a drop of blood was collected from the brachial or foot vein for molecular sexing using the primers 294F, cFR, and 3224R as described by Ellegren (1996).

Since multivariate measures of size are preferable to univariate ones (Freeman and Jackson 1990), we used principal component analysis, particularly the first axis (PC1), to combine bill and flipper measurements of adult birds. PC1 had the highest degree of

correlation with the different variables measured on adults. We extracted separate PC1s for males and females. In both sexes, bill length had the strongest correlation with our derived index of size (0.76 for females and males). In females, bill depth and flipper length had also a high positive correlation with PC1 (0.73 and 0.68, respectively), whereas in males these correlations were negative and much weaker (-0.59 for both measurements). PC1 accounted for over 53% of total variance in size of adult females and 50% for adult males. An index of body condition was calculated as the residuals from the linear regression of body mass on PC1 factor scores ($r = 0.28$, $n = 219$, $P < 0.001$, for males and $r = 0.31$, $n = 161$, $P < 0.001$, for females). An index of sexual dimorphism within pairs was calculated as the ratio of male body size to female body size multiplied by 100 (Wagner 1999). This index reaches 100 when the trait we are measuring is identical in males and females; lower values indicate that males are larger than females.

To assess the effects of phenotypic traits and degree of sexual dimorphism within pairs on breeding performance of individuals, we used their brood size as well as two potential measures of offspring quality: body condition and immunocompetence of fledglings. In a number of bird species, body mass of fledglings has been shown to correlate positively with their survival as juveniles and probability of recruitment (see the review in Magrath 1991). More recently, it has also been suggested that T-cell-mediated immunity influences survival prospects in birds (Christe et al. 1998; Soler et al. 1999; Tella et al. 2000a). These two evaluators of offspring viability could therefore reflect parental quality in addition to brood size.

Since fledgling body mass in Magellanic and other species of penguins may vary greatly between days, depending on feeding rates (Gandini et al. 1992; Boersma et al. 1990), to obtain an index of body condition we used the lower of the two masses determined 24 h apart. Therefore, we reduced the potential effect of recently ingested food on body mass. Body mass of fledgling Magellanic penguins was also influenced by bill length, flipper length, and sex (M.G. Forero, J.L. Tella, M. Bertellotti, G. Blanco, and J.A. Donazar, unpublished data). Therefore, as an index of body condition we obtained the residuals from an analysis of covariance with log body mass as the dependent variable, sex as a fixed factor, and log-transformed flipper and bill lengths as covariates ($r^2 = 0.342$, $F_{[3,304]} = 51.890$, $P < 0.001$).

T-cell-mediated immune response (CMI) of fledglings was measured using the phytohaemagglutinin (PHA) skin-testing technique (Goto et al. 1978; Smits et al. 1999). It is based on the injection of a mitogen (PHA) under the skin of birds, which produces a prominent perivascular accumulation of T-lymphocytes followed by macrophage infiltration (Goto et al. 1978; McCorkle et al. 1980). This technique has been routinely used to evaluate thymus-dependent immune function in vivo in poultry (e.g., Tsiagbe et al. 1987; Cheng and Lamont 1988). More recently, the intensity of skin swelling as response to PHA injection has been proved to correlate with a number of components of fitness in free-living birds (e.g., Saino et al. 1997; Moreno et al. 1998; Tella et al. 2000a). We injected 0.1 mL of 2 mg/mL PHA-P (Sigma) in phosphate-buffered saline intradermally at a marked point on the right external foot web. The thickness of the right foot web was measured (to the nearest 0.001 mm) by the same researcher with a micrometer at the injection site three times just before and 24 h (± 15 min) after the injection. Since repeatability of the three measurements was high ($r = 0.99$, $F_{[29,89]} = 59765.1$, $P < 0.001$), the mean of these measurements was used to calculate the CMI response, i.e., the change in thickness between the day of injection and the following day (for more details see Tella et al. 2001).

Statistics were performed using SPSS and SAS programs. All test were two-tailed except for assortative mating analyses. We used Pearson's rank correlation for analyses of morphometric assortative mating, except for the number of pectoral spots, which

was not normally distributed and thus required Spearman's rank correlation. Brood size was treated using non-parametric tests for univariate analyses (Kruskal–Wallis test). Since both body condition (Merilä 1996) and CMI (Brinkof et al. 1999; Christe et al. 2000; Tella et al. 2000b) of siblings are influenced by sharing of genes and rearing environments, we computed the within-nest average values for those nests with two chicks to avoid pseudo-replication in correlation analyses. The potential influence of variation in size of individuals among colonies was a concern, so to control for colony effects in previous analyses we used separate models for each phenotypic trait using the PROC MIXED procedure of SAS (SAS Institute Inc. 1996), applying normal error and identity link function. For the brood-size analyses we used the SAS macro program GLIMMIX (Littell et al. 1996), applying Poisson error and logarithmic link function. Since some individuals belonged to the same colonies, we fitted colony as a random term in all previous models. Because we lacked some measurements from some individuals, sample sizes varied somewhat between analyses.

Results

We measured 400 adult penguins (231 males and 179 females). Mean values for body measurements and phenotypic traits were calculated separately for each sex. Males were larger than females for all variables (Student's t tests, all $P < 0.001$) except the number of pectoral spots (Mann–Whitney U test, $P = 0.48$) (Table 1). The previous results were similar when we made separate multivariate models for each phenotypic trait, including the trait as the dependent variable, sex as a fixed effect, and colony as a random effect. The effect of sex was significant for all phenotypic traits (all $P < 0.0001$) except the number of pectoral spots ($P = 0.155$). In addition, the effect of colony was only significant for bill depth ($P = 0.001$) and body mass ($P = 0.02$), and the interaction between sex and colony was not significant for any phenotypic trait (all $P > 0.08$). These results indicate that differences between the sexes in the measured phenotypic traits were significant in the six sampled colonies despite the variation in some of these measurements among colonies.

Coefficients of variation (CVs) showed that structural-size measurements of penguins were less variable than body mass and thickness of the pectoral band, this variability being slightly higher in females than in males (Table 1). The least variable trait was flipper length (Table 1). Dimorphism indexes showed that body mass and bill depth were the most dimorphic measurements and that flipper length was the measurement which was most similar between the sexes (Table 1).

We trapped both members of the pair at 119 nests. We examined correlation coefficients between members of the pair for the three body-size variables (flipper length, bill length, bill depth), PC1 as an index of overall body size, the number of pectoral spots, and the thickness of the pectoral band, body mass, and body condition. We found positive assortative mating by bill depth (Table 2, Fig. 1). No other structural-size measurements, either number of pectoral spots or thickness of the pectoral band, were correlated within pairs. Additionally, body masses of pair members were positively correlated. Body condition also tended to be positively correlated within pairs, but this relationship was not significant (Table 2). As body mass could vary considerably throughout the breeding season and according to breeding effort, we performed separated correlations for birds that bred successfully and birds that did not attempt to breed or

Table 1. Mean and variability in phenotypic traits of male and female Magellanic penguins (*Spheniscus magellanicus*).

	Mean ± SD	Range	n	CV	Dimorphism index ^a
Body mass					
Females	3709 ± 348	3000–5000	169	9.38	82.6
Males	4490 ± 406	3400–5500	221	9.04	
Flipper length					
Females	158.0 ± 6.3	140–177	172	4.0	94.7
Males	166.8 ± 6.7	148–190	228	4.0	
Bill length					
Females	53.7 ± 2.4	46.8–60.8	179	4.5	91.5
Males	58.7 ± 2.3	51.2–64.5	231	4.0	
Bill depth					
Females	20.5 ± 1.0	17.8–23.6	179	4.9	85.2
Males	24.1 ± 1.3	20.0–29.6	231	5.5	
Pectoral band					
Females	16.3 ± 4.9	6.4–35.6	178	30.2	87.6
Males	18.7 ± 5.2	2.1–37.1	231	27.9	
Pectoral spots					
Females	2.0 ^b	0–10	167	1–3 ^c	92.3
Males	2.0 ^b	0–12	215	1–4 ^c	

Note: Coefficients of variation (CV) are indicated separately for each sex.

^aCalculated as (mean value for females/mean value for males) × 100.

^bMedian.

^cThe 25 and 75% percentile.

Table 2. Correlations between phenotypic traits of mated pairs of Magellanic penguins (n = 119).

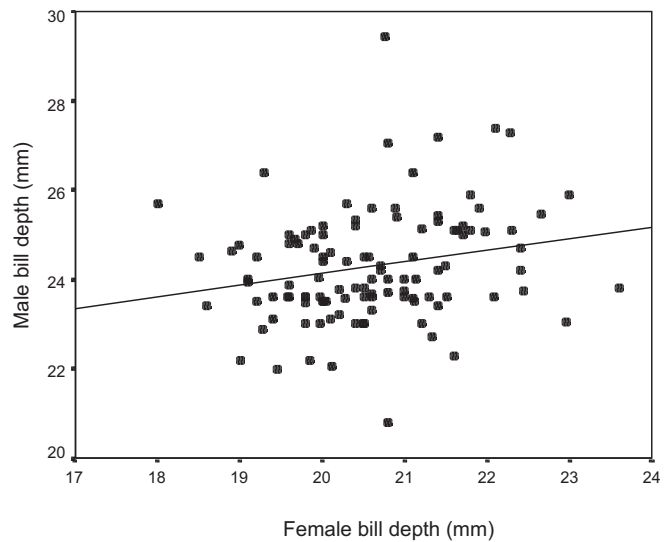
Variable	r	n	P
Body mass	0.18	100	0.03
Flipper length	0.06	104	0.24
Bill length	-0.11	111	0.13
Bill depth	0.22	111	0.01
PC1	-0.02	104	0.43
Body condition	0.12	93	0.121
Pectoral band	0.00	119	0.49
Pectoral spots ^a	0.04	96	0.35

^aSpearman’s rank correlation was performed for this trait.

bred unsuccessfully. These analyses revealed that body-mass correlations within pairs were only significant for successful breeding pairs (Fig. 2). Again, differences in body size and body mass among colonies could have biased the previous results. Therefore, we also performed multivariate analyses, introducing each male body measurement as the dependent variable, the female body measurement as the independent one, and colony identity as a random effect. When controlling for colony effects the results remained similar to those obtained univariately; only bill depth ($P = 0.009$) and body mass ($P = 0.03$) were positively related between the two members of the pair.

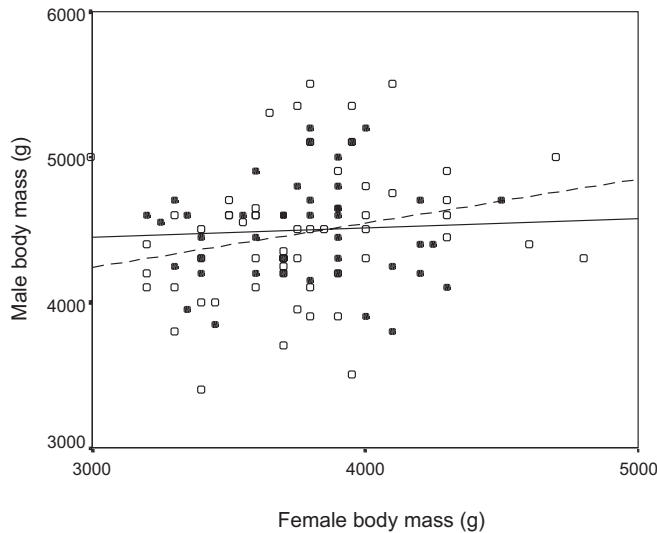
We explored the effects of phenotypic characteristics and degree of sexual dimorphism within pairs on brood size, body condition, and immune response of fledglings. Only sexual dimorphism in flipper length within pairs affected breeding success: the less dimorphic pairs raised a higher number of offspring (Kruskal–Wallis test, $H_{[2,103]} = 7.36$,

Fig. 1. Bill depths of females plotted against those of males for mated pairs of Magellanic penguins (*Spheniscus magellanicus*).



$P = 0.025$) (Fig. 3A). This effect was due to differences in flipper length among females ($H_{[2,170]} = 6.23$, $P = 0.04$) but not to differences in flipper length between males that differed in breeding success ($H_{[2,226]} = 1.136$, $P = 0.57$) (Fig. 3B). We found no significant effects of body size or degree of dimorphism within pairs on body condition (Spearman’s rank correlations, all $P > 0.20$) or immune response of offspring (Spearman’s rank correlations, all $P > 0.24$). As these three measurements of breeding performance could vary among colonies, we corroborated these results by testing the models with each breeding-performance measure-

Fig. 2. Relationship between male and female body masses within pairs. Separate regressions are shown for pairs that bred successfully ($r = 0.24$, $n = 57$, $P = 0.03$; -- □ --) and pairs that did not attempt to breed or bred unsuccessfully ($r = 0.06$, $n = 43$, $P = 0.36$; —■—).

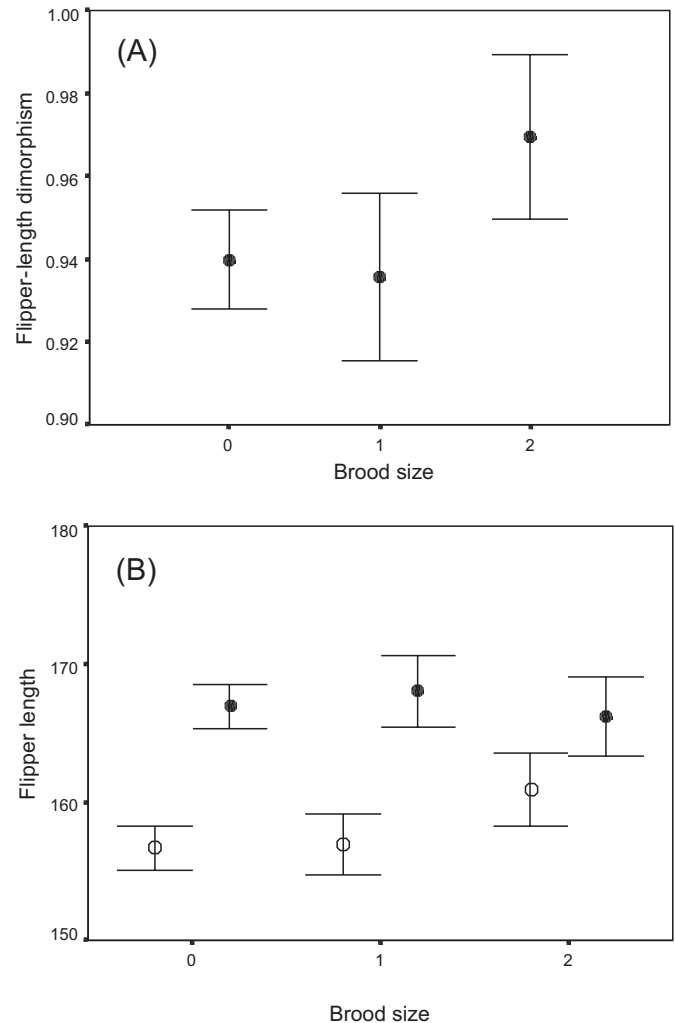


ment as the dependent variable, colony as a random effect, and the phenotypic characteristic of the parents or degree of within-pair sexual dimorphism as the independent variable. Again, independently of variation of breeding performance between colonies, only the previously exposed variables affected brood size ($P = 0.01$ and $P = 0.02$ for flipper-length dimorphism and female flipper length, respectively).

Discussion

All species of penguins exhibit some degree of sexual size dimorphism, males generally being heavier and having a larger bill and larger flippers than females (see the review in Agnew and Kerry 1995). However, the extent of this dimorphism varies among species and among populations of the same species (Fairbairn and Shine 1993; Agnew and Kerry 1995). In most penguin species, dimorphism is expressed to its greatest extent in bill depth and length (Agnew and Kerry 1995). To our knowledge, the only data previously available on dimorphism indexes for Magellanic penguins were those reviewed by Agnew and Kerry (1995) from two different colonies (Scolaro et al. 1983; J. Thompson, unpublished data). By sampling a higher number of colonies and individuals, we also found that in Magellanic penguins, bill depth was the most dimorphic body measurement and flipper length was the least dimorphic. However, we found that body mass was more dimorphic than bill length. Nonetheless, comparisons of data on sexual dimorphism in body mass for any species of penguin should be carefully done (Croxall 1995). It is known that large changes in body mass typically occur throughout the breeding cycle of penguins, and there could even be stages when females are heavier than males (Agnew and Kerry 1995). Because of this fact, comparisons should be done only among individuals with the same breeding status and sampled at the same stage of the breeding cycle.

Fig. 3. Relationship between dimorphism within pairs and breeding success (brood size) (A) and between flipper lengths of male (●) and female (○) parents and brood size (B).



Additionally, in this work we explored sex differences in the thickness of the pectoral band and the number of pectoral spots, two plumage traits present in this and other related species of penguins and previously ignored in morphometric studies (Willians 1995). Males had a wider pectoral band than females, suggesting that this trait could be a secondary sexual characteristic. What may be more important is that CVs for this trait are much higher in both sexes (ca. 30%) than CVs for any other phenotypic trait ($CV = 4\text{--}9\%$; see Table 1). Information from other species suggests that secondary sexual characters, particularly those evolved in sexual selection, show higher CVs (usually larger than 10%) than ordinary morphological characters (Møller 1994; Evans and Barnard 1995; Forero and Tella 1997). Determining whether or not the pectoral band is implicated in sexual selection in this species would require additional studies.

Sexual selection through intrasexual competition for mates is one of the most common theories for explaining sexual di-

morphism in birds (Hedrick and Temeles 1989; Davis and Speirs 1990; Andersson 1994). Magellanic penguins, as well as other species of penguins, fight with conspecifics during the breeding period using the bill as a weapon (Lamey 1993; Moreno et al. 1995; Viñuela et al. 1995). Data on this and other penguins species show that yearlings have a smaller bill than adults (Mínguez et al. 1998; M.G. Forero, J.L. Tella, M. Bertellotti, G. Blanco, and J.A. Donázar, unpublished data), suggesting the importance for adults of having a stronger bill. Furthermore, the bill is also used in courtship rituals in many penguin species (Willians 1995). Therefore, the bill of the Magellanic penguin should be more prone to sexual dimorphism than other body measurements. An alternative explanation for the evolution and maintenance of sexual dimorphism in this trait is the intersexual competition hypothesis (see Introduction). The separation between the sexes in the exploitation of feeding resources has been considered evidence in favor of this hypothesis (Selander 1972; Hedrick and Temeles 1989; González-Solís et al. 2000). In fact, it has been suggested that selection to avoid competition for food (by exploiting prey of different sizes) promotes sexual dimorphism in the bills of the Adèle penguin (*Pygoscelis adeliae*) (Ainley and Emison 1972), eudyptid penguins (*Eudyptes* spp.) (Warham 1975), the Galápagos penguin (*Spheniscus mendiculus*) (Boersma 1976), and the Gentoo penguin (*Pygoscelis papua*) (Willians 1991). Although some works have been published on diet and feeding behavior in Magellanic penguins (Gosztonyi 1984; Scolaro and Badano 1986; Blanco et al. 1996; Frere et al. 1996; Gandini et al. 1999; Scolaro et al. 1999), none have explored differences in food choice between males and females of this species. However, recent data (Forero et al. 2001) indicate that males and females consume different proportions of prey types during the chick-rearing period. These data, while suggesting that avoidance of intersexual competition for food may have some effect on the evolution and maintenance of sexual dimorphism in this species, are not conclusive because cause and effect are unclear.

A complementary functional explanation is that dimorphism may result from intersexual selection through mate choice, with females choosing larger males (Davis and Speirs 1990). To demonstrate that this mechanism is acting in the Magellanic penguin, larger, preferred males should obtain better territories or more resources than smaller males and then derive advantages in terms of breeding output (Andersson 1994). However, we found no effect of male size on breeding performance in this species. Despite this, we cannot discard female mate choice as a force driving dimorphism in the Magellanic penguin, since there could be some long-term fitness consequences that we were not able to measure through our study.

To our knowledge, this is the first study to explore assortative mating in penguins. Our results indicate that there is significant assortment with respect to bill depth and body mass. A number of previous studies have reported examples of positive assortative mating by some aspect of bill size in other seabird species (Coulter 1986; Stern and Jarvis 1991; Wagner 1999). Assortative mating may arise from active mate choice by one or both sexes, or it may result from patterns of passive contact between phenotypes (Burley 1983).

Some authors have argued that positive assortative mating by bill size in seabirds can be explained by a positive correlation between age and bill size (Coulson et al. 1981; Shaw 1985; Reid 1988; Bradley et al. 1995; Jouventin et al. 1999). Even if assortative mating by age exists, it could be a passive effect due to age-related time of arrival at the breeding place after winter migration. Owing to a lack of information on the age of the individuals we sampled, any interpretation of our results must be viewed with caution. However, characteristics such as the high mate-fidelity rate (see the review in Dubois et al. 1998) and the difference in bill size between yearlings and adults (M.G. Forero, J.L. Tella, M. Bertellotti, G. Blanco, and J.A. Donázar, unpublished data) indicate that assortative mating by bill depth in this species could be the consequence of active or passive assortative mating by age together with a potential progressive increase in this trait after sexual maturity.

Body masses of pairs were also positively correlated. We found the same trend for body condition, but it was not significant. This result is similar to those reported for other species of birds (Choudhury et al. 1992; Heitmeyer 1995; Rosenfield and Bielefeldt 1999; Wagner 1999). However, body mass is usually an unreliable measurement in birds because it tends to fluctuate throughout the breeding cycle (Moreno 1989). So it is possible that the pattern of nonrandom pairing in relation to body mass that we report is related to the synchronous change in body mass within pair members, since both male and female Magellanic penguins show a high degree of parental investment and lose their body reserves synchronously during the breeding period (Boersma et al. 1990). This suggestion is supported by the fact that positive assortative mating was significant only in those pairs that bred successfully, for which changes in body mass of males and females must be more similar than those within pairs that failed to breed.

When assessing the potential effects of male and female phenotypic traits and within-pair sexual dimorphism on breeding performance, we found that only sexual dimorphism in flipper length had an effect on breeding success, i.e., less dimorphic pairs raised a higher number of offspring. This effect was due to that fact that females which raised two offspring had larger flippers than those that raised only one offspring or failed to breed, while flipper lengths did not differ in males whose breeding success differed. Although breeding success in this and other species of penguins is affected by such factors as nest density and nest cover and location (Davis and McCaffrey 1986; Scolaro 1990; Frere et al. 1992; Barbosa et al. 1997; Stokes and Boersma 1998), it is mainly determined by variation in weather conditions and food availability between years (Boersma et al. 1990; Frere et al. 1998; Stokes and Boersma 1998). The flipper is a very important structural character for locomotion in penguins, which have large feeding ranges (see the review in Croxall and Lishman 1987). Data on Magellanic penguins show that during the chick-rearing phase of the breeding cycle, parents can travel up to 120 km per day (Wilson et al. 1995). Thus, the flipper should be of an optimal size for foraging and parental-care duties. In this sense, de León et al. (1998) showed that flipper size of adult chinstrap penguins (*Pygoscelis antarctica*) has a significant effect on the amount of food delivered to the chicks, and parents with larger flippers carried larger

meals. We suggest that females with larger flippers are able to forage more efficiently and offer better food provisioning to chicks, and thus to raise larger broods.

The enhancement of reproductive success in females with larger flippers could be a selective force causing an increase in flipper length in females, thus reducing sexual dimorphism in this trait. According with this reasoning, flipper length was the least dimorphic trait in our large sample of Magellanic penguins (Table 1), as is the case for other penguin species (see the review in Agnew and Kerry 1995). The complete disappearance of sexual dimorphism in flipper length, however, would only be possible if heritability of female flipper length is high and (or) if female offspring with larger flippers have higher survival prospects. Few estimations of heritability of dimorphic traits in penguins are available (Moreno et al. 1999). In the case of Magellanic penguins, flipper length is mainly affected by environmental conditions during growth, heritability being very low (M.G. Forero, J.L. Tella, M. Bertellotti, G. Blanco, and J.A. Donazar, unpublished data). On the other hand, Moreno et al. (1999) found that there is strong natural selection favoring survival of fledgling chinstrap penguins with larger flippers. Unfortunately, they did not explore this effect separately for males and females, so there remains the possibility that long flippers are favored in fledglings of both sexes. We suggest that although the evolutionary origin of sexual dimorphism in this species remains to be determined, natural selection and differences in female quality may explain the reduction in sexual dimorphism in flipper length compared with other body measurements in this species.

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